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Breeding Biology and Status of the California Least Tern *Sterna antillarum browni* at Alameda Point, San Francisco Bay, California

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Abstract.—The largest breeding colony of the endangered California Least Tern (*Sterna antillarum browni*) north of San Luis Obispo County occurs at Alameda Point, San Francisco Bay, California. Data on population size, reproductive success, and food habits were collected since the colony's inception in 1976, while more specific data on breeding chronology (dates of active nesting and nest initiation dates), clutch size, hatching success, and size of prey dropped at the breeding site were collected from 2000-2004. The number of breeding pairs increased by 10.4% per year, making this colony the largest colony in San Francisco Bay and representing 6% of the state population. Breeding success varied but is generally superior to the state's combined productivity numbers. Of the 32 Least Tern sites monitored in 2004, only five other colonies had higher breeding success than Alameda Point in that year. Despite the colony's success, both hatching and breeding success have declined since the mid-1990s. Terns at this urban location forage in central and south San Francisco Bay, characterized by both marine and estuarine water. Dropped prey collected since 1981 indicate that silversides (family Atherinopsidae) were the most abundant prey in all years. Breeding success was positively correlated with the proportion of Northern Anchovy (*Engraulis mordax*, family Engraulididae), the second most common prey collected, suggesting that this high-energy fish may be beneficial to these terns. Potential factors limiting growth of this crucial northern Least Tern colony include predation and human disturbance, an inadequate protected nesting area, and environmental variability and its effects on prey abundance. *Received 3 July 2006, accepted 31 March 2007.*

Key words.—Least Tern, breeding success, population status, dropped prey, Alameda Point, San Francisco Bay, estuary, environmental stochasticity.

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The California Least Tern (*Sterna antillarum browni*), the subspecies occupying the coastal areas of western North and Central America, has been on federal and state endangered species lists since 1970 and 1971, respectively. Least Terns arrive at California nesting locations in late April, where courtship and pair formation activities last into early May (Thompson *et al.* 1997). Egg-laying and incubation generally begins in mid-May, and pairs may renest following a loss of their first clutch (Massey and Atwood 1981). Nests are simple scrapes made on non-vegetated substrates, usually consisting of one to three eggs, and are incubated for 19-25 days (Thompson *et al.* 1997). Chicks are mobile and leave the nest at only two days after hatching, and first flight happens at approximately day 20 after hatching (Thompson *et al.* 1997). Least Terns usually start breeding in their third year (Massey and Atwood 1981), and they forage for small fishes in the surface waters (Thompson *et al.* 1997). The Least Tern population declined primarily due to loss of habitat to coastal human recreation and residential development (Thompson *et al.* 1997). There are 32 Least Tern sites monitored in California, and only three sites exist north of San Luis Obispo County (Marschalek 2005); the largest of these three sites is located at Alameda Point, San Francisco Bay, California. Alameda Point hosted the largest and most stable California Least Tern colony in northern California since 1977 (California Department of Fish and Game (CDFG), unpublished data). Due to the colony's high productivity over the years, it has been considered a 'source' of Least Terns for the California metapopulation (Caffrey 1995). Least Terns have attempted to nest at other sites in the San Francisco Bay area but have failed to breed successfully at most locations.

The objectives herein are 1) to describe the breeding phenology and success of Least Terns at Alameda Point and 2) to evaluate the status of this northern population. Discussion on the factors that may be limiting the growth of this population is also presented.

STUDY AREA

The Alameda Point Least Tern colony is located in the northern reaches of south San Francisco Bay (37°47'N, 122°19'W; Fig. 1). San Francisco Bay is the estuary of the Sacramento and San Joaquin Rivers (Cloern 1991) and is located in a major metropolitan area on the west coast of North America. Human population densities inhabiting the San Francisco Bay area have increased approximately 20% from 1980 to 1990 (from 319.1 people/km^2 to 384.0 people/km^2), and shipping and commerce industries move an estimated \$20-\$30 billion in goods annually (Emmett *et al.* 2000).

