Forster's Tern, Caspian Tern, and California Gull Colonies in San Francisco Bay: Habitat Use, Numbers and Trends, 1982-2003

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Abstract.—We analyzed data on numbers and annual trends of breeding terns and gulls based on censuses of all colonies of the Caspian Tern (*Sterna caspia*), Forster's Tern (*S. forsteri*) and California Gull (*Larus californicus*) in the San Francisco Bay estuary from 1982 to 2003. All species used nesting substrates that were flat, largely non-vegetated, had a wide view in all directions, and were composed of sand, gravel, or earth. The estuary supported 17, 13, and seven colonies of each species, respectively. Nesting terns were primarily on salt evaporation pond islands and tidal islands. The largest colony of California Gulls was on a deactivated salt pond. Total numbers of each species in 2003 were about 2,300, 2,450 and 21,200 breeding birds, respectively. Numbers of Forster's Terns declined significantly during the study, while California Gulls increased, and the number of Caspian Terns was stable. Numbers of each species at each colony site have shown considerable annual variation. We attribute the lack of colony site fidelity of each species, and the decline among Forster's Terns, primarily to mammalian predation, human disturbance, and possibly annual variation in food availability. Flat, minimally vegetated islands, which are few in the estuary, are critical for maintaining nesting terns and California Gulls. Yet, the planned restoration of 65% (9,050 ha) of the salt pond complex of the San Francisco Bay estuary will likely remove some of the salt pond islands and levees where 20% of the Caspian Terns (438 birds), 80% of Forster's Terns (1,958) and 96% of California Gulls (20,210) were nesting in 2003. We recommend that restoration plans should include the creation of sizeable tracts of islands specifically designed to provide nesting habitat for these larids. These replacement sites should be in place soon after the restoration has been implemented; i.e., well before scheduled completion. This is especially important because severe habitat limitation would lead to competition for nesting space among the three species, a situation expected to result in exclusion of the terns by the gull, which nests earlier, are larger, more abundant, and more aggressive. *Received 20 December 2003, accepted 19 August 2004.*

Key words.—Breeding larids, California Gull, Caspian Tern, Forster's Tern, *Larus californicus*, *Sterna caspica*, *Sterna forsteri*, nesting habitat, colony site fidelity, San Francisco Bay estuary.

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In North America, the Caspian Tern (*Sterna caspia*), Forster's Tern (*S. forsteri*) and California Gull (*Larus californicus*) nest on interior marshes, lakes, and reservoirs in Canada and USA and Pacific coast estuaries (Winkler 1996; Wires and Cuthbert 2000; McNicholl *et al.* 2001). The terns also nest in estuaries on the Atlantic and Gulf coasts (Wires and Cuthbert 2000; McNicholl *et al.* 2001), and Baja California (Howell and Webb 1995).

On the Pacific coast, the San Francisco Bay estuary (SFBE) supports colonies of all three larids. However, 95% of the historic SFBE marshes and tidal flats have been converted to salt evaporation ponds, agricultural lands, and other development (Goals Project 1999). This conversion has resulted in 42% and 79% decreases in tidal flat and marsh habitat, respectively, and a 20 fold increase in salt pond habitat. Nevertheless, the SFBE supports over one million waterbirds throughout the year (Page *et al.* 1999; Takekawa *et al.* 2001). Among them, the Caspian Tern, Forster's Tern, and California Gull nest primarily on tidal islands, islands in salt ponds, and salt pond levees, mainly in the south of SFBE (Harvey *et al.* 1992).

In the SFBE, the Caspian Tern feeds exclusively on fish that are 8 to 23 cm in length (D. D. Roby and K. Collis, unpubl. data); Forster's Tern generally feed on smaller fish (1-10 cm length) and arthropods (McNicholl *et al.* 2001). Feeding habitats used by both species include the sea, open bay, salt ponds, slough channels, marshes, and nearby reser-

voirs and streams (Harvey *et al.* 1992). The California Gull feeds in the same habitats as the terns, as well as on refuse in landfills adjacent to the SFBE (Goals Project 2000).

Approximately 34,000 breeding pairs of Caspian Terns nest in North America (Cuthbert and Wires 1999) and are present at SFBE only during the breeding season. They are thought to have first nested at SFBE in 1916 (Grinnell and Miller 1944). The colony grew from seven nests in 1922 to 378 nests in 1943; 299 nests were recorded there in 1966 (DeGroot 1931; Miller 1943; Gill 1972). By the late 1960s, four more colonies had been discovered at Bair Island, Mowry, Turk, and Baumberg (Fig. 1; Gill 1972; Harvey *et al.* 1992). This species has nested at north bay salt pond levees (Napa River marsh) since the 1970s (Madrone Associates 1977; Jones and Stokes 2003). Shuford and Craig (2002) estimated that in 1979 the SFBE supported 52% of the Caspian Terns then breeding on the Pacific Coast. Due primarily to the increasing numbers breeding at the Columbia River in Oregon (Roby *et al.* 2002), the SFBE supported only 6.5% of the Caspian Terns breeding on the coast in 2001 (Shuford and Craig 2002).

