

## SECOND-WAVE NESTING OF THE CALIFORNIA LEAST TERN: AGE COMPOSITION AND REPRODUCTIVE SUCCESS

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**ABSTRACT.**—The nesting season of the California Least Tern (*Sterna albifrons browni*) has often been characterized by two waves of nesting, but the composition of the later wave and reasons for its occurrence have not been well understood. In 1980, a group of late-nesting birds, many of them banded and color-banded, presented a unique opportunity for study. Most of the banded birds were identified as 2-yr-old terns nesting for the first time; several were older, renesting pairs that had failed earlier at a colony close by. The chronology of the second wave, age composition, clutch size, behavior of 2-yr-old parents, fledging success, and postfledging dispersion were documented. Implications of these new data are discussed. *Received 20 October 1980, accepted 13 February 1981.*

BREEDING colonies of California Least Terns (*Sterna albifrons browni*) are frequently characterized by two waves of nesting during one season. Usually egg laying begins the first or second week in May after the terns have been in the area for 1–4 weeks, and the first wave of laying is complete in 10–14 days. By mid-June, when most of the chicks have hatched, a second and usually smaller group of courting and nesting terns is often observed. The second period of egg laying is more prolonged than the first, and hatching may continue throughout July and occasionally into August (Atwood et al. 1977, 1979). The composition of the late-nesting group has long been a subject of interest and speculation, with several explanations appearing to be reasonable. The second wave could be comprised of one or more of the following groups: (1) renesting terns that failed on their initial nesting attempts, (2) late arrivals making their first attempts, and (3) birds that arrived with the first wave of migrants but delayed nesting until later in the season.

Renesting after loss of eggs or chicks has been reported in many tern species, including Black Noddy (*Anous tenuirostris*) (Ashmole 1962), Common Tern (*Sterna hirundo*) (Palmer 1941), Sooty Tern (*S. fuscata*) (Ashmole 1963), and Arctic Tern (*S. paradisaea*) (Cullen 1956). There are also many references to the staggered arrival of seabirds on their breeding grounds and of prolonged nesting periods. The Laysan Albatross (*Diomedea immutabilis*) (Fisher 1969), Kittiwake (*Rissa tridactyla*) (Coulson and White 1958), Sooty Tern (Robertson 1964, Harrington 1974), Sandwich Tern (*S. sandvicensis*) (Veen 1977), and Arctic Tern (Coulson and Horobin 1976) have all shown a pattern of early return by older, experienced birds and late arrival of first-time breeders. In the Kittiwake, the young birds both arrive later and lay eggs later than experienced breeders (Coulson and White 1958). Hays (1978) found that young Common Terns nested later and with less synchrony than older individuals. In the Arctic Tern, laying time has been synchronous despite the late arrival of first-time breeders (Coulson and Horobin 1976).

Until 1978, we assumed that reneesters formed the major component of late-nesting groups of Least Terns. Banding returns had given evidence that some of the pairs

that lost eggs or chicks early in the season could later be found renesting either at the same colony or one close by (Massey and Atwood pers. obs.). We had also observed periodically that a breeding colony under heavy pressure from predators or human disturbance would abandon a site and immediately thereafter a similar-sized group would "materialize" at another, nearby site and begin nesting. The evidence, although circumstantial, was often convincing that the two groups were the same. In 1978, however, we documented through banding that some of the late-nesting terns were 2 yr old and thus were nesting for the first time (Massey and Atwood 1978). Our data at the time suggested that 2-yr-old breeding Least Terns were not common and that the usual age of first breeding was 3 yr. The size of the 2-yr-old component in the second wave could not be assessed.

In 1980 an opportunity became available for close observation of a second wave of nesting Least Terns under ideal conditions. Among the group were a number of banded 2-yr-old birds, including several that were paired. We were able to observe the behavior and assess the competence of birds nesting for the first time and to evaluate the contribution made by a group of late-nesting terns to the season's total fledgling population.

#### METHODS

A large-scale, long-term program of banding Least Tern chicks in southern California was begun in 1976 and has continued each year since, with 259 chicks banded in 1976, 297 in 1977, 407 in 1978, and 612 in 1979 (Collins et al. 1979). Since 1978, chicks at major colonies in Los Angeles and Orange counties have been color-banded with a year and colony code, so that many returning birds are now identifiable in the field as to age and natal colony. In 1980 we began to color-band adults individually as they were trapped.