The nesting area is located on the runway complex of the former Naval Air Station, Alameda. The breeding site (hereafter referred to as "the site") was enclosed in 1981 by a 0.91-m high electric fence with hardware cloth near the bottom that acted as a chick barrier (Collins 2000). The fence was designed and erected to reduce access by mammalian predators and perching by avian predators. The fence lost its charge in 2001, but still provided an effective barrier to ground-based predators. In April 2004, the U.S. Fish and Wildlife Service (USFWS) replaced the derelict electric fence with a 1.2-m high chain link fence, and the fence was shifted north 20 m to avoid a storm water drain and a highly vegetated portion of the original tern colony. With the new fence in 2004, the site was expanded from 2.4 to 3.9 ha. The substrate within the enclosure consists of asphalt covered with soil, pea gravel, sand, and oyster shells, all of which were added to improve the breeding habitat. Cylindrical clay tiles, wooden A-frame structures, and driftwood were randomly placed in the site to provide shelter and protection for nestlings. Cinder blocks were also placed in a grid system within the site to form approximately 20 m × 20 m grid cells to aid in the mapping of nest locations.

METHODS

Through contracts with the U.S. Navy and USFWS, the colony was managed and protected by the Golden Gate Audubon Society (1979-1999), PRBO Conservation Science (2000-2001) and USFWS (2002-2004). Golden Gate Audubon Society personnel monitored the colony almost exclusively from outside the site and occasionally entered the colony to collect dead nestlings, non-viable eggs, and dropped prey (Collins 2000). However, PRBO and USFWS biologists entered the site on a regular basis to collect the necessary data (see below). Due to these methodological differences between Golden Gate Audubon Society monitors and PRBO and USFWS monitors, results on breeding chronology, clutch size, egg fates, and hatching success were only compared for years 2000-2004. When possible, mean clutch size and mean hatching success estimates from previous years were taken from CDFG annual monitoring reports and compared to the 2000-2004 results. Estimates on population size, breeding success, and dropped prey composition were compared for all years (1976-2004).

Nest Surveys

From 2000-2004, nest surveys were conducted in the site from every three days (early in the breeding season) to once weekly (later in the breeding season) in the

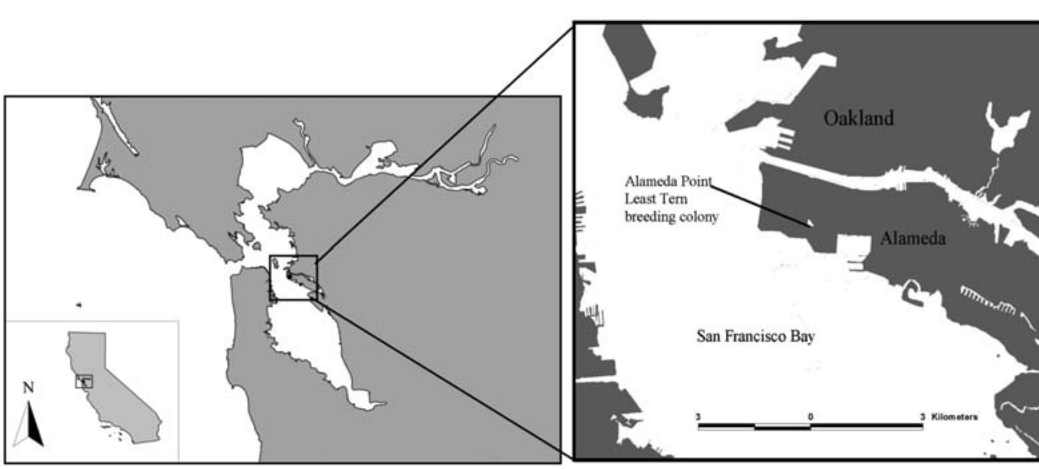

Figure 1. Location of the Alameda Point Least Tern colony, San Francisco Bay, California.