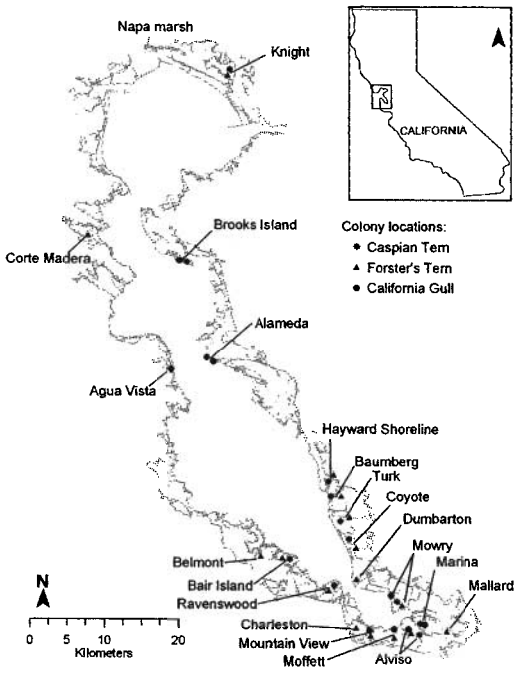

Figure 1. San Francisco Bay estuary with locations of nesting colonies of the Caspian Tern, Forster's Tern, and California Gull. Almaden Lake (not shown on the map) is approximately 25 km south of the Alviso colony.

The number of breeding Forster's Terns in North America is estimated to be about 20,100 pairs (McNicholl *et al.* 2001). Previously found in small numbers only during winter in the SFBE, Forster's Tern was first found breeding there in 1948, when approximately 110 nests were counted in the south bay (Sibley 1952). They increased to 1,200 breeding pairs by 1971, 2,000 in 1972 (Gill 1977), and to about 2,500 pairs in 1981 (Harvey *et al.* 1992). In 1988, Carter *et al.* (1990) estimated that 1,775 pairs were breeding in the SFBE. This number constituted 22% of the 8,095 pairs thought to be nesting that year on the Pacific Coast (McNicholl *et al.* 2001).

Winkler (1996) roughly estimated that about 250,000 pairs of California Gulls breed in North America. In 1980, a colony was found with twelve nests on a salt pond island in the south of SFBE, representing the first time that these gulls are known to have nested in an estuarine habitat (Jones 1986). Overall, numbers of California Gulls appear to be increasing throughout their range (Winkler 1996).

There are about 13,900 ha of salt ponds in the SFBE, consisting of 11,000 ha in the south bay and 2,900 ha in the Napa River marsh of the north bay (Siegel and Bachand 2002; H. T. Harvey and Associates/P. Williams and Associates 2003; Jones and Stokes 2003). Restoration of 6,130 ha of the salt ponds in the south SFBE and all of the north bay complex to tidal marsh and flats is about to begin (references above, Goals Project 1999; 2000). These projects could reduce the amount of nesting habitat available to these larids, although the expected impact to the SFBE breeding numbers is unknown without details on the location, numbers and status of breeding birds on a colony level. Therefore, to assess potential impacts of the salt pond restoration on these species, the objective of this study was to summarize existing data on their colony distribution, numbers, annual trends, and use of nesting habitat in the SFBE.

METHODS

Study Area

The study area was the SFBE, California (37.8°N, 122.3°W), including the wetland area from the Napa River marsh in the north bay, to Alviso in the south bay (Fig. 1). The study area includes 34,500 ha, with 40% salt ponds, 31% tidal flats, and 29% tidal marsh (Goals Project 1999).

Census Protocol

San Francisco Bay Bird Observatory (SFBBO) biologists and volunteers have counted numbers of breeding individuals in each of 22 years (1982-2003) at most of the known Forster's Tern, Caspian Tern, and California Gull colonies in the SFBE (Fig. 1). A "colony" was considered as a location used by pairs of nesting larids. Other agencies also provided data on numbers of terns and gulls breeding at colonies during our study. These agencies were: East Bay Regional Parks District (Brooks Island and Hayward Shoreline colonies), and the San Francisco Bay National Wildlife Refuge Complex (Alameda, Knight and Mowry).

Colony censuses were conducted during five four-day periods each year. The periods coincided with courtship, egg laying, incubation, chick rearing, and fledging. However, there was variability in observation frequency and time of day that colonies were counted. As a result, number of nesting birds may have been underestimated, although these underestimations were not likely to be of a magnitude to affect the results reported here. In addition, numbers of birds nesting at some colonies were assessed by entering the colony and counting all nests with eggs or chicks. Although this method provides an accurate census, it was employed infrequently to avoid disturbance. For estimates of colony size, we used either peak adult counts, or peak nest counts. We multiplied nest counts by two, rounded adult counts to the next even number, and used either the adult count or twice the nest count, whichever number was greater.

Counting nests and multiplying by two may provide an underestimate of colony size if all nests have not been initiated at the time of the count. In addition, not all nests may be visible when counting nests from distant locations, a factor that can also result in underestimation of colony size. Therefore, although our census protocol was standardized, thus yielding count data that are comparable over time, the counts are probably underestimates.

Analyses

Linear regression was used to examine the relationship between year and larid numbers at each colony. Colony count was analyzed as the dependent variable; independent terms were linear year and curvilinear (quadratic) year. The total number of terns nesting in the SFBE in a given year was calculated as the number of terns summed across colonies if all major colonies were counted.

Following Seber (1977) and Kleinbaum *et al.* (1988), multiple regression was used to examine the relationship between colony site fidelity (the dependent variable, measured as the number of years that a given colony site was occupied between 1982 and 2003) of each larid species and the following four independent variables: i) amount of area (m^2) available at the colony site and adjacent area, ii) nesting substrate stability; and for terns only, iii) distance to nearest California Gull colony (km), and iv) average number of birds nesting at the nearest gull colony.