The site of this study was NASA Island, a small, round landfill approximately 120 m in diameter that juts out into the Anaheim Bay saltmarsh (Seal Beach National Wildlife Refuge, Seal Beach Naval Weapons Station, Orange County, California). A connecting road to the "island" allows for vehicular access. The island was leveled, topped with sand and otherwise prepared as a Least Tern nesting site in 1978. The terns used it for nesting in 1979 and 1980.

All California Least Tern nesting sites are monitored annually as part of the recovery program for this endangered species, with most colonies visited at least once weekly throughout the breeding season. The Anaheim Bay colony was visited 12 times between 11 April and 15 June 1980 during the initial wave of nesting. Eight to 10 pairs nested in this period. Observations were made mostly from a car, as it was possible to drive around the perimeter of the island and see all of the nests without disturbing the birds. The approximate number of nesting pairs, general location of nests, and a clutch-size sample were noted; these data are taken routinely at all colonies. Nests were not marked. We checked for banded adults with the aid of a 15-60× spotting scope. Hatching success was recorded, and chicks were banded at each visit during the hatching period. Until mid-June the colony received only routine attention.

In early June there was noticeably heightened activity in the colony as a second wave of nesting began (see Results: *Chronology*). The colony became the focus of close attention and between 15 June and 13 August was visited every other day. All nests were marked, nest locations mapped, and clutch sizes recorded. Adults were checked for bands, and banded birds were trapped on nests whenever possible.

Trapping was done late in the incubation period, using a drop trap over the nest. Birds trapped early in the season have usually returned to their eggs within 15 min of the time the trap was set. We found in this study that many of the late nesters were trap-wary, even after their eggs were started. Because Least Terns do not tolerate handling well and desertion during the incubation period has occurred, we suspended trapping efforts if unsuccessful after 30 min.

Of the 66 Least Terns nesting in the second wave at Anaheim Bay, 19 were already banded on arrival. Fifteen of the banded birds were trapped in order to read their bands; the unbanded mates of three banded birds were also trapped and banded.

Hatching success was tabulated, and all chicks were banded with red anodized U.S. Fish and Wildlife Service bands. Behavior of 2-yr-old adults toward their chicks, particularly during the first critical days,

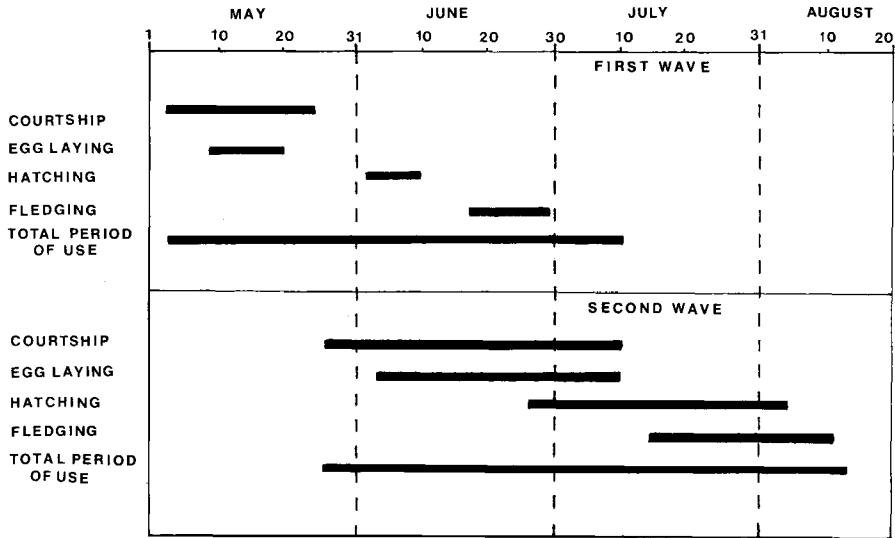


Fig. 1. Chronology of the California Least Tern nesting colony in Anaheim Bay, 1980.

was observed at several nests. The chicks were watched throughout the prefledging period to obtain data on fledging success. Postfledging movements and behavior were observed both at the colony and at known postseason fishing and flocking sites in the vicinity.