morning hours. Two to four monitors would space themselves apart to cover the approximate 20-m distance between the rows of cinder block grid markers. Monitors walked in a sinusoidal pattern to locate eggs and chicks. This was repeated in the opposite direction for the next row of grid markers until the entire site was investigated. The fence allowed for confinement of chicks to the breeding area, thereby increasing the probability of adults to reunite with their chicks. Excessive disturbance was prevented by adhering to the CDFG monitoring protocols: disturbance was temporary (i.e., breeders were kept off of nests for no more than 15 min), no surveys were conducted during certain climatic conditions (e.g., high winds, extreme cold, or extreme heat), and no obvious deleterious effects from survey-related disturbances were apparent. Nests were marked using two-inch diameter washers vertically cemented into small plaster of Paris mounds. Daily nest surveys were conducted from outside the site to supplement information gained from in-site monitoring. Dead chicks were collected and counted during each in-site survey. Abandoned and failed-to-hatch eggs were collected at the end of each season. Data from individual nests were used to determine breeding chronology (date of peak nesting and nest initiation dates), clutch size, hatching success, overall productivity, and population size for the colony. Analysis of variance (ANOVA) and Bonferroni adjusted t-tests were used to test for interannual differences in nest initiation dates, clutch sizes, and hatching success. Data on annual mean clutch size and annual mean hatching success were taken from CDFG reports for 1993-1999 (found on the CDFG Habitat Conservation Planning Branch publication website: http://www.dfg.ca.gov/hcpb/info/bm_intro.shtml) and were compared to the 2000-2004 period to evaluate changes in these breeding parameters.

Interannual Trends in Productivity

Varying methods were used throughout the study to estimate productivity. Prior to 2000, fledglings were counted daily, and composite counts of fledglings throughout the season were added for a total count (Collins 2000). From 2000-2004, the number of fledglings produced each year was determined from nest data and morning counts of chicks (i.e., nestlings not yet fully feathered) and fledglings (i.e., nestlings that were completely feathered) in the site and the surrounding tarmac from early June through early August. The minimum number of fledglings produced in a season was determined from the highest count of fledglings, and the maximum number of fledglings was calculated from the number of chicks known to have hatched minus the number of chicks located that died or were depredated. The average of the minimum and maximum number of fledglings was used for each year's fledgling production estimate, and this was divided by the number of breeding pairs to calculate the breeding success in each season. A second-order regression equation was fit to the annual breeding success estimates to show the variability in productivity through the years. Spearman-rank correlations between annual breeding success and annual means of clutch size, hatching success, and nest initiation date were calculated to see if these different breeding parameters were correlated with one another; this non-parametric statistic was used because these variables were not normally distributed. To evaluate trends in the breeding success of the Alameda Point colony relative to the state population, a frequency distribution of this colony's breeding success from 1976-2004 was compared to a similar histogram created for the state of California's combined breeding success numbers from 1971-1998.

Effects of Weather on Productivity

During 2000, a major heat wave apparently affected tern productivity. In an effort to understand the relationship between air temperature and ground temperature at the site, two Taylor® Dual Maximum-Minimum thermometers were used to track air and ground temperatures. Daily maximum, minimum, and the current measurements of air and ground temperatures were simultaneously recorded from 11 April to 27 July, 2001 between 05.45 and 19.10 h. The resulting linear regression equation ($y = 1.0018x + 6.6952$, $r^2 = 0.6504$) was used to make predictions of daily maximum ground temperatures (y) based on daily maximum air temperatures (x) in 2000 to examine the potential effects of heat on tern productivity during the heat wave in that year. The daily maximum air temperatures in 2000 were downloaded from the Center for Operational Oceanographic Products and Services website (within the National Oceanic and Atmospheric Administration's National Ocean Service (NOAA-NOS-CO-OPS: http://co-ops.nos.noaa.gov/data_res.html)), using data collected from the Alameda weather station (station #9414750), located approximately 0.6 km south of the Alameda Point Least Tern colony.

Population Estimates

The number of breeding pairs in each season was estimated differently by different monitors. CDFG employed the use of a standard breeding pair protocol (Method I; Marschalek 2005), where the number of nests initiated prior to 15 June is added to half of the nests initiated after 15 June. However, this method was not used in each year of the study and breeding chronology data were not available for all years. Instead, estimates of breeding pairs that were provided to CDFG for annual monitoring reports were used. The number of breeding pairs in each year was log-transformed and linear regression was used to estimate the population growth over time.

General Food Habits: Dropped Prey Composition

Prior to 2000, dropped fish were collected opportunistically during the breeding season and identified to the lowest taxonomic category possible (Collins 1995). From 2000-2004, dropped fish were collected during each in-site nest survey. Each specimen was identified to the lowest taxonomic level possible. Challenging specimens were identified with the assistance of biologists at the National Marine Fisheries Service, Santa Cruz, California and the Port of Oakland, California. Prey composition was described for most years since 1981. The coefficient of variation was calculated for the most common prey families to characterize their relative variabilities in the dropped prey. Using the 20 most commonly found species of prey, a Shannon-Weiner diversity index was calculated for each year. Spearman-rank correlations between the Shannon-Weiner index, the most common families of prey collected, and annual breeding success were calculated to see if breeding success was correlated with dropped prey diversity. Significant correlations with breeding success were evaluated further with linear regression analysis, and variables were transformed to properly evaluate linear trends.

RESULTS

Population Status 1976-2004

The estimated number of breeding pairs at Alameda Point increased from ten pairs in 1976 to 379 pairs in 2004. The average rate of growth was 10.4% per year (B = 0.0986, SE = 0.014, $P < 0.001$; Fig. 2).

Breeding Biology 2000-2004

Breeding Chronology. Breeding chronology differed among years, with the peak count of active nests occurring earlier in 2001 (1 June) than in the other four years (9 June in 2000, 5 June in 2002, and 2 June in 2003 and 2004). The breeding effort ended much sooner in 2002 (10 July) than in the other years (27 July in 2004, 29 July in 2001, and 2 August in 2000 and 2003).

Nest initiation dates differed significantly among years (ANOVA: $F_{4,1716} = 54.36$, $P < 0.001$; Table 1). The mean nest initiation date was earlier in 2001 than 2000, 2003 and 2004 (Bonferroni inequalities: $P < 0.001$), while 2000 had the latest mean nest initiation date compared to all years ($P < 0.001$). Nest initiation date was also significantly earlier in 2002 than 2003 ($P = 0.009$) and 2004 ($P = 0.016$).

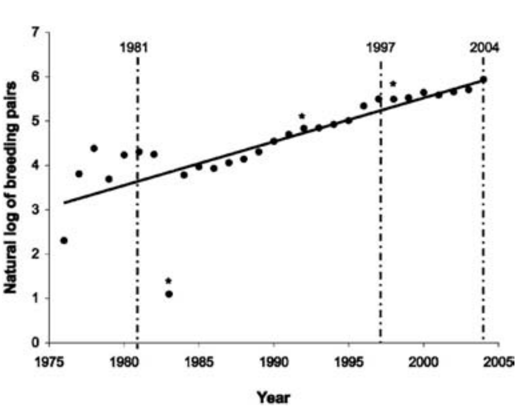

Figure 2. Estimated population size of the Alameda Point Least Tern colony from 1976-2004. (* = El Niño years. Years of important site changes are noted: 1981 = electric fence was erected; 1997 = Naval Air Station closure; 2004 = chain link fence erected.)

Table 1. Mean nest initiation dates for the Alameda Point Least Tern colony from 2000-2004.

Year	Mean nest initiation date ± SD	N
2000	5 June ± 13	312
2001	22 May ± 10	275
2002	24 May ± 10	326
2003	28 May ± 15	368
2004	26 May ± 15	440

Clutch Size and Hatching Success

Clutch size differed significantly among years (ANOVA: $F_{4,1715} = 23.11$, $P < 0.001$; Table 2A), with 2001 having a significantly larger clutch size than 2000 (Bonferroni inequality: $P = 0.002$), 2003 ($P = 0.003$), and 2004 ($P < 0.001$). Clutch size in 2004 was significantly smaller than in all other years ($P < 0.001$).

Hatching success was significantly different among years (ANOVA: $F_{4,1687} = 15.61$, $P < 0.001$; Table 2B), with 2001 having significantly higher hatching success than all other years (Bonferroni inequalities: $P < 0.001$). A total of 105 eggs in 2000 (18.3%) failed to hatch, a high percentage relative to years 2001, 2002 and 2004. A total of 44 eggs in 2002 (7.0%) were depredated, representing four times the number of depredated eggs in 2000.

Mean clutch size and mean hatching success for the 2000-2004 period were 1.86 ± 0.11 eggs SD (N = 5) and 0.73 ± 0.09 SD (N = 5), respectively. Comparatively, mean clutch size and mean hatching success for the 1993-1999 period were 1.85 ± 0.21 eggs SD (N = 7) and 0.83 ± 0.05 SD (N = 7), respectively.

Colony Temperature. NOAA-NOS-CO-OPS data indicated maximum daily air temperatures for the 10 June-20 June, 2000 period ranged from 17.3-30.6°C. Using the regression equation from the Methods, maximum ground temperatures in the site for the same time period ranged from 24-40.8°C.

Breeding Success and General Feeding Habits 1976-2004

Productivity. The estimated number of fledglings produced was 215, 320, 238, 178, and 268 from 2000-2004, respectively. Breeding success (number of fledglings/breeding pair) increased through the 1970s and 1980s

Table 2. Clutch sizes and egg fates for the Alameda Point Least Tern colony from 2000-2004.

	Year				
	2000	2001	2002	2003	2004
(A) Clutch size (% nests)					
1-egg	55 (17.6)	17 (6.2)	40 (12)	68 (18.5)	148 (33.6)
2-eggs	251 (80.4)	247 (89.8)	267 (82)	287 (78.0)	281 (63.9)
3-eggs	6 (2.0)	11 (4.0)	18 (5)	13 (3.5)	10 (2.3)
4-eggs	0	0	0	0	1 (0.2)
5-eggs	0	0	1 (1)	0	0
Mean ± SD (N)	**1.84** ± 0.41 (312)	**1.98** ± 0.32 (275)	**1.93** ± 0.42 (325)[a]	**1.85** ± 0.45 (368)	**1.69** ± 0.52 (440)
(B) Egg fates (% eggs)					
hatched	360 (62.6)	489 (89.9)	435 (68.7)	516 (75.8)	554 (74.6)
failed to hatch	105 (18.3)	28 (5.1)	56 (8.8)	75 (11.0)	63 (8.5)
abandoned	19 (3.3)	7 (1.3)	30 (4.7)	63 (9.2)	78 (10.5)
depredated	11 (1.9)	1 (0.2)	44 (7.0)	0	1 (0.1)
died while hatching	1 (0.2)	0	0	0	1 (0.1)
unknown	79 (13.7)	19 (3.5)	64 (10.1)	25 (3.7)	46 (6.2)
unknown if attended[b]	0	0	4 (0.6)	0	0
incidental take	0	0	0	2 (0.3)	0
TOTAL	575	544	633	681	743
Mean hatching success ± SD (N)	**0.67** ± 0.39 (284)	**0.89** ± 0.26 (275)	**0.67** ± 0.42 (326)	**0.70** ± 0.43 (368)	**0.70** ± 0.43 (440)

[a]Results do not include the 5-egg clutch.
[b]Undetermined if nest was attended during 21 day incubation period; egg did not hatch.

but decreased since the mid-1990s, particularly after the Naval Air Station's closure in 1997 ($y = -0.005x^2 + 19.82x - 19740$, $r^2 = 0.348$; Fig. 3). Breeding success was positively correlated with mean annual clutch size ($r_{11} = 0.890$, $P < 0.001$), while mean annual hatching success ($r_{11} = 0.415$, n.s.), and mean nest initiation date ($r_4 = -0.700$, n.s.) did not correlate significantly with breeding success. Clutch size and hatching success had a nearly significant positive correlation with one another ($r_{11} = 0.437$, $P = 0.156$).

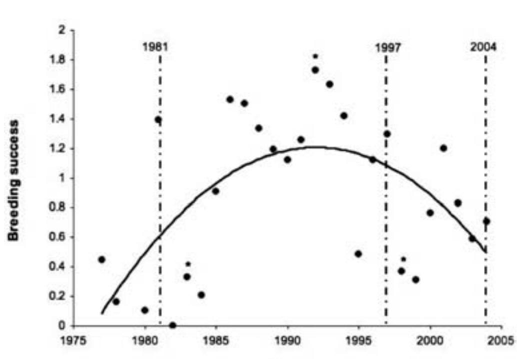

Figure 3. Breeding success (fledglings / breeding pair) of the Alameda Point Least Tern colony from 1976-2004. (* = El Niño years. Years of important site changes are noted: 1981 = electric fence was erected; 1997 = Naval Air Station closure; 2004 = chain link fence erected.)

Breeding success at Alameda Point was evaluated by a method similar to Akçakaya *et al.* (2003). They showed the frequency distribution of breeding success (fledglings/breeding pair) for all California Least Tern colonies in California and Baja California, Mexico for 1971-1998. A histogram of breeding success for the Alameda Point Least Tern colony was created for 1976-2004 (Fig. 4).

Dropped Prey Composition. Silversides (family Atherinopsidae) were the most abundant prey items found for all years except 1987 and 1992 (Fig. 5). The principle silverside species identified were Jacksmelt (*Atherinopsis californiensis*) and Topsmelt (*Atherinops affinis*). Northern Anchovy (*Engraulis mordax*, family Engraulididae) was the next most numerous prey species collected, making up the majority of collections in 1987 and 1992. Pacific Herring (*Clupea harengus*, family Clupeidae) and surfperch species (family Embiotocidae) were also abundant in collec-

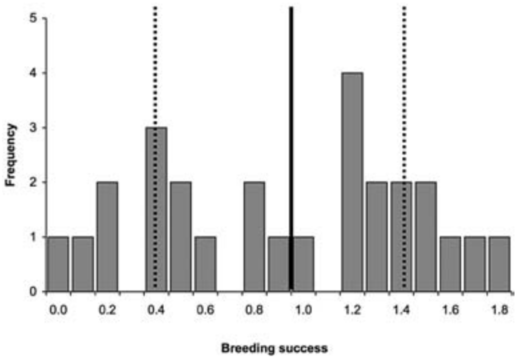

Figure 4. Frequency distribution of breeding success (fledglings/breeding pair) at the Alameda Point Least Tern colony from 1976-2004. (Note: the solid line represents the mean, and the dashed lines represent ± 1 SD of the mean.)

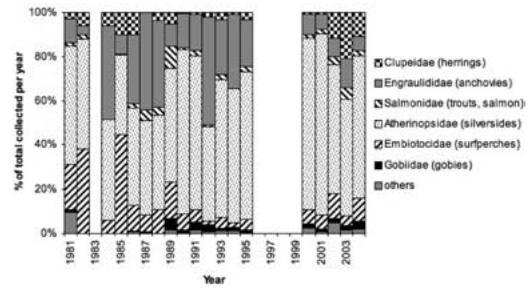

Figure 5. Least Tern dropped prey collected at Alameda Point from 1981-1982, 1984-1995, and 2000-2004. (Years 1981-1995 from Collins (1995).)

tions. The coefficients of variation for Atherinopsidae and Engraulididae were 23.4% and 70.3%, respectively.

Integration of Breeding Parameters and Diet. Spearman-rank correlations revealed a significant positive correlation between annual breeding success and the percentage of Engraulididae in the annual dropped prey collection ($r_{18} = 0.547$, $P = 0.015$), while the percentage of Atherinopsidae and the percentage of Engraulididae were negatively correlated with each other ($r_{18} = -0.402$, $P = 0.088$). The annual percentages of Engraulididae were log-transformed to obtain the linear regression equation relating breeding success to northern anchovy ($y = 0.7287x + 0.1598$, $r^2 = 0.241$; Fig. 6).

DISCUSSION

Population Status, Reproductive Success, and General Feeding Habits

The Alameda Point colony comprised 97% of the San Francisco Bay region's Least Tern population, was the seventh largest colony out of the 32 Least Tern sites in California, and represented approximately 6% of the Least Tern population in California in 2004 (Marschalek 2005). The estimated 10.4% per annum growth rate may be contentious because different methods for determining the number of breeding pairs were employed by different monitors. In addition, Least Terns at Alameda were not banded, so pairs and renesting attempts could not be positively identified. However, the 2000-2004 breeding chronology data showed that breeding may have started at different times in different years, but there was no clear evidence of major renesting events. The El Niño/Southern Oscillation event in 1983 likely caused the decline in breeding pairs at Alameda Point and southern California colonies (Massey *et al.* 1992). Despite the urban environment that the terns of this colony contend with, this colony has been the largest, most stable colony in the San Francisco Bay Area for decades.

When comparing egg and hatching success data with other 31 California Least Tern colonies in 2004, the Alameda Point colony ranked fifth in the number of eggs laid and fourth in the number of chicks hatched. In 2004, this colony was responsible for all of the fledglings estimated in the San Francisco

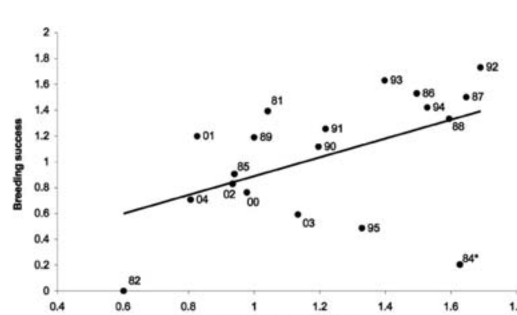

Figure 6. Least Tern breeding success and the percentage of Engraulididae in the dropped prey. (Each point is labeled with the two-digit year. * = possible outlier.)

Bay Area and ranked second of all colonies in California for fledgling production (Marschalek 2005).

When comparing breeding success with other California nesting sites in 2004, only five other colonies had higher fledgling-per-pair ratios than Alameda Point (Marschalek 2005). Some of the variability in breeding success may be due to the difficulty in estimating fledgling production in each year, as finding and counting all fledglings in the site was difficult. Despite the shortcomings in productivity estimates, the frequency distribution of annual breeding success estimates is not unimodal, similar to that shown by Akçakaya *et al.* (2003) for the California state population. However, unlike Akçakaya *et al.* (2003), the Alameda Point colony has not experienced a high frequency of total breeding failure years. In 13 of the 27 years of breeding success data, this colony produced more than one fledgling per breeding pair and is apparently more successful than the state population.

Given the continued growth of the Alameda Point colony and its relatively high productivity, this colony may be the 'source' population for the San Francisco Bay region (Pulliam 1988). However, other sites in San Francisco Bay (e.g., Oakland Airport, Bay Farm Island, Bair Island) have not been successful through the years. Predators, construction and human recreation activities have disrupted Least Terns from breeding and forced them to other locations, as was found in 1974 at Bay Farm Island (Bender 1974). The only other Least Tern colony in the San Francisco Bay region that has managed to persist is located in Pittsburg, approximately 50 km northeast of Alameda Point. Since its inception in 1984, this colony has only grown from seven breeding pairs to twelve breeding pairs in 2004 (CDFG, unpublished data). Therefore, the Alameda Point colony remains a crucial colony for the San Francisco Bay.

The dropped prey results indicate that Least Terns forage mainly on pelagic, slender-bodied schooling fishes. These results corroborated findings in other Least Tern diet studies (Atwood and Minsky 1983; Atwood and Kelly 1984; Wilson *et al.* 1993; Elliott 2005). While Atherinopsidae and Engraulididae were the most common families collected, the larger coefficient of variation value for Engraulididae implies their availability to the Alameda Point Least Tern colony fluctuates greatly. Despite being the secondary prey and having greater variability, Northern Anchovy appeared to have a positive influence on annual breeding success. A small increase in anchovy abundance can have a considerable impact on breeding success; using the equation generated in the Results, increasing Northern Anchovy from 1% to 5% of the dropped fish can result in a breeding success increase from 0.16 to 0.67 fledglings per breeding pair. The Northern Anchovy contains more lipids and energy content than Topsmelt (Dahdul and Horn 2003), which may contribute to improved breeding success in Least Terns.

Factors Limiting Growth of the Alameda Point Least Tern Colony

This colony continues to be the only large, stable colony in northern California. However, while clutch size has not changed, hatching success and reproductive success have declined since the mid- to late-1990s. Herein, the different factors that may be limiting the reproductive success (and future growth) of the Alameda Point Least Tern colony are discussed.

Predation and Human Disturbance

Least Tern breeding success can be affected by predation and disturbance events. Both avian and terrestrial predators take eggs and chicks, particularly when adults leave the nest to mob predators (Burger 1989; Thompson *et al.* 1997). Egg predation appeared most prevalent in 2002, with 35 of the 44 depredated eggs discovered early in the breeding season (24 May). Since Least Terns can renest as quickly as four days after the loss of eggs (Massey and Fancher 1989), this might explain the lack of evidence for renesting (i.e., renesting occurred early and could not be separated from the first-nesting attempts) and the relatively early end to breeding activity in that year.

Fortunately, the Alameda Point colony has not had the heavy predation pressures of other colonies. First, this colony always had a fence enclosing the breeding area, thereby keeping most terrestrial predators out. Second, there are large, open, non-vegetated areas adjacent to the site, allowing the terns to see predators coming from a great distance. Third, the lack of tall vegetation and buildings near the site do not encourage breeding and/or perching by potential predators (Caffrey 1995). Finally, the colony has benefited from effective predator management, as well as a strong monitor presence to help document and locate predators (Caffrey 1995; Collins 2000).

With the closure of the Naval Air Station in 1997 and the use of adjacent areas by people anticipated to increase, predator and human-related disturbances may have a greater impact on the breeding success of the Alameda Point colony in the future.

Habitat Constraints

The Alameda Point colony is confined by the presence of the fence, and since 2004 it yielded a 3.9 ha space for approximately 380 pairs to breed, which translates to 97.4 breeding pairs per ha. This was an improvement from the estimated 125.4 breeding pairs per ha in 2003 with the previous fence line. In comparison, three other large (i.e., >200 breeding pairs) Least Tern colonies in California had variable breeding pairs per ha ratios. According to population data collected in 2002, Mission Bay/Mariner's Point (San Diego County) hosted 110 breeding pairs per ha (Virginia Johnson, site monitor, pers. comm.), which was a slightly higher ratio than the Alameda Point colony. However, in 2002, the Ormond East colony at Naval Base, Point Mugu (Ventura County) contained an average of 33.4 pairs per ha (Martin Ruane, CIV (Environmental), U.S. Navy, pers. comm.), and Huntington State Beach (Los Angeles County) held 56.0 pairs per ha (Anne Hoeker, U.S. Fish and Wildlife Service, pers. comm.). The Alameda Point breeding site may be too small to accommodate the growing Least Tern population, and density-dependent effects may be causing the declining breeding success. It remains to be seen whether the expansion of the breeding area in 2004 will enhance breeding success for the terns.

Environmental Stochasticity

Large-scale climate events such as El Niños and their effects on the prey of estuarine seabird populations have not been studied extensively. The effects of El Niño events on the Alameda Point colony varied, with 1983 and 1998 having reduced breeding success while 1992 did not show the same result (Fig. 3). Since dropped fish were not collected in a few El Niño years, it is difficult to make conclusions on the effects of El Niños on Least Tern prey. The Alameda Point Least Terns have historically foraged most often in the south San Francisco Bay environment (Collins and Feeney 1995; PRBO unpublished data), and El Niños have enhanced phytoplankton production and zooplankton biomass in the south Bay through increased river inflow (Ambler *et al.* 1985; Cloern 1991). However, secondary mechanisms (e.g., wind speed, cloud cover) have confounding effects on El Niños (Cloern 1991). So different climate events have affected the biota of south San Francisco Bay in different ways, which may explain the variable breeding success results of the Least Terns to El Niños.

Other environmental factors, such as heat waves, also have an impact on breeding success. Too much exposure to temperature extremes could terminate further development of the embryo in the egg or cause heatstroke in small, less mobile chicks (Thompson *et al.* 1997). Least Tern chicks died from heat-stroke during a hot spell in Oklahoma when air temperatures reached 33.2-35.5°C (Overstreet and Rehak 1982). The substrate of the Alameda Point site retains heat, as daily maximum ground temperatures in 2001 almost always exceeded the daily maximum air temperatures. In 2000, air temperature data indicated two days (13-14 June) reached 30-34°C, which corresponded to ground temperatures of 30-40°C and could cause considerable heat stress on tern eggs and chicks. These high temperatures undoubtedly led to some of the 105 (18.3%) failed-to-hatch eggs found during that season.

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