Amount of available nesting area was calculated using aerial photography and GIS (ArcMap 8.3, ESRI, Inc. 2002). All exposed habitat in the immediate area of colonies was considered as available nesting habitat, including, for example, islands and levees adjacent to colonies but not in use in a particular year.

Nesting substrate stability was measured as: 1) highly stable, 2) of intermediate stability, and 3) unstable. Substrate stability at locations observed during this study to be highly vulnerable to disturbance from factors including flooding/draining of salt ponds, tidal action, or human disturbance were considered less stable, i.e., either unstable or of intermediate stability, depending on the frequency of these disturbances at respective sites. Locations where these types of disturbances were not observed were categorized as stable. Stable nesting habitat was considered as the most favorable (because of the best chances for breeding success), and unstable habitat as least favorable. Substrate type was not included in these analyses because it was highly correlated with nesting substrate stability (Table 1). Both were categorical, and the former included eight substrate categories and the latter, only three. Therefore, we chose to retain substrate stability in regression analyses (due to its simplified presentation potential) and present the analyses related to substrate type separately.

For these analyses, values of colony site fidelity were normalized using log-transformation (calculated as: log [number of years that site was occupied + 0.1]), which is considered appropriate for data having a Poisson distribution (Kleinbaum *et al.* 1988). All habitat variables except substrate type (see above) were initially entered into the models. Insignificant terms were dropped, one at a time, in order of increasing, but insignificant, P-values. We then retested eliminated terms by putting them, one at a time, back in the model. The model was considered complete if no terms could be added or dropped.

One-way ANOVAs and Sidak multiple comparison tests (an improved version of the Bonferroni test; SAS Institute, Inc. 1985) were used to compare parameters

Table 1. Pearson correlation coefficients (r) between nesting habitat variables; N = 30 colonies. The relationship having the r-value in bold was significantly correlated ($P < 0.001$).

	Nesting substrate	Available area	Substrate stability	Distance to nearest gull colony
Available area	0.10			
Substrate stability	**-0.65**	-0.34		
Distance to nearest gull colony	0.00	0.09	0.22	
Number of gulls at nearest colony	-0.07	-0.17	-0.10	-0.01

among the three larid species. Variables included colony site fidelity, area available at colony sites, nesting habitat stability, and mean number of birds per colony. Unpaired t-tests were used to compare distance to nearest gull colony, and mean number of gulls at nearest colony, between the two tern species. Averages are reported as the mean and one standard error.

RESULTS

Number of Colonies and Colony Size

Within the SFBE, there were 13, 17, and seven colony sites used by Caspian Terns, Forster's Terns, and California Gulls, respectively, during one or more years from 1982 to 2003 (Appendices 1, 2, and 3). Mean number of birds at a given site (averaged among years when colonies were occupied) was 296 Caspian Terns (SE ± 87, N = 13 colonies), 218 Forster's Terns (SE ± 37, N = 17), and 1,424 California Gulls (SE ± 849, N = 7). Mean size of gull colonies was significantly larger than that of either of the terns (Sidak tests, both $P < 0.05$). Mean colony size differed little between the two tern species (Sidak test, n.s.).

Number of Caspian Terns

The number of Caspian Terns breeding within the SFBE was stable from 1982 to 2003 (linear: $r_{12} = 0.28$, n.s., quadratic: n.s.; Fig. 2, Appendix 1). The yearly average was 2,070 birds (SE ± 116, range = 1,002-2,636 birds).

Variation in Caspian Tern Counts at Different Colony Sites

There was considerable variation in number of terns breeding at each of the 13 colony sites except Hayward Shoreline and Ravenswood, where numbers never exceeded four birds (Appendix 1). The Alameda colony was established in 1985 and abandoned in1998. In 1991, however, this colony was the largest in the SFBE, when an estimated 2,040 birds, or 95% of those recorded, were present. Several colonies were established during the study: Alviso and Ravenswood (initiated in 1997), Agua Vista (2002), Brooks Island (1985), and Coyote (1993). Several others were present when the study began, but were deserted before 2003: Bair Island (deserted in 1995), Mowry (1997), and Turk (1988). Several sites were used intermittently, including Marina (used only in 1992), Baumberg, and Coyote. Because of the lack of stability among Caspian Tern colonies (and see Colony site fidelity), analyses to examine temporal trends in numbers of birds occupying different colonies were not conducted.

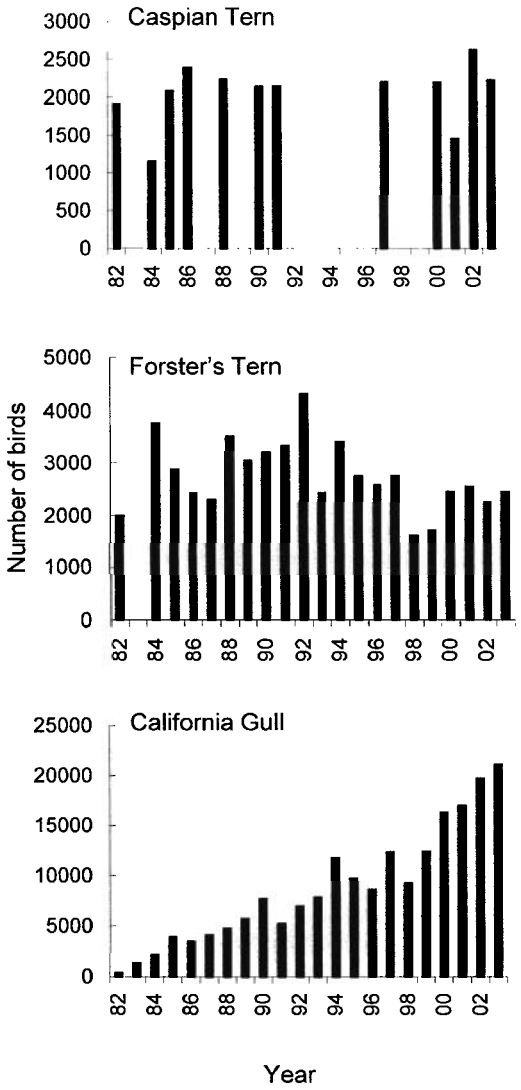

Figure 2. Number of Caspian Terns, Forster's Terns, and California Gulls breeding in the San Francisco Bay estuary during 1982 to 2003. Years with incomplete counts at primary colonies are not included. See Appendices 1, 2, and 3 for size of individual colonies by year.

The largest Caspian Tern colony each year differed across the 22 years (Appendix 1), involving Alameda, Bair Island, Brooks Island, Mowry, Turk, and Knight. The number of these terns at the largest colonies was 1,100 birds at Bair Island in 1982, 2,040 at Alameda in 1991, and 1,720 birds at Brooks Island in 2003. The Brooks Island colony has been the largest since at least 1997.

Number of Forster's Terns

The yearly average of Forster's Terns was 2,710 terns (SE ± 143, N = 21 years, range = 1,628-4,312 birds; Fig. 2, Appendix 2). There was a significant decline in total number of breeding Forster's Terns between 1984 and 2003 ($r_{13} = -0.49$, $P < 0.03$).

Variation in Forster's Tern Counts at Different Colony Sites

There was substantial variation in number of Forster's Terns breeding at different colony sites (Appendix 2). Numbers at five colonies increased significantly between 1982 and 2003, including those at Mountain View, Mallard Slough, Belmont, Corte Madera, and Turk; four were stable (Charleston, Coyote, Hayward Shoreline, and Ravenswood); and five decreased (Alviso, Bair Island, Baumberg, Dumbarton, and Moffett, Table 2).

Colonies with highest numbers of Forster's Terns differed across the 22 years, and included those at Moffett, Bair Island, Baumberg, Mallard Slough, Hayward Shoreline, Turk, and Knight. The largest colony at the beginning of this study (1982) and middle (1992) was at Moffett (655-1,000 birds); however, only three colonies had >300 birds at the end of the study (Baumberg, Belmont, and Turk; Appendix 2).

Number of California Gulls

There was a yearly average of 8,739 breeding California Gulls (SE ± 1,245, range = 412-21,106, N = 22 years; Fig. 2, Appendix 3), however, the number increased markedly and progressively ($r_{20} = 0.95$, $P < 0.001$) from 412 birds in 1982 to 21,106 in 2003 (Fig. 2).

Variation in California Gull Counts at Different Colony Sites

Between 1982 and 2003, numbers of California Gulls increased significantly at each of the SFBE colony sites of this species (Table 3, Appendix 3). The largest and oldest gull

Table 2. Results of regression analyses for the relationship between Forster's Tern colony count and year. No quadratic effects were significant; only linear effects are reported. Variance explained (r^2) reported for each model. Sample size = number of years that colony was counted. 1 = Mountain View, 2 = Mallard Slough, 3 = Alviso, 4 = Almaden Lake, 5 = Bair Island, 6 = Baumberg, 7 = Belmont, 8 = Charleston, 9 = Corte Madera, 10 = Coyote, 11 = Dumbarton, 12 = Hayward Shoreline, 13 = Mowry, 14 = Moffett, 15 = Ravenswood, 16 = Turk, and 17 = Knight. Analysis not conducted for colonies 4, 13, and 17 due to missing data for most years.

Colony	Sample size (years)	r^2-value	Regression coefficient ± standard error	P-value
1	14	0.58	13.46 ± 3.31	<0.01
2	17	0.41	10.18 ± 3.18	<0.01
3	21	0.40	-10.91 ± 3.10	<0.01
5	22	0.34	-15.78 ± 4.95	<0.01
6	22	0.30	-25.45 ± 2.96	<0.01
7	11	0.61	36.0 ± 9.67	<0.01
8	17	0.01	-1.36 ± 3.25	n.s.
9	21	0.24	2.30 ± 0.94	<0.05
10	20	0.18	-4.57 ± 2.29	n.s.
11	20	0.24	-12.23 ± 5.13	<0.05
12	16	0.07	20.13 ± 28.34	n.s.
14	20	0.32	-47.67 ± 16.56	<0.01
15	22	0.04	-4.14 ± 4.63	n.s.
16	22	0.71	25.97 ± 3.75	<0.0001
Total	21	0.12	-36.37 ± 22.93	n.s.

Table 3. Results of regression analyses for the relationship between California Gull colony count and year. Quadratic effects of year were tested for each colony; only the quadratic relationships that were significant are reported. Variance explained (r^2) reported for each model; variance explained reported for a quadratic term = variance explained by the linear term plus that of the quadratic. All linear relationships also are reported. Sample size = number of years that colony was counted. 1 = Alviso, 2 = Marina, 3 = Mountain View, 4 = Mowry, 5 = Moffett, 6 = Alameda, 7 = Brooks Island.

Colony	Sample size (years)	r^2-value	Regression coefficient ± standard error	P-value
1	22	0.87	506.2 ± 43.1	<0.001
2	22	0.61	128.2 ± 23.0	<0.001
Quadratic	22	0.70	9.0 ± 3.63	<0.05
3	22	0.40	21.17 ± 5.8	<0.01
Quadratic	22	0.56	2.39 ± 0.9	<0.05
4	22	0.55	144.8 ± 29.2	<0.001
Quadratic	22	0.65	10.77 ± 4.69	<0.05
5	22	0.54	32.67 ± 6.74	<0.001
6	19	0.49	9.23 ± 2.29	<0.001
7	19	0.36	21.71± 7.0	<0.01
Quadratic	19	0.71	3.49 ± 0.79	<0.001
Total	22	0.90	853.5 ± 63.2	<0.001

colonies were at Alviso, Mowry, and Marina. Smaller and more recently established colonies were at Mountain View, Moffett, Alameda, and Brooks Island. Numbers of gulls varied appreciably between years in all colonies except at Alviso and Brooks Island. Colonies at Marina, Mountain View, and Mowry were deserted during several years of the study. Regression analyses indicated that the relationship between colony count and year was curvilinear (quadratic) at Marina, Mountain View, Mowry, and Brooks Island colony sites. At the Marina, Mountain View, and Brooks Island sites this was due to colony stability during approximately the first 15 years of the study followed by an increase during the later 90s and early 2000s. At the Mowry colony the increasing numbers were followed by stability during the latter part of the study (Table 3, Appendix 3).

Nesting Habitat Preference

All three species nested on five to six different habitat types (Fig. 3), however, 59% and 46% of the Forster's Tern and Caspian Tern colonies, respectively, were located on salt pond islands. Other habitats used by Forster's Terns were tidal islands, sewage treatment pond islands, salt pond levees, and freshwater lake islands, in order of decreasing importance. Other habitats used by Caspian Terns were tidal islands, salt pond levees, sewage treatment pond islands, pier pilings, and bare high marsh, also in order of decreasing importance.

The California Gulls nested on a variety of habitats, although four of the seven colonies were located on salt pond islands and salt pond levees. The largest colony (Alviso) was located on a dry salt pond not in commercial use. One gull colony was located on a tidal island and another on bare high marsh habitat.

Averaged across years, 42% of the Caspian Terns nested on tidal islands, 71% of the Forster's Terns nested on salt pond islands, and 65% of the California Gulls nested on a dry salt pond (Fig. 3). The average number of birds at colonies located on a given nesting habitat showed no correlation with number of colonies located on each habitat (Appendices 1, 2, and 3, Fig. 3).

Colony Site Fidelity

Colony site fidelity (number of years of occupation at a given colony site, 1982-2003) among Caspian Tern colony sites (6.8 years, SE ± 1.4; N = 9 sites counted each year; Appendix 1) was significantly lower than colony site fidelity of Forster's Terns (16.7 years, SE ± 2.1; N = 10 sites; Appendix 2) and California Gulls (15.8 years, SE ± 2.5; N = 5 sites;

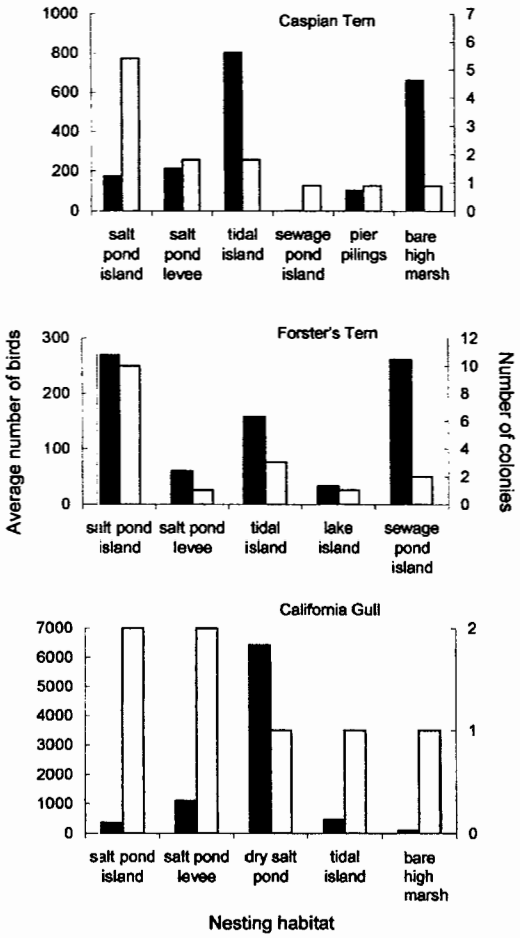

Figure 3. Average number of Caspian Terns, Forster's Terns and California Gulls using different nesting habitats (1982 to 2003) in relation to number of colonies found on respective habitats.

Sidak tests, both $P < 0.05$; Appendix 3). Colony site fidelity differed little between the gull and Forster's Tern (Sidak test, n.s.).

Colony Site Characteristics

Available nesting habitat at colony sites (range = 180 m^2 at Corte Madera to 656,600 m^2 at Bair Island) and nesting habitat stability differed little among the species (Sidak tests, all n.s.). Comparisons between the two tern species indicated that there was little and no significant difference in distance to nearest California Gull colony ($t_{28} = 0.49$, n.s.), and in average number of gulls nesting at the nearest colony ($t_{28} = 0.50$, n.s.).

The multiple regression model relating the effects of four habitat variables to colony site fidelity among Caspian Tern colonies did not relate site fidelity to any of the four terms. However, the model for Forster's Tern colony site fidelity was highly significant, explaining 99% of the variance in site fidelity. Forster's Tern site fidelity was highest at sites having the largest available areas, and that were nearest to California Gull colonies. Colonies of these terns were also more persistent at unstable locations compared to intermediately stable or stable sites (Sidak tests, all $P < 0.05$; Table 4). In contrast, colony site fidelity among California Gulls was higher at stable sites than at intermediately stable or unstable sites (Sidak tests, both $P < 0.05$; Table 4).

DISCUSSION

During the study period, numbers of breeding Forster's Terns at SFBE declined, those of Caspian Terns were stable, and numbers of California Gulls increased markedly. Nevertheless, numbers of birds in each colony of each species differed among years. Some of this annual variation may have been due to undercounting during censuses. Desertion of colony sites also occurred in some years in each species, although site fidelity was lower in the Caspian Tern compared to the other two larids.

Both tern species experienced low fledging rates in the SFBE during at least the last few years (Roby *et al.* 2003a; SFBBO, unpubl. data). Therefore, it is suspected that the high rate of fluctuation in numbers among Forster's Tern and Caspian Tern colonies could also be related to their low fecundity, as breeding site fidelity of seabirds is thought to depend, at least in part, on reproductive success in the previous year (Burger 1982; Cuthbert 1988; Danchin *et al.* 1998; Quinn and Sirdevan 1998).

The fluctuations in colony site fidelity were unlikely to be related to emigration from the SFBE because no tern or California Gull colonies are closer than 180 km from the SFBE (two small Caspian Tern colonies in Monterey Bay; Carter *et al.* 1990; Winkler 1996; McNicholl *et al.* 2001; Roby *et al.* 2003b).

Table 4. Results of multiple regression analyses for the relationship of colony site fidelity with amount of area (m^2) available at the colony site, nesting substrate stability, distance to nearest California Gull colony, and average number of birds nesting at nearest gull colony (average number for all study years). See Methods for definition of substrate stability, which was analyzed as categorical; all other terms analyzed as continuous. The dependent variable, colony site fidelity, was measured as the number of years that a given colony site was occupied between 1982 and 2003. Colony site fidelity was log-transformed (see Methods). DF = numerator df. Values reported are those obtained after all insignificant terms had been removed from the models.

	Regression coefficient ± standard error	P-value	DF
Caspian Tern: model not significant, all terms rejected			
Forster's Tern: Model $F_{(4, 5)} = 115.7$; 98.9% of variance explained			
Colony area (m^2)	$3.37^{-06} \pm 2.95^{-07}$	<0.001	1
Substrate stability	—	<0.001	2
Distance to nearest gull colony (km)	-0.022 ± 0.009	<0.05	1
California Gull: Model $F_{(2, 2)} = 25.9$; 96.3% of variance explained			
Substrate stability	—	<0.05	2

There was no evidence that the decline among Forster's Terns and low site fidelity in Caspian Terns was affected by nesting habitat stability (including fluctuating water levels in salt ponds) or disturbance/predation by California Gulls. Indeed, Caspian Terns were not affected by either of the two factors and Forster's Terns had highest colony site fidelity on the least stable nesting substrate, and at sites closest to California Gull colonies.

Potential factors that were not measured were predation by the Red Fox (*Vulpes vulpes*) and human disturbance (primarily salt pond maintenance and recreational boaters) at colony sites. Both of these factors were suspected to have affected colony size and breeding success at SFBE Caspian Tern colonies in 2003 (Roby *et al.* 2003a). The Red Fox was first observed at the SFBE in 1986, and soon thereafter was established in or adjacent to tidal marshes and salt ponds throughout the south bay (Goals Project 2000). In 1991, Red Fox predation resulted in the abandonment of a heronry and the tern colonies on Bair Island. The Red Fox probably caused similar declines at Baumberg, Moffett and Alviso colonies, when low water levels created land bridges to colony sites (Ryan and Parkin 1998).

The fact that colony site fidelity among Forster's Terns was highest at colonies closest to the nearest California Gull colony is surprising. For example, displacement of terns occurred when California Gulls colonized areas adjacent to the tern colonies, and gulls also ate tern eggs and chicks (CMS, pers. obs.). Other than chance, our best explanations for the positive relationship between tern site fidelity and proximity to gull colonies is that: 1) the gulls may serve as a buffer or warning system reducing the effects of disturbance and predation (the gulls vigorously mob predators that approach their colonies; Tinbergen 1960); and/or 2) there may be a relationship with available food supply (both the gulls and terns may place their colonies adjacent to locations where prey availability is high). We believe that the latter explanation is most likely because the tern's colonies averaged 9-11 km from the nearest gull colony, a distance that would not likely provide tern colonies protection by gulls responding to predators intruding into their colonies.

Nesting Caspian Terns rely on the most available forage fish near the colony, a characteristic that may facilitate the frequency of shifts in colony location among these terns in response to changing conditions throughout their range (Collis *et al.* 2002). However, we have no information on variation in food supply in different regions of the SFBE, although the reduced counts of breeding Caspian Terns and Forster's Terns during the strong 1982-83 El Niño, as well as the lower incidence of breeding among the latter during El Niños in 1986-87 and 1997-98, indicate that food shortage could have been an important factor to SFBE terns in those

years, as appreciable reductions in food available to seabirds occurred along the Pacific coast of North America during each of those El Niño events (Ainley *et al.* 1995; Oedekoven *et al.* 2001).

Two findings of this study indicated that nesting space was limited in the SFBE. The first showed that colony site fidelity among Forster's Terns was positively related to available nesting area at colony sites, indicating these terns preferred larger colony sites where more space was available for nesting. However, few of these larger colonies persisted to the end of the study. Nest site limitation was also suggested by the fact that Forster's Terns had highest site fidelity on the least stable (i.e., least favorable) nesting habitat where the breeding failure may be higher compared to that on stable habitat. Being the smallest of the three larids, they are more likely to be excluded on the more stable and favorable nesting habitat if the latter habitat is preferred by the two larger larids, as was found for the California Gull.

The second finding regarding limited nest space was colony habitat preference among terns and gulls in the SFBE was not related to colony size. The lack of a relationship between average number of birds at colonies located on a given nesting habitat and number of colonies located on respective habitats also suggests nesting habitat limitation because it would be expected that 1) colonies would be established most frequently on the most preferred (i.e. most stable) habitat (e.g., Ainley *et al.* 1995), and 2) respective colonies would be the largest because they would attract more individuals to the most preferred habitat. As this did not prove to be the case, nesting space may be limited at the more preferred nesting habitat.

The results of this study show that the preservation of islands with flat nesting substrate (minimally vegetated and composed of sand, gravel, earth), with a low potential for flooding, land-bridging, or disturbance, and with a wide view in all directions are critical for maintaining numbers of larids in the SFBE. Indeed, the evidence from this study indicates that such nesting habitat is extremely limited, a conclusion also reached by Roby *et al.* (2003a). Given that the planned restoration of 65% of the 13,900 ha of salt ponds in the SFBE will likely remove many of the salt pond islands and levees where 80% (1,958 birds), 20% (438 birds) and 96% (20,210) of the Forster's Terns, Caspian Terns, and California Gulls, respectively, were nesting in 2003, there could be serious problems for these birds unless restoration plans include creation of new islands specifically designed to provide them with nesting habitat.

Managers of aquatic habitat having tidal islands also should be encouraged to maintain water levels at a depth that will prevent land bridging, allowing access to mammalian predators and human disturbance, as well as flooding during the breeding season. Exclusion of human visitors from islands used by nesting larids is advisable, as well as eradicating the Red Fox. However, the creation of new nesting habitat is crucial for continued presence of terns in the SFBE. With reduction of the salt pond complexes, failure to do so would likely lead to severe competition for nesting space among the three species, and possibly the exclusion of the terns by the gulls, that begin nesting earlier in the year, are larger, more abundant, and more aggressive. Because the marsh restoration process will require many years to complete, the installment of suitable colony sites should occur soon after the restoration process has begun.

The limitation of nesting space to larids breeding in the SFBE has broader implications regarding use of the SFBE as a location to accommodate Caspian Terns nesting in the Columbia River (a colony of 11,200 birds in 1998—the largest Caspian Tern colony in the world; Collis *et al.* 2002). The possibility that the SFBE could serve as a breeding site for terns emigrating from the Columbia River is another reason for the creation of additional nesting space during the restoration projects in the SFBE.

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Appendix 1. Counts of breeding Caspian Terns by year at all colonies within the San Francisco Bay estuary. 1 = Alameda, 2 = Alviso, 3 = Marina, 4 = Agua Vista, 5 = Bair Island, 6 = Baumberg, 7 = Brooks Island, 8 = Coyote, 9 = Hayward Shoreline, 10 = Mowry, 11 = Ravenswood, 12 = Turk, and 13 = Knight. Zero = no birds present; dash = colony not counted. Total number is the number of terns summed across colonies, which was done only if all major colonies were counted in a given year. Mean = average colony count during years when colony site was counted. Occupied = number of years colony was occupied.

	Colony													
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
1982	0	0	0	0	1100	0	0	0	—	316	0	500	—	1916
1983	0	0	0	0	422	64	0	0	—	378	0	138	—	1002
1984	0	0	0	0	0	0	0	0	—	440	0	718	—	1158
1985	200	0	0	0	20	0	—	0	—	746	0	1128	—	2094
1986	520	0	0	0	400	250	—	0	—	906	0	324	—	2400
1987	—	0	0	0	800	0	—	0	—	650	0	60	—	—
1988	—	0	0	0	1616	0	218	0	—	412	0	0	—	—
1989	—	0	0	0	800	0	—	0	—	578	0	0	—	—
1990	1188	0	0	0	450	0	120	0	—	316	0	0	76	2150
1991	2040	0	0	0	0	0	—	0	—	116	0	0	—	2156
1992	—	0	70	0	156	0	—	0	—	42	0	0	—	—
1993	—	0	0	0	160	0	—	32	—	136	0	0	—	—
1994	—	0	0	0	170	0	—	0	—	138	0	0	—	—
1995	—	0	0	0	0	0	—	48	2	210	0	0	—	—
1996	248	0	0	0	0	0	—	0	4	24	0	0	—	—
1997	570	174	0	0	0	0	1000	60	2	0	4	0	400	2210
1998	534	54	0	0	0	74	—	46	2	0	4	0	200	—
1999	2	90	0	0	0	158	—	0	2	0	2	0	—	—
2000	0	190	0	0	0	154	1612	4	2	0	2	0	242	2206
2001	0	196	0	0	0	150	1024	0	2	0	2	0	84	1458
2002	0	190	0	134	0	110	1650	0	2	0	2	0	546	2634
2003	0	82	0	78	0	70	1720	0	0	0	0	0	286	2236
Mean	663	139	70	106	554	129	1049	38	2	360	3	478	262	
Occupied	—	7	1	2	11	8	—	5	—	15	6	6	—	

Appendix 2. Counts of breeding Forster's Tern colonies by year at all colonies in the San Francisco Bay estuary. 1 = Mountain View, 2 = Mallard Slough, 3 = Alviso, 4 = Almaden Lake, 5 = Bair Island, 6 = Baumberg, 7 = Belmont, 8 = Charleston, 9 = Corte Madera, 10 = Coyote, 11 = Dumbarton, 12 = Hayward Shoreline, 13 = Mowry, 14 = Moffett, 15 = Ravenswood, 16 = Turk, and 17 = Knight. Zero = no birds present; dash = no census. Numbers in parenthesis are extrapolations where data were missing for one year but not the preceding or the following years. Total number is the number of terns summed across colonies, which was done only if all major colonies were counted in a given year. Knight Island (17) counts were excluded when calculating totals because of missing data for all but four years. Mean = average colony count during years when colony site was counted. Occupied = number of years colony was occupied.

	Colony																	
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
82	—	—	244	0	300	428	0	—	0	50	240	0	0	656	80	0	—	1998
83	—	—	(189)	0	0	194	0	—	0	56	256	0	—	—	0	0	—	—
84	—	22	134	0	300	788	0	—	0	248	80	0	60	1880	194	60	—	3766
85	—	(50)	296	0	700	484	0	—	0	20	416	0	0	530	380	0	—	2876
86	—	70	394	0	400	660	0	150	0	124	382	—	0	0	150	98	—	2428
87	—	88	198	0	150	706	0	110	0	72	382	—	0	256	270	64	—	2296
88	—	48	422	0	0	936	0	100	0	170	192	52	0	1522	0	74	—	3516
89	30	34	306	0	50	956	0	120	0	110	500	150	0	514	80	150	46	3046
90	(28)	158	204	0	0	350	0	230	0	80	140	76	—	1232	230	200	270	3198
91	26	896	306	0	0	106	0	102	0	(60)	(394)	180	—	786	384	104	—	3342
92	184	162	314	0	120	880	18	70	0	40	648	404	0	1000	472	0	—	4312
93	50	104	320	0	116	542	(38)	264	0	116	182	328	0	246	120	0	—	2426
94	80	52	154	0	0	294	58	104	0	220	34	1600	0	242	224	356	—	3418
95	76	122	174	0	36	592	60	246	0	120	254	480	0	46	154	390	—	2750
96	140	112	200	0	50	162	76	64	0	54	282	512	0	324	166	428	—	2570
97	194	106	148	0	4	228	144	146	0	138	150	452	0	254	192	600	—	2756
98	120	30	194	0	58	168	32	40	0	40	42	396	0	146	72	290	—	1628
99	100	164	38	34	0	92	110	42	0	44	90	328	0	178	10	492	—	1722
00	126	374	174	0	0	124	388	66	0	0	40	610	0	(100)	24	434	—	2460
01	196	274	52	0	0	68	488	66	(21)	0	106	782	0	20	24	484	—	2560
02	222	114	18	0	0	50	256	96	42	0	62	556	0	120	288	434	1314	2258
03	278	230	154	0	0	386	324	220	134	0	134	78	0	122	0	382	274	2442
Mean	123	161	212	34	190	418	166	124	88	98	228	436	60	509	185	296	476	
Occupied	—	—	22	1	12	22	12	—	18	22	—	—	22	19	17	—	—	

Appendix 3. Counts of breeding California Gulls by year at all colonies within the San Francisco Bay estuary. 1 = Alviso, 2 = Marina, 3 = Mountain View, 4 = Mowry, 5 = Moffett, 6 = Alameda, 7 = Brooks Island. Zero = no birds present; dash = colony not counted. Total number is the number of gulls summed across colonies. Mean = average colony count during years when colony site was counted. Occupied = number of years colony was occupied.

	Colony							
Year	1	2	3	4	5	6	7	Total
1982	412	0	0	0	0	0	0	412
1983	1342	0	0	46	0	0	0	1388
1984	2000	150	0	44	0	0	0	2194
1985	3000	374	0	554	0	0	0	3928
1986	3000	98	0	398	0	0	0	3496
1987	4000	100	0	22	0	0	0	4122
1988	4600	180	0	30	0	0	0	4810
1989	5310	434	0	0	0	0	0	5744
1990	7600	122	2	0	0	0	0	7724
1991	5250	0	0	0	0	0	0	5250
1992	5500	200	0	1294	0	0	0	6994
1993	6912	234	200	416	82	40	0	7884
1994	9000	300	350	1540	556	20	0	11766
1995	7236	4	74	2010	300	100	0	9724
1996	6558	1410	0	174	282	200	0	8624
1997	6256	1722	164	3000	1000	200	0	12342
1998	6562	1628	0	480	400	200	—	9270
1999	9380	2118	146	476	248	50	—	12418
2000	11482	1986	0	2526	254	80	10	16338
2001	11216	3056	278	1824	624	—	—	16998
2002	11302	3590	510	3120	712	—	486	19720
2003	13644	1010	862	4310	384	—	896	21106
Mean	6435	985	287	1237	440	111	464	
Occupied	22	19	9	18	11	—	—	