## RESULTS

*Chronology of the colony.*—The chronology of the nesting colony in Anaheim Bay during the 1980 season is shown in Fig. 1 and can be summarized as follows.

*First wave:* the usual time of arrival of Least Terns in the Los Angeles/Orange County area has been around the last week in April (Massey 1974), but in 1980 the birds arrived earlier than usual and were first seen in aerial courtship over the bay on 11 April. Early arrival did not result in earlier nesting; ground courtship began on 3 May, and the first eggs were laid about 9 May. By 20 May the first wave of laying was complete, and 8–10 pairs were nesting. Hatching began on 2 June. All of the eggs hatched, and 10 of the chicks were banded. The first fledglings were seen on 21 June.

*Second wave:* on 27 May, while the first group was still incubating, three pairs of Least Terns were observed in ground courtship, a 2-yr-old banded male among them. By 9 June five pairs of adults, including two banded pairs, were courting and scrape-making, and the first eggs of the second wave had been laid (on 5 June). A flock of 30–40 “extra” Least Terns was frequently seen loafing and preening at the edge of the nesting area. Most of the first-wave chicks had hatched. Many of the courting and nesting birds were color-banded and identifiable as either renesting pairs or 2-yr-olds. Egg laying continued over the next 36 days, with the last clutch completed on 11 July. During this period 33 pairs nested. Hatching began on 26 June and continued through 4 August. The first fledglings were seen on 17 July. Although the colony suffered some problems from predation, the activity level remained high through 9 August. On that date there were approximately 40 Least Terns in evidence, including several half-grown chicks and 10–12 fledglings being

TABLE 1. Ages of banded, breeding California Least Terns.

	Age (yr)				Total
	1	2	≥3	Unknown	
Birds nesting at Anaheim Bay in 1980 ( <i>n</i> = 23)					
First nesting wave	0	0	2	2	4
Second nesting wave	0	12 (63%)	3 <sup>a</sup> (16%)	4 (21%)	19
Birds nesting in Los Angeles and Orange Counties, 1976–1980 ( <i>n</i> = 62)					
First nesting wave	0	2 (5%)	39 (95%)	0	41
Second nesting wave	0	16 (76%)	5 <sup>a</sup> (24%)	0	21

<sup>a</sup> All renesting after initial failures.

attended by their parents, plus a mixed flock of adults and fledglings from other colonies and several 1-yr-old birds. On 11 August the site was virtually deserted, with one pair of adults tending a 9-day-old chick. Not all of the pre fledged chicks seen on 9 August could have fledged before the site was vacated and were presumed lost to predators. On 13 August the site was completely deserted, and a search of the area revealed fresh tracks of red fox (*Vulpes fulva*) and striped skunk (*Mephitis mephitis*) and the wings of 2 pre fledged chicks.

*Age composition.*—Table 1 shows the age composition of the first and second waves of nesting Least Terns in Anaheim Bay in 1980. There were 4 banded adults in the first wave; 2 were color-banded and identifiable as ≥3 yr of age; the ages of the other 2 were not ascertained. There were no color-coded 2-yr-olds in the group. At other colonies in the area 23 banded birds were trapped during the first wave of nesting in May; only one was 2 yr old, and it was mated with a 3-yr-old bird.

In the second wave at Anaheim Bay there were 19 banded adults; 12 were identified as 2 yr of age, 3 were older (and renesting) birds, and the ages of the remaining 4 were not ascertained (Table 1). Of the 33 nests in the second wave, 10 (30%) had at least one 2-yr-old pair member, and at two nests both adults were 2 yr old. Only two nests (6%) were known second attempts by older, renesting birds.

The 2-yr old component was not confined to the second wave at Anaheim Bay. On brief, routine visits to other colonies in late June, we observed five color-coded nesting 2-yr-olds. Postseason flocks at Harbor Lake and Belmont Shore, where California Least Terns congregate from all local colonies to forage and roost (Atwood and Massey in prep.), contained numerous 2-yr-olds, totalling many more than could be accounted for by the nesting group at Anaheim Bay.

Table 1 summarizes the age composition of banding recoveries of nesting Least Terns in California from 1976–1980, including the birds at Anaheim Bay in 1980. The data are based on age at date of first recovery, as many of the birds have been recovered while nesting in subsequent years. Other known-age birds have been seen only postseason or found dead on breeding colonies; if their breeding status was uncertain they were omitted from the table. In the first nesting wave there have been only 2 recoveries of 2-yr-old terns, while the late-nesting group has been dominated by 2-yr-olds. The five banded birds ≥3 yr of age in the late-nesting group were all renesting; we have seen no instances of older birds that have delayed their initial nesting attempts until late in the season.

*Egg laying.*—The prolonged egg-laying phase of the second nesting wave was characterized by rather even spacing (Table 2). Two-yr-old terns were laying throughout the 36-day period, and the two known reneesters were among the first and last to lay eggs.

TABLE 2. Egg-laying period—second nesting wave, Anaheim Bay 1980.

	Date of laying of first egg															
	June								July							
	1	4	8	12	16	20	24	28	1	4	8	12				
Total number of nests ( $n = 29$ ) <sup>a</sup>		1	2	1	2	2	1	2	2	1		4	2	3	1	3
Nests of 2-yr-old terns ( $n = 10$ ) <sup>b</sup>				1	1	1	1	1	1			1	1	2		1
Nests of terns $\geq 3$ yr of age ( $n = 2$ ) <sup>c</sup>					1											1

<sup>a</sup> The total number of nests in the second wave was 33; laying dates of four abandoned nests could not be determined.

<sup>b</sup> Twelve 2-yr-old terns nested in the second wave at 10 nests; in two instances both pair members were banded 2-yr-olds.

<sup>c</sup> Three birds  $\geq 3$  yr of age nested in the second wave at two nests; both pair members were banded and were  $\geq 3$  yr old at one nest.

*Clutch size.*—Clutch sizes of first- and second-wave nests in Anaheim Bay in 1980 are shown in Table 3. A marked increase in the number of one-egg nests was apparent in the second wave. Representative samples of clutch sizes at two other colonies were taken during the first wave of nesting in 1980 and showed only a small percentage of one-egg nests. Samples were not taken of second-wave clutch sizes at other colonies.

Ten nests in the second wave at Anaheim Bay where one or both members of the pair were 2 yr old showed about the same high proportion (30%) of one-egg clutches as did the entire group of late-nesting terns, and there were no three-egg clutches (Table 3).

*Hatching success.*—All of the eggs in the first nesting wave at Anaheim Bay hatched successfully, but only 82% (44/54) in the second wave hatched. Four nests were apparently abandoned after laying, as no bird was ever seen incubating the eggs. Two others were deserted during the incubation period. One was abandoned early; the other, a re-nest containing the last eggs laid in the colony, was abandoned after 25 days, the eggs still unstarred. Two eggs failed to hatch at nests where the other egg hatched: one of them was infertile; the other did not survive pipping.

*Behavior of 2-yr-old parents.*—Behavior of adult Least Terns toward their newly hatched chicks has been observed frequently, and first feedings have been described (Massey 1974). Both parents are usually in close attendance upon the first post-hatching day, one brooding the chick(s) and the other either standing by and guarding or bringing food in response to signals from the chick(s). For a successful first

TABLE 3. Clutch sizes of first- and second-wave nests at several California Least Tern colonies in 1980.

Colony	Number of eggs			
	1	2	3	$\bar{x} \pm SE$
<b>First wave</b>				
Venice Beach (36/150) <sup>a</sup>	3 (8%)	31 (86%)	2 (6%)	1.97 $\pm$ 0.063
Huntington Beach (29/65)	3 (10%)	25 (86%)	1 (3%)	1.93 $\pm$ 0.069
Anaheim Bay (6/10)	1 (17%)	2 (33%)	3 (50%)	2.33 $\pm$ 0.333
<b>Second wave</b>				
Anaheim Bay (33/33)	11 (33%)	21 (64%)	1 (3%)	1.70 $\pm$ 0.092
Anaheim Bay—nests of 2-yr-old birds (10/10)	3 (30%)	7 (70%)	0	1.70 $\pm$ 0.153

<sup>a</sup> Sample size = 36 nests, colony size = 150 nests. The  $2 \times 3$  table of clutch size/colony was subjected to a  $\chi^2$  test and revealed a significant difference in clutch size between the first and second waves of nesting ( $P < 0.01$ ).

TABLE 4. Fledging success at several California Least Tern colonies of varying sizes in 1980.

Colony	Number of nesting pairs	Minimum number of fledglings	Fledglings/nesting pairs <sup>a</sup>	Fledging success
Venice Beach	150-165	240	1.45	Good
Huntington Beach	70-90	85	0.94	Moderate
Los Cerritos	7	6	0.86	Moderate
Bolsa Chica	20-26	15	0.58	Moderate
Anaheim Bay (total)	38-43	24	0.56	Moderate
First wave	8-10	5	0.50	Moderate
Second wave	33	19	0.58	Moderate
Second wave (nests of 2-yr-old birds)	10	8	0.80	Moderate

<sup>a</sup> Minimum number of fledglings/maximum number of nesting pairs.

feeding, the parent must present a small fish to the chick so that the chick can swallow it head first.

Two nests at Anaheim Bay with first-time parents were watched for several hours on the first posthatching day. At one nest where two chicks were about 5 h old, both parents exhibited awkward and uncertain behavior in trying to feed them. Of three fish brought during a 45-min interval, none was successfully fed to a chick, even though both chicks were begging for food. One parent presented a fish repeatedly tail first to a chick. All three fish were eventually eaten by the parents. At the second nest where there were two newly hatched chicks, only one parent was in attendance during a 1.5-h period of observation. The attending parent brooded but did not respond to begging behavior by its chick. There was no feeding during the period of observation despite persistent begging by one chick.

Despite the difficulties both these pairs experienced on the first day, the first pair, when observed again the following day, fed their chicks several times in a smoothly functioning manner. Both pairs were ultimately successful in rearing young. One chick from the first nest was recaptured on the colony at 13 days of age and presumably fledged a week later (Massey 1974); both chicks from the second nest fledged and were seen intermittently on the colony with their parents for 15 days after fledging.

Awkward parental behavior has been observed many times in the past but has not been associated with a particular time in the season, and review of our field notes did not yield usable reference data on this aspect of parental behavior. It may also occur with experienced parents; it definitely occurs in some new parents.

*Fledging success.*—Criteria for fledging success were established in 1979 after a number of seasons of censusing the Least Tern population in California (Atwood et al. 1979). The minimum number of fledglings per maximum number of breeding pairs is ascertained for each colony whenever possible. If a colony has produced 1.0-1.5 fledglings/nesting pair, success is considered good, 0.5-1.0/pair is a moderate success, and 0-0.5/pair is poor. Fledging success is never easy to establish, and at some colonies the estimates are very rough.

The number of chicks fledged from the initial nesting group at Anaheim Bay in 1980 could be estimated only roughly; approximately 5-10 youngsters probably fledged from 8-10 nests, with success characterized as moderate (Table 4).

Fledging success could be gauged with greater accuracy for the second wave. All chicks were banded with red anodized service bands and were distinguishable from first-wave chicks. Many were recaptured on the colony throughout the pre-fledging

period, and chicks that survived the first week were known to have a good chance of fledging (Massey 1974). Many also had color-banded parents and could be identified in association with their parents. Using all these indicators, we were able to document a minimum of 19 fledglings and possibly as many as 35. Thus, the second wave at Anaheim Bay showed moderate success, with a minimum of 0.58 fledglings/pair (Table 4).

The 10 nests in the second wave where at least one parent was a 2-yr-old bird produced a minimum of 8 fledglings. The ratio was 0.8, considered a moderate success.

Table 4 shows fledging success at several California Least Tern colonies in Los Angeles and Orange Counties in 1980. The data for colonies other than Anaheim Bay are for the whole season rather than in terms of first and second waves of nesting. The overall contribution from Anaheim Bay was in the same range as that from several other small colonies, and the second wave of nesters was comparable to the first in terms of percentage success.

*Postfledging period.*—The first fledglings from the second wave were seen making short flights on the Anaheim Bay nesting grounds on 17 July. For the next 3 weeks, until the nesting site was deserted on 13 August, fledglings were present at every visit. Some stayed on the colony during the day and were seen there for as long as 16 days postfledging. Others moved to Harbor Lake for daytime foraging and preening, where one juvenile was seen 28 days after it had fledged from Anaheim Bay.

The postfledging group did not stay on the colony at night but flew off just before dusk to join the roosting flock at Belmont Shore in Long Beach, about 5 km west (Atwood and Massey in prep.).

The last identifiable fledglings and adults from Anaheim Bay were seen in the area (at Belmont Shore) on 29 August, 6 weeks after fledging began.

#### DISCUSSION

The second wave of nesting California Least Terns appears to have a large component of 2-yr-old birds breeding for the first time, as well as a group of older, reneating birds that failed on the season's first attempt. The one group we have not seen represented in the second wave is the age class  $\geq 3$  yr nesting for the first time in the season. All banded birds  $\geq 3$  yr of age recovered thus far that were nesting late in the season have been known to be making second attempts. The phenomenon of an older bird delaying its first breeding attempt until June or July has not been encountered and is unlikely to be a significant contributor to second-wave nesting.

Age of first breeding has been reported for several of the larger *Sterna* species. Arctic Terns generally begin breeding in the 3rd yr (Cullen 1957); some Common Terns breed in the 3rd yr but most begin at age 4 (Austin 1945, Nisbet 1978); Sooty Terns usually delay until the 5th yr (Harrington 1974). In a detailed study of a Sandwich Tern colony where 20% of the birds were ringed, Veen (1977) found only one 2-yr-old nesting. Age of first breeding was 3–4 yr, and the majority of the breeding population was 5–11 yr old. Full maturity and successful breeding at the age of 2, as exhibited by the California Least Tern, appears to be exceptional.

In 1978, Least Terns in nonbreeding (*portlandica*) plumage appeared in fair numbers on California breeding colonies midway through the season and stayed until the end, moving with the breeding birds and fledglings postseason to local fishing and flocking areas. Five were banded and identifiable as 1-yr-old birds (Massey and

Atwood 1978). We have since determined that birds in *piki* plumage are also 1 yr of age, and that 2-yr-olds, with rare exceptions, wear full adult plumage (Atwood and Massey in press). In 1978 we began to color-band chicks with a year-code and in 1980 we were able to determine that the vast majority of 2-yr-olds also arrives later in the season. On 21 May 1980, 6 weeks after the first wave of migrants had arrived, 2-yr-old color-coded Least Terns were seen at several colonies coincident with the first sightings of 1-yr-old birds. Thereafter, both age classes were seen in increasing numbers. It is now apparent that both 1- and 2-yr-old Least Terns arrive late and together on the breeding grounds, but the 2-yr-olds are returning, for the most part, to breed. One-yr-old birds have been observed in preliminary courtship behavior but have not been seen either copulating or nesting. Nor do they return to the breeding grounds in large numbers. In some seasons only a few have been seen, and the greatest number in the past 10 yr was 30 in 1977 (Massey and Atwood 1978). The percentage of 2-yr-olds that returns to breed has not been determined. An estimate should be obtainable in 1981, when presumably all of the surviving 1978 cohort will be among the breeding population, and their number can be compared with the number that returned in 1980.

The percentage of 2-yr-olds in the second wave at Anaheim Bay was probably much larger than we were able to document. Only 25% of the late-nesting terns were banded and thus identifiable; we suspected from their behavior that many of the unbanded birds were also 2 yr old. At two nests there were pairs of 2-yr-olds; it is reasonable to assume that at nests where one adult was known to be 2 yr old its unbanded mate was that age also. The asynchronous return of these younger birds to the breeding grounds would mitigate against their mating with older birds (except for those older terns that had lost mates during the breeding season).

The composition of a second nesting wave at a given colony could depend upon the success of the first wave, both there and at nearby colonies. When a colony has abandoned a site early in the season, there has been good circumstantial evidence that the birds have re-nested as a group at a nearby site. Thus, in some seasons and at some colonies, re-nesting terns could be the major component of the second wave, but in a good season there would be a very small re-nesting group.

Smaller clutch sizes, lower hatