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DEMOGRAPHY OF A CALIFORNIA LEAST TERN COLONY INCLUDING EFFECTS OF THE 1982-1983 EL NIÑO¹

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Abstract. In a seven-year study (1983-1989) of banded California Least Terns (*Sterna antillarum browni*) breeding at Venice Beach, a number of demographic parameters were examined. Survival of breeding adults was found to be age-related, with young breeders age two and three years showing lower return rates than adults equal to or greater than four years. The return rate of banded hatchlings as breeding adults was 0.16, and annual hatchling productivity per individual adult was 1.00. Combining the survival data with available information on intercolony exchange rates, we computed the expected breeding life of an adult (once it has bred) as 9.63 years, with a lifetime productivity of 1.49. The extraordinary El Niño (ENSO) of 1982-1983 had major adverse effects on the population dynamics of the colony for a period of five years. Values were computed for "normal" and "ENSO" years.

Key words: Tern; demography; El Niño; survival; productivity; breeding life; ENSO; Least Tern; *Sterna antillarum*.

INTRODUCTION

The breeding biology of the California Least Tern (*Sterna antillarum browni*) has been scrutinized since it was listed as an endangered species in 1970. Age of first breeding (Massey and Atwood 1978), breeding chronology (Massey and Atwood 1981), foods and foraging (Atwood and Minsky 1983, Atwood and Kelly 1984), site fidelity (Atwood and Massey 1988) and reneating patterns (Massey and Fancher 1989) have been analyzed. In this paper, we address increasingly complex questions about Least Tern demography including the age profile of a colony, adult survival rates, expected breeding life of an adult, and lifetime reproductive potential. The study is based on banded breeding adults at the Venice Beach colony in Los Angeles County, California.

The study was begun in 1983 and was expected to span four to five seasons. It became apparent in 1984 that the extraordinary El Niño/Southern Oscillation (ENSO) of 1982-1983 would have prolonged effects on the Least Tern population and the study was extended through 1989.

STUDY SITE

The colony is located on the beach at the south end of the community of Venice in Los Angeles, California, and has been protected and monitored since 1977. The number of breeding pairs quadrupled between 1977 and 1980 (Table 1). Permanent chain-link fencing was installed in 1979; the enclosure has since been enlarged several times and is now 108 × 154 m. Small mesh fence at the base of the chain-link fence prevents chicks from running out onto the public beach.

METHODS

Banding of Least Tern chicks in California dates back to 1969. However, from 1976 to 1989, a concerted effort was made to band as many chicks as possible, particularly in southern California colonies. The banding program was under the auspices of Charles T. Collins of California State University, Long Beach, California. Banding at Venice was done from 1978 to 1989 (Table 1); no chicks were banded in 1977, the first year of the colony.

At Venice, all nests were marked with numbered stakes from 1978 on, and the course of the nests followed through hatching. The statewide

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population has been monitored since 1977; annual summaries are available from the California Department of Fish and Game (1979–1989, unpubl. data).

We began to color-band known-age adults (banded as chicks) in 1979 in several southern California colonies, including Venice. From 1979 to 1982 we were sampling, rather than trapping systematically, to collect data on inter-colony movements.

This study encompasses the years 1983 to 1989, when we checked Venice nests systematically to find and color-band all banded, breeding adults. To minimize disturbance and possible desertion, trapping was not begun until late in the incubation period, was done in the cool hours of early morning, and only one pair member was trapped in a day.

Many two and three-year old terns nesting for the first time were trap-wary, but could often be classified as to hatching year and natal colony by their bands. We were sometimes able to read band numbers from the blind as well.

Productivity was measured by estimating fledging success and then calculating the fledging/pair ratio. Fledglings were counted at bi-weekly intervals in a roosting flock of Venice adults and fledglings that congregated each evening adjacent to the nesting site. Numbers were pooled to give an estimate of the total output of the colony (Massey, unpubl. data). The fledging/pair ratio was obtained by dividing the number of fledglings by the number of breeding pairs. The latter figure was derived by adding the number of nests in the first nesting wave and the estimated number of two-year-olds in the second wave (Massey and Atwood 1981).

Capture-recapture methodology based on the Jolly-Seber model has been useful in estimating population demographics from banding data (Spendelov and Nichols 1989). However, we found the age-dependent version of the Jolly-Seber model (Pollock et al. 1990) unsuitable for this application because the estimates were highly variable with many survival estimates exceeding 1.0. Population growth combined with an increasing proportion of banded adults may have artificially inflated these estimates.

As an alternative that would preserve the range of the estimates, we adapted techniques from censored survival estimation methodology to this study. This required indirect estimation of the failure (death) and censoring (emigration) rates,

TABLE 1. Demography of the Least Tern population in California and at Venice Beach 1977–1989.

	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
California													
Number of breeding pairs	775	832	1,000	1,160	1,067	1,130	1,264	1,046	1,003	960	945	1,253	1,240
Estimated number of fledglings	449	418	696	769	733	511	894	518	682	902	632	1,130	764
Productivity ratio ¹	0.58	0.50	0.70	0.66	0.69	0.45	0.71	0.50	0.66	0.94	0.67	0.90	0.62
Venice colony													
Number of breeding pairs	35	67	87	157	150	150	140	82	96	104	109	165	137
Estimated number of fledglings	37	75	145	240	200	60	140	94	113	113	82	192	134
Productivity ratio	1.1	1.1	1.7	1.5	1.3	0.4	1.0	1.2	1.2	1.1	0.8	1.2	1.0
Number of chicks banded	0	87	157	291	139	208	173	84	158	117	92	285	149
Percent of returns ²	NA ³	10	10	4	9	2	2	4	9	7	NA ⁴	NA ⁴	NA ⁴

¹ Number of fledglings/pair of adults.
² Based on number of chicks banded each year that returned as adults to breed.
³ Not applicable—no chicks banded in 1977.
⁴ Not applicable—chicks banded 1987–1989 did not reach age of major first breeding during the study.

because failures could not be explicitly observed. This left all observations censored in the traditional sense. Given the discrete time scale available (records only reflect appearance during each breeding season), the standard exponential estimator (number of deaths divided by the total time on test [Kalbfleisch and Prentice 1980, Lawless 1982]) provided the basis for our estimator.

To determine the rate of death, as opposed to emigration for adults that disappeared from the colony, we began by counting as potential deaths all failures to return to breed at Venice that could not be verified as censorings. These counts excluded birds known to have moved to other colonies, as well as those that reappeared at Venice later, presumably having spent some period undetected in one of the less-thoroughly monitored colonies. The remaining number of failures was multiplied by the proportion of disappearances where the bird was presumed dead because it was not verifiably alive. By this means, we estimated that 81% of the terns that were never seen again had died (confidence interval 0.72, 0.87).

The less intense monitoring of other colonies compared to Venice diminished the precision of this estimate, and may have resulted in some underestimation of the final survival rates, even after adjustment. However, this approach achieved far greater stability and yielded more sensible estimates than the capture-recapture model. The essential difference is that capture-recapture methods estimate the true population size from recapture rates, while the approach we used estimates the relative rates of death and censoring from the rate of long-term disappearances.

Post-breeding survival rates were estimated as described above, stratified by age. Ninety-five percent bootstrap confidence intervals for these rates were used to assess possible variation in survival rates across age groups.

The survival rate of Venice-hatched chicks to at least one breeding season was estimated separately. Without equally intense monitoring at all colonies it was impossible to determine the number of Venice-hatched chicks that bred elsewhere. However, we estimated this from the rate at which non-Venice chicks chose to breed at Venice, assuming that the number of emigrants would about equal the number of immigrants. This might underestimate the emigration rate

from Venice, as it is one of the most productive colonies; but the resulting estimate almost surely improves upon raw return rates.

These survival rates were combined with pooled rates for the hatchling productivity (half the number of hatchlings per pair) to estimate expected breeding life and lifetime breeding productivity. Ninety-five percent bootstrap confidence intervals for these estimates were based on the percentile method (Efron and Gong 1983, Efron and Tibshirani 1986). These confidence intervals incorporate several variance components (hatchling productivity, disappearance rate, and three survival rates).

Separate estimates and confidence intervals contrasted the ENSO years with "normal" years. Projections of lifetime productivity for the ENSO years were based upon the rate estimates for 1982 and 1983.

RESULTS

The population at the Venice colony increased rapidly for the first three years, then plateaued from 1980–1983 (Table 1). In 1984, it plunged 40% and did not recover until four years later. The statewide population followed roughly the same course (Table 1).

Overall productivity was significantly greater at Venice than over the rest of the state (*t*-test, $P < 0.001$). In fact, only in 1982 did the statewide average exceed Venice's productivity. At Venice, the productivity ratio (fledglings per pair) was higher than 1.0 in all but two seasons, while the statewide ratio never exceeded 0.9 (Table 1).

During the seven-year study period, the Venice breeding population ranged from 82 to 165 pairs. Each year we were able to see $\geq 90\%$ of the individuals; in 1983, 22% of those seen were banded, by 1989 the number had risen to 48%. During the course of the study there were 186 individually color banded birds, 154 of which had been banded as chicks and were thus of known age.

The percentage of banded chicks that returned to Venice as breeding adults is shown in Table 1. The years that produced the smallest percentage of returning adults were 1982–1983. In 1982, 208 chicks were banded but many did not survive to fledge (see below—brief description of the 1982 season). The productivity ratio was 0.4, and only 2% returned as adults to breed. In 1983 the productivity ratio was back up again (1.0)

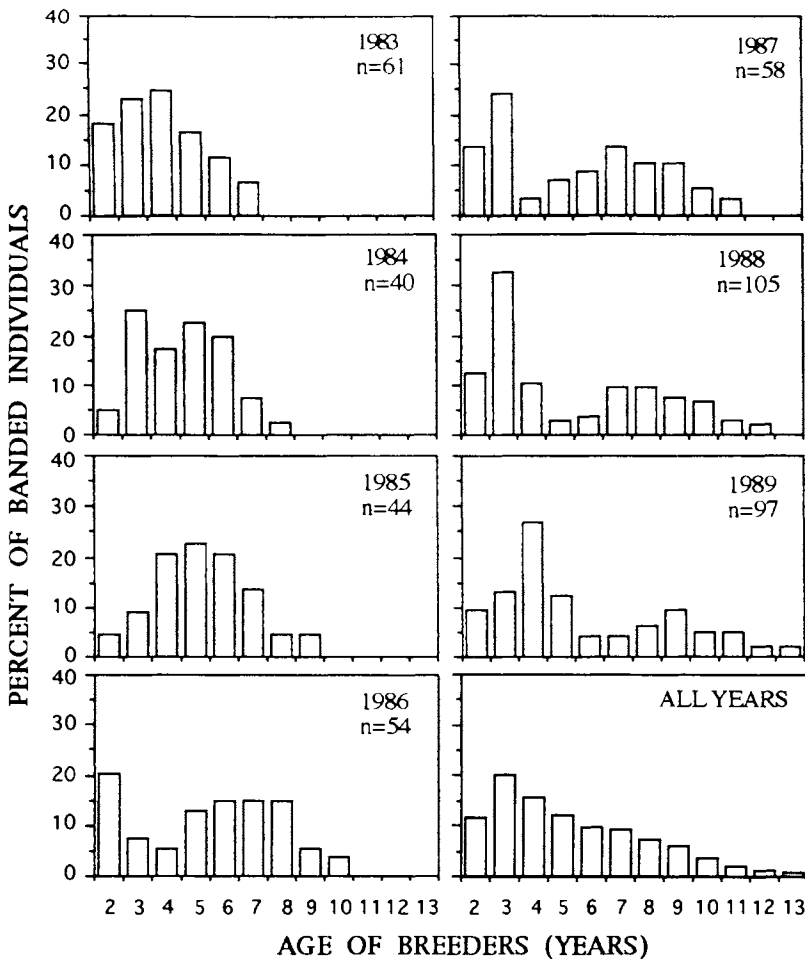


FIGURE 1. Age profile of banded adults breeding at Venice, 1983-1989.

but very few fledglings of that year survived the two-year interval until age of first breeding.

Table 2 shows the age at which 186 banded adults were first known to breed. While many bred at age two years, the largest age group was the three-year-olds. The few that were trapped

at age equal to or greater than five years presumably began their breeding lives elsewhere and later emigrated to Venice.

The age profile for banded adults in the colony each year is shown in Figure 1. The composite graph combines data for all seven seasons and

TABLE 2. Age of adults at Venice Beach when first trapped on nests (154) or identified by color code (32); n = 186.

Number of adults	Age (years)									
	2	3	4	5	6	7	8	9	10	
Trapped	37	64	37	6	5	2	2	0	1	
Identified by color code	21	11	0	0	0	0	0	0	0	
Total	58	75	37	6	5	2	2	0	1	
Percent	31	40	20	3.2	2.7	1.1	1.1	0	0.5	

TABLE 3. Return rate of banded adults breeding at Venice (both known and unknown age).

	1983	1984	1985	1986	1987	1988	1989
Total returns ¹	0	37	42	58	59	64	76
Total possible returns ²	0	56	48	65	69	74	104
New birds	56	11	23	11	15	40	32
Return rate (%)	—	66	88	89	86	86	73

¹ Adults that nested at Venice the previous year.

² Banded adults trapped for the first time and unbanded mates of banded birds.

shows that peak breeding age was three years, and 80% were age two to seven years. The oldest banded breeding birds were 13 years. Pooling the data, however, had the effect of smoothing the annual differences and creating a "model" age profile which masked the ramifications of the 1982–1983 ENSO. When examined year by year, major changes in the curves were revealed after 1983. Because of the importance of this event to Least Terns, the demography of the colony is described briefly by year. The 1982 breeding season is included because ramifications of this disastrous year were felt throughout the study.

1982. The first sign of an atypical nesting season was seen at many southern California colonies very soon after the terns' arrival in April. During the courtship phase, when males were bringing fish to their prospective mates, it was noted that the fish were smaller than usual, comparable to the size fish fed to young chicks (Atwood and Kelly 1984). Egg laying was delayed and clutch size reduced (Minsky, unpubl. data). The chick growth curve lagged behind other years (C. T. Collins, pers. comm.), and egg abandonment and chick mortality were high (Atwood and Kelly 1984). Statewide fledgling production decreased 30% (Table 1).

At Venice, an additional problem was caused by an American Kestrel (*Falco sparverius*) that took about 100 chicks just prior to fledging (Minsky, unpubl. data). The combination of a food dearth and unusually heavy predation resulted in a 70% reduction in the fledgling crop from the previous year and the lowest fledgling/pair ratio during the study period (Table 1). Ramifications of this virtual loss of an annual cohort were seen during the rest of the study.

1983. All phases of the breeding cycle occurred on schedule, indicating that the food supply had returned to normal. Productivity at Venice was 1.0 (Table 1). The age profile reflected the short history of the site; the oldest banded adults were

age seven years (Fig. 1), and 82% of the breeding birds were age two to five years.

1984. The statewide breeding population dropped 17%, the first decrease since censusing began (Table 1). At Venice, the population dropped 41%. Two factors were operating: 34% of the banded adults that bred in 1983 did not return in 1984 or thereafter (Table 3), and the two-year-old cohort was very small (Fig. 1). The season proceeded uneventfully at Venice and the colony had a high productivity ratio (1.2). However, the number of fledglings was not large because of the reduced number of breeding pairs (Table 1).

1985. The number of breeding pairs at Venice increased slightly, although the statewide population was still decreasing (Table 1). But the number of two-year-old breeders at Venice was again very low. It was becoming evident that both adults and juveniles had died in large numbers during the winter of 1983–1984. The age profile was bell-shaped, with very small numbers of young and old breeders (Fig. 1). It also showed a shift to the right, with 77% age four to seven years. Productivity was almost twice the statewide ratio (Table 1).

1986. There was no substantial gain in number of breeding pairs at Venice, but the two-year-old age class returned in strength for the first time since 1983 (Fig. 1). It was the only year when there were more two-year-old than three-year-old breeding birds. Despite the influx of two-year-olds, 57% of the birds were age five to eight years, showing a continuing shift towards older breeders. In Venice and throughout California, fledgling production was high (Table 1).

1987. Breeding numbers remained depressed, both statewide and at Venice. Productivity was down sharply from 1986 (Table 1). At Venice, reduced productivity was attributed to chick starvation (the number of dead chicks was higher than in 1986 but not comparable to 1982) and

TABLE 4. Demographic analysis.

		Normal years		ENSO years§	
		Estimate	95% Confidence Interval	Estimate	95% Confidence Interval
Return rates					
Hatchling*	S_h	0.16	(0.13, 0.18)	0.03	(0.01, 0.05)
Young breeders†	S_y	0.81	(0.72, 0.87)	0.82	(0.66, 0.96)
Older breeders‡	S_a	0.92	(0.88, 0.95)	0.79	(0.68, 0.89)
Demographic parameters					
Hatchling productivity**	P_H	1.00	(0.84, 1.20)	0.98	(0.88, 1.08)
Breeding life††	L	9.63	(6.55, 14.48)	4.97	(3.46, 8.10)
Lifetime productivity‡‡	P_L	1.49	(0.93, 2.34)	0.15	(0.06, 0.30)

* Percentage of chicks hatched at Venice that return as adults to breed.
 † Annual survival rate for birds breeding at ages two and three.
 ‡ Annual survival rate for birds breeding at ages four or older.
 ** Hatchlings produced per breeder per year.
 †† Expected number of breeding years per adult: $L = 1 + S_y + S_y/(1 - S_y)$.
 ‡‡ Number of progeny per adult expected to survive to breeding age: $P_L = S_h \times P_H \times L$.
 § Estimates based on data from the 1982–1983 El Niño Southern Oscillation.

predation. The age curve was now bi-modal, a configuration that persisted through the rest of the study (Fig. 1). The two-year-old contingent was again large but the biggest group was age three years.

1988. The breeding population increased 25% statewide and 34% at Venice (Table 1). Fledgling production was high in the state (0.9) and even higher at Venice (1.2). At Venice, the population increase was due to an influx of new breeders age two and three years, the older age classes did not change appreciably (Fig. 1). The curve was similar to 1987; 56% of the breeding birds were age two to five years. Again, many of the three-year-old age class were nesting for the first time (25/34). The oldest breeding birds were age 12 years; two-thirds had nested at Venice for at least six seasons.

1989. The statewide population remained at the 1988 level but it was not a productive year. Food supply appeared normal, but many colonies were plagued by predators and statewide fledgling productivity was 0.62 (Table 1). At Venice, there was a 17% reduction in the number of breeding pairs, but productivity was high at 1.0 (Table 1). The age profile was similar to 1988, except that the peak age group was four-year-olds rather than three-year-olds. There was also a return in pattern to the first year of the study, with the majority of birds (62%) again two to five years of age. The most reduced age class was the three-year-olds. While 15 out of 18 returned, only three new nesters were found; in sharp contrast to the large contingent of first-time nesting three-year-olds seen in most other years. The two

oldest birds (age 13) had been nesting at Venice for seven and ten seasons.

The virtual loss of two age classes can first be seen in 1984 and 1985, and can clearly be followed through subsequent seasons (Fig. 1). By 1989, most breeding birds were again in the two to five year range, as in 1983, but the oldest were age 13 years. This reflected the duration and stability of the colony, by then in its 13th season. There was still a bimodality in the age curve, with more adults aged eight and nine years (pre-ENSO) than age six and seven years.

Table 4 summarizes demographic analyses. The rate at which Venice-hatched chicks survived to breed at least once in California was estimated at 0.16. The overall survival rate for adults, once they had returned to breed, was 0.88. However, there was a difference in rate of return according to age. Terns age two and three years had a lower rate of return than those four years

TABLE 5. Age-dependent survival rates.

Age	n	Survival estimate	95% Confidence Interval
2	31	0.82	(0.69, 0.93)
3	73	0.80	(0.72, 0.88)
4	64	0.90	(0.83, 0.96)
5	52	0.92	(0.85, 0.98)
6	43	0.93	(0.85, 0.98)
7	43	0.87	(0.78, 0.96)
8	31	0.87	(0.76, 0.97)
9	20	0.92	(0.80, 1.00)
10	10	0.76	(0.50, 1.00)
11	3	1.00	(1.00, 1.00)
12	2	0.60	(0.17, 1.00)

or older (Table 5). When "young breeders" were separated from "older breeders," survival rates were 0.81 and 0.92, respectively. After age three years, the survival rate appeared constant through age nine years. Combining these survival estimates with pooled rates for the hatchling productivity (half the number of hatchlings per pair) yields an expected individual breeding life of 9.63 years and a lifetime breeding productivity of 1.49 (Table 4).

DISCUSSION

Survival estimates for several other tern species, using various capture-recapture methods, have fallen within the same range as those reported here for the Least Tern (Arctic Terns [*S. paradisaea*], 0.87–0.88 [Coulson and Horobin 1976]; Common Terns [*S. hirundo*], 0.92 [Di Costanzo 1980]). More recently, a modified version of the Jolly-Seber model was used for the endangered Roseate Tern (*S. dougallii*), and the annual adult return rate was estimated at 0.74–0.75 (Spindel and Nichols 1989). Survival of fledglings to age of first breeding for this species was 0.156 (Nichols et al. 1990).

Age distribution curves for other species of breeding terns peak at one to two years after age of first breeding and taper gradually to zero (e.g., Common Tern [Austin 1942], Arctic Tern [Coulson and Horobin 1976]). For the Least Tern, complications introduced by the 1982–1983 ENSO make it difficult to see a "normal" curve. However, the composite age profile shown in Figure 1 that pools data over 7 seasons probably represents "normal" age distribution. Barring another strong El Niño event, the curve should return to the standard unimodal shape by 1995.

"Normal" is a questionable term here because ENSO events are natural and recurring phenomena, and thus must be considered normal. In 1987 a mild ENSO occurred after the breeding season and ended before the 1988 breeding season (Kerr 1987). The 1987 season's poor fledgling productivity (Table 1) may have been related to that event, just as reduced productivity was manifested in 1982 before the accepted onset of the 1982–1983 El Niño. The 1982–1983 ENSO, however, was extraordinary, and probably delineated the most severe impacts such an event can have on breeding Least Terns. The timing of this study was fortuitous in that it encompassed this event.

Under severe ENSO conditions survival rate

drops to 0.80, breeding life to 4.97 years, productivity to 0.15, and hatchling return rate to 0.03 (Table 4). These contrasts are dramatic. It is also important to note that while the adult return rate at Venice would apply to all colonies, as there are few hazards to adults in California during the breeding season, breeding success at Venice is usually greater than at most other colonies. Thus, annual and lifetime productivity values at most other colonies would be lower for both normal and ENSO years.

The timing of the 1982–1983 El Niño in southern California's coastal waters is difficult to establish. The first recorded changes in ocean temperature were along the west coast of South America and in the central equatorial Pacific in June 1982. By October 1983, sea-surface temperatures had returned to normal (Rasmussen 1984). Warming then moved northward and satellite imagery detected a warming trend off southern California beginning in December 1982 and peaking in March 1983 (Feidler 1984). However, sea-surface temperatures off southern California were elevated from September 1982 through February 1983 and again September–December 1983 (Oceanographic Monthly Summaries published by the National Oceanic and Atmospheric Administration [NOAA]).

Whether the ocean warming began in September or December, it was well after the 1982 seabird breeding season in California. Effects on seabird breeding colonies, however, were already being seen along the California coast by April of 1982. On the Farallon Islands, the breeding season for most species was delayed, beginning in late May to June instead of the usual late April to early May (Ainley et al. 1986). Also in late April, 1982, we first noticed an altered food supply in southern California Least Tern colonies. Pelagic Cormorants (*Phalacrocorax pelagicus*) and Pigeon Guillemots (*Cepphus columba*) showed poor fledgling productivity on the Farallon Islands in 1982 (Ainley et al. 1986), as did Least Terns on the mainland.

By the 1984 breeding season, oceanic conditions had returned to normal in the eastern Pacific and most California seabirds (including those on the Farallon Islands and Least Terns) had a normal breeding season. However, depressed numbers of breeding adults characterized many species on Christmas Island in the central Pacific Ocean (Ainley et al. 1986), as well as the Least Tern in California. These data suggest that sea-

birds, particularly in California, suffered from diminished food supply as early as April 1982, well before ocean temperature changes were detected.

Our analyses are based on the four to five month breeding season in California; knowledge about the wintering range of the California Least Tern is patchy. The northern limit of the winter range appears to be in Colima, Mexico (Massey 1981). However, the bulk of the population may be distributed along the Pacific Coast of Central America and perhaps to Colombia, as Least Terns migrate through Costa Rica (Stiles and Smith 1980) and are seen regularly in small numbers in Panama (Vaucher 1988). Identification of the wintering range and a study of events affecting the species' demography in the two-thirds of the year they spend away from their breeding grounds in the United States should be part of the recovery program for this endangered species.

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