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SITE FIDELITY OF LEAST TERNS IN CALIFORNIA[1]

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Abstract. The degree to which Least Terns (*Sterna antillarum*) exhibit year-to-year fidelity to particular colony sites, as well as fidelity toward their natal colony sites, was examined using banding recoveries obtained in California. Individuals had high rates of return to colony sites where they had nested during the preceding year; of those few birds that switched colony sites between successive years, most moved only short distances from the previous area. Least Terns also showed a significant tendency toward nesting at their natal colony site. These results suggest that the species may be more philopatric than has been postulated previously, and that long-term protection and management of current colony sites is therefore an important conservation goal.

Key words: Sterna antillarum; *Least Tern; site fidelity; philopatry; banding recoveries; endangered species; California.*

INTRODUCTION

Many populations of the Least Tern (*Sterna antillarum*) and its Old World counterpart, the Little Tern (*Sterna albifrons*), appear to be threatened or declining as a result of destruction or disturbance of their nesting areas (Massey 1974, Fisk 1975, Lloyd et al. 1975, Galli 1978, Haddon and Knight 1983, Burger 1984, Cramp 1985, U.S. Fish and Wildlife Service 1985). Consequently, conservation efforts have generally focused on protection of the species' active nesting sites. However, observations at many colony sites, especially those located in unstable habitats, have suggested that Least Terns exhibit relatively little fidelity to breeding areas (Drost 1953, Nisbet 1973, McNicholl 1975), raising the question of whether long-term maintenance and protection of present colony sites is an effective management approach.

Since the California Least Tern (*S. antillarum browni*) was given Federal and State endangered status in 1970, various aspects of the species' biology on the west coast of the United States have been described (Massey 1974; Massey and Atwood 1978, 1981; Atwood and Minsky 1983; Atwood and Kelly 1984; Atwood 1986; Keane 1987; Minsky 1987). A major research emphasis in this population has involved the annual banding of young and the recovery of banded, breeding adults. Here we examine, based on banding recoveries, the degree to which individual Least Terns exhibit year-to-year fidelity to particular colony sites. Additionally, we discuss the extent to which individual Least Terns return to their natal colony sites to breed.

METHODS

From 1973 to 1983 a total of 5,425 Least Tern chicks were banded with aluminum USFWS bands at breeding colonies in California (Table 1, Fig. 1). During the 1976 to 1986 nesting seasons banded adults were searched for from blinds placed within or adjacent to colonies; principal study sites were located in Orange County (Huntington Beach) and Los Angeles County (Venice Beach and Terminal Island, including separate nesting areas at Ferry Street and Reeves Field). Less intensive searches for banded birds were also conducted at other breeding colonies in southern California and northern Baja California.

Banded adults were selectively captured, usually during the last 10 days of incubation when nest abandonment is less likely, using simple wire mesh drop traps placed over nest scrapes. When these procedures were deemed too disruptive to the nesting activities of particular pairs, band numbers were read in the field using a 15 to 60× spotting scope. A total of 328 known-age birds (i.e., birds banded as chicks) were recovered; of these, 303 were given unique color-band combinations at the time of their capture as adults.

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TABLE 1. Numbers of Least Tern chicks banded in California, 1973 to 1984.

Colony[a]	Year											
	73	74	75	76	77	78	79	80	81	82	83	84
HB	4[b]	—	—	—	35	115	98	105	66	61	69	104
VB	—	—	—	—	—	112	168	218	213	178	173	47
TI	—	—	5	44	111	—	—	—	19	48	40	7
MISC	87	44	21	301	151	159	355	360	401	277	633	596
Total	91	44	26	345	297	386	621	683	699	564	915	754

[a] Colony site abbreviations as follows: HB = Huntington Beach; VB = Venice Beach; TI = Terminal Island; MISC = colonies other than HB, VB, or TI.
[b] Number of chicks banded.

Additionally, 104 nesting birds were trapped and uniquely color-banded as adults of unknown age. Throughout the following analyses only recoveries of breeding individuals known to be associated with either active nests or juveniles are considered; banded birds that were only observed courting or loafing in the nesting areas and recoveries of dead individuals have been excluded.

To evaluate the fidelity of Least Terns to their natal colonies we followed a modified version of the method used by Blokpoel and Courtney (1982) to correct for the effects on recovery data of unequal banding and recovery efforts. The assumptions we have made in using this approach, as well as the particular details of the calculations, are best explained using a simplified hypothetical example.

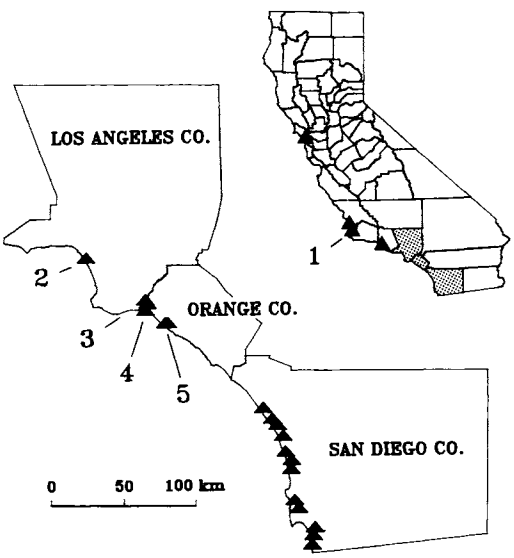

FIGURE 1. California Least Tern chick-banding localities, 1973 to 1984. Shaded counties on state map shown in enlargement. Colony sites mentioned in text labelled as follows: 1 = Vandenberg Air Force Base; 2 = Venice Beach; 3 = Terminal Island; 4 = Anaheim Bay; 5 = Huntington Beach.

First, in the absence of more exact information, the total number of banded fledglings produced at a colony in a given year was estimated by multiplying the total number of chicks banded with a correction factor for chick mortality. This correction factor was defined as the number of fledglings estimated to have been produced divided by the total number of eggs estimated to have been laid in the colony; these values were obtained from unpublished census and banding data of the California Least Tern Recovery Team. For instance, at a hypothetical colony A where 75 chicks were banded and 88 fledglings were produced from a total of 110 two-egg nests, $(75) \times (88/220) = 30$ banded chicks would be estimated as having survived to fledging. For the sake of example, hypothetical colonies B and C produced estimated banded cohorts of 66 and 43 fledglings, respectively.

These values were then used to calculate expected frequencies of natal and nonnatal colony recoveries at a given colony site. If breeders were randomly distributed with respect to their natal colonies, recoveries of banded nesting birds would proportionately reflect the initial cohorts banded at each colony site. Thus, in the example above, a total of $(30 + 66 + 43) = 139$ banded individuals (from colonies A, B, and C) could potentially have been recovered, of which $(66/139) = 0.475$ would represent the expected frequency of natal colony recoveries at site B; the expected frequency of nonnatal colony site recoveries at B would be $(1 - 0.475) = 0.525$. Using these proportions, if 25 banded adults were recovered as breeders at colony site B, then $(25) \times (0.475) = 11.88$ would be the number expected to have originally hatched at colony B, whereas $(25) \times (0.525) = 13.13$ would be the

TABLE 2. Fidelity to natal colony sites in Least Terns.

Colony[a]	Year	Total recoveries	Observed recoveries from natal colony site	Expected recoveries from natal colony sites[b]	χ^2
HB	1983	24	11	4.30	12.72**
HB	1984	27	9	4.54	5.36*
HB	1985	15	5	2.52	2.93
HB	1986	26	9	3.69	8.90**
VB	1983	52	30	16.74	15.45**
VB	1984	44	28	13.82	21.21**
VB	1985	44	28	13.33	23.16**
VB	1986	50	30	14.55	23.13**

[a] Colony abbreviations as follows: HB = Huntington Beach, VB = Venice Beach.
[b] Assuming random distribution of breeders relative to their natal colony sites.
[c] Based on 2 × 1 contingency table comparing observed vs. expected numbers of recoveries at natal and nonnatal colony sites. Chi-square significance levels (df = 1) indicated as follows: ** = $P < 0.01$; * = $P < 0.05$.

number expected to have hatched at colonies other than B. These expected values were then compared with the observed results using a 2 × 1 chi-square contingency table. Because of small numbers of recoveries obtained at most study colonies in any given year, only data from Venice Beach (1983 to 1986) and Huntington Beach (1983 to 1986) were analyzed using this approach.

RESULTS

NATAL COLONY SITE FIDELITY

Based on recoveries at Venice Beach and Huntington Beach, Least Terns breed at their natal colony sites more frequently than would be predicted if birds nested randomly relative to the colonies where they were hatched (Table 2). Unfortunately, similar examination of natal site fidelity at other colony sites was impossible due to the constraints of sample size. Although these data indicate that Least Terns in California tend to breed at their natal colony site, additional analyses using recoveries from localities other than Venice Beach and Huntington Beach is certainly desirable.

YEAR-TO-YEAR COLONY SITE FIDELITY

Examination of the frequency with which banded birds found breeding at a colony in one year returned to that same site during the following year indicates that individual Least Terns maintain a very high degree of colony site fidelity from year-to-year. At Venice Beach, where virtually all nesting birds were checked for bands during 1983 to 1986, the mean annual rate of return during this period was 78%; excluding the 1984 value, when only 34 individuals returned of the 59 that had been present at the colony in 1983, the mean annual rate of return at this site was 85% (Table 3). Even if one naively assumes that no mortality has occurred between breeding seasons, and that all of each year's "missing" individuals (birds present at a nesting site in one year that failed to return to that site in the following year) moved from Venice Beach to other less intensively studied areas where they were overlooked, an obvious pattern of strong site fidelity by individual breeding Least Terns was still evident.

These results agree with Burger's (1984) analysis of Least Tern site fidelity in New Jersey, which was based not on observations of banded

TABLE 3. Annual and intercolony variation in site fidelity in breeding Least Terns.

Colony	Year				$\bar{x}$
	1983[a]	1984	1985	1986	
Venice Beach	86 (21)	58 (59)	82 (54)	86 (66)	78
Huntington Beach	54 (13)	42 (31)	52 (31)	79 (19)	57
Terminal Island	50 (22)	38 (34)	36 (50)	47 (38)	43

[a] Percent of the previous year's banded population (n indicated in parentheses) that was documented as breeding during the specified year. Thus, of 21 banded individuals that nested at Venice Beach in 1982, 86% returned to breed at this site in 1983.

individuals but rather on year-to-year occupancy of established nesting areas; in this study, she found that "turnover rates for Least Terns are less than half those for other species that are often considered to have high colony and nest site stability." We note that even the relatively intense levels of human disturbance associated with research activities at the Venice Beach colony site, often involving intrusion into the nesting colony on 3 to 4 days per week throughout the breeding season, failed to cause reduced levels of site fidelity.

Pronounced colony site fidelity was less evident at Huntington Beach and Terminal Island (Table 3), probably mostly because of failure to locate all of the banded birds that were actually present at these less thoroughly studied (relative to Venice Beach) sites. Approximately equal time and effort in searching for banded birds was expended at Huntington Beach each year from 1983 to 1985, and return rates varied from 42 to 54%. However, when more intensive observations were made at this colony in 1986 (comparable to the recovery efforts at Venice Beach during 1983 to 1986), the return rate dramatically increased to 79%, suggesting that the 1983 to 1985 Huntington Beach values represent substantial underestimates (Table 3). Recovery efforts at Terminal Island from 1983 to 1986 were similar in magnitude to those at Huntington Beach during the period 1983 to 1985; these annual return rates (36 to 50%) probably also represent underestimated, minimum values (Table 3).

Movement between colony sites in successive years was infrequently documented in California Least Terns. In 304 cases where individuals were recovered as breeders during two consecutive seasons (thus eliminating mortality as a complicating factor to observed patterns of site fidelity), the same colony site was used during both years in 240 instances (79%). Seventy-seven percent of the 64 birds that did change colony sites in successive years moved distances of less than 15 km; of the 15 individuals that did emigrate farther than 15 km, 10 moved to the next nearest colony site. Thus only 8% of the Least Terns that switched colonies between successive breeding seasons emigrated to sites that were not either (a) within 15 km of the initial nesting area or (b) the next nearest colony site to the initial nesting location. Although more rigorous interpretation of these data is prevented by the complicating effects of unequal recovery efforts at different colony sites, nonetheless we believe that these results suggest that California Least Terns seldom move between colony sites, and that when emigration does occur, only short distance movements are usually involved.

Because comparable recovery efforts were made from year-to-year at each specific colony (with the exception of Huntington Beach in 1986, when coverage was substantially increased from 1983 to 1985 levels), annual differences in intracolony return rates might reflect either variations in emigration rates or differences in survivorship during the nonbreeding season. At all three nesting areas the return rates in 1984 were less than in nearly all other years of study at these colonies (Table 3). We believe that these results best suggest increased levels of mortality in the California Least Tern population between the 1983 breeding season and the beginning of the 1984 season; none of the missing birds have been subsequently relocated, and we presume these individuals to have died rather than to have moved to other colony sites. In the absence of even basic knowledge regarding the migratory route or wintering grounds of this subspecies, we can only speculate as to possible causes of this putative increase in mortality. During the 1983 breeding season, El Niño conditions severely impacted many seabird populations along the Pacific coasts of North, Central, and South America (Cane 1983, Schreiber and Schreiber 1984). Although we saw no evidence of reduced reproductive success in California Least Terns during the 1983 breeding season (Atwood and Kelly 1984), it is possible that as the population migrated south after the nesting season it encountered depleted or limited food resources associated with El Niño. Elevated levels of mortality caused by these food shortages would then have been reflected in the reduced return rates observed in 1984.

FACTORS AFFECTING COLONY SITE FIDELITY

A variety of factors, all of which are in general related to reproductive success, may cause Least Terns to move from one colony site to another (Burger 1984, Kotliar and Burger 1986). Principal among these may be the physical stability of the site itself, including the overall configuration of the colony site as well as specific characteristics such as the amount of vegetation cover. On Terminal Island, the exact geographic location and physical characteristics of two Least

Tern nesting areas varied almost annually from 1975 to 1986; at Huntington Beach the colony site has remained essentially constant in its ecological characteristics and specific location for over 10 years due to annual vegetation control and management efforts (California Least Tern Recovery Team, unpubl. data). Birds in the Huntington Beach colony exhibited higher levels of site fidelity each year than those breeding at Terminal Island (Table 3). Unfortunately these limited data may be compromised by the possible effects of unequal sampling effort at each colony site. Although approximately equal amounts of time were spent looking for banded birds at each of these sites during 1983 to 1985, systematic surveys (such as at Venice Beach) were not conducted at Huntington Beach or Terminal Island, and we cannot exclude the possibility that the minor observed differences in site fidelity are merely an artifact of the sampling protocol. Additional study of Least Tern site fidelity, especially in areas where the physical and ecological characteristics of colony sites are frequently altered from year-to-year, would provide valuable information concerning the relationship between site fidelity and the stability of nesting areas.

Predation may also influence the year-to-year fidelity of individual Least Terns to their breeding colonies, although available data concerning the effects of this factor fail to indicate a clear pattern. No courtship or nesting activity occurred at Anaheim Bay in 1983 following predation during 1982 in which 15 of 16 nests were destroyed by red foxes (*Vulpes fulva*); four of the seven banded breeders present during the preceding year were documented as having moved in 1983 to two nearby nesting areas. However, in a seemingly analogous situation that unfortunately did not involve known banded birds, colony sites at Vandenberg Air Force Base were occupied by approximately equal numbers of terns during 1984 and 1985, despite the fact that nearly 100% of the nesting attempts in 1984 failed due to nocturnal predation by coyotes (*Canis latrans*) (California Least Tern Recovery Team, unpubl. data).

In a better documented example based on observations of banded individuals, significant diurnal predation definitely failed to influence site fidelity at Venice Beach between 1982 and 1983. During a 3-week period in 1982, over 100 juvenile terns, representing approximately 60% of the colony's total chick production for the year, were taken at Venice Beach by a female American Kestrel (*Falco sparverius*) thought to be feeding juveniles (California Least Tern Recovery Team, unpubl. data). Of 21 banded individuals that nested at this site in 1982, 18 (86%) returned to breed in 1983. Although the reproductive success of each of these birds in 1982 is not known, many or all probably suffered at least some losses of chicks to predation, and certainly all were subject to the disturbance caused by the kestrel's repeated raids on the nesting area.

Burger (1984) similarly noted that predation had variable effects on Least Tern site occupancy in New Jersey, and we concur with her suggestion that the magnitude of losses to predators as well as the past history of a site's use may be important factors in determining whether or not abandonment would occur. Additionally, we suspect that situations in which nesting adults are threatened by nocturnal predators such as mammals or owls may be more likely to result in a site's abandonment than even intense levels of diurnal predation on chicks or eggs (or human disturbance associated with research). Unfortunately, without detailed monitoring of breeding activities the presence and extent of nocturnal predation on Least Tern colonies is rarely noted, and site abandonment or reproductive failure may be wrongly attributed to other more easily observed causes such as diurnal predators or human disturbance. More intensive study is needed to clarify the relationship between predation and Least Tern site fidelity, as well as the frequency with which human disturbance is responsible for abandonment of established colony sites.

Recovery data indicate that breeding age was not an important variable related to site fidelity. Linear regression analysis based on recoveries of known-age Least Terns at Venice Beach indicated that age was a poor predictor of site fidelity ($r^2 = 0.068$, $P = 0.619$).

Similarly, there was no clear evidence that declines in available food supplies had an impact on Least Tern site fidelity. Breeding colonies throughout the southern California breeding range were characterized in 1982 by lowered clutch sizes, depressed rates of chick growth, and increased levels of egg abandonment and chick mortality, all considered to be indirect indicators of food shortage (Atwood and Kelly 1984). Of 17 banded individuals that nested at Venice Beach in 1981, 10 (58%) were recorded at this site in 1982. Although this rate of return is less than

observed at this colony during subsequent years (Table 3), systematic searches for banded birds were not begun at Venice Beach until 1983, and it is likely that some birds present in 1981 were merely overlooked in the following year. Of 21 banded individuals that nested at Venice Beach during the 1982 food shortage, 18 (86%) returned to the site in 1983.

CONCLUSIONS

These results suggest that in both fidelity to the natal colony site and in year-to-year colony site fidelity, Least Terns may be far more "faithful" to their nesting areas than has been postulated previously based on observations made at unstable or disturbed colony sites. It should not be assumed that *Sterna antillarum* inherently lacks the site fidelity characteristic of many other terns. Instead, future research should focus on identifying the circumstances that cause specific breeding colonies to deviate from the basic pattern of well-developed site fidelity. Variables such as the physical/ecological stability of the colony site or the extent and type of predation may significantly affect the faithfulness of Least Terns to their nesting areas; however, at the present time, information concerning the influence of these factors on colony site fidelity is largely anecdotal.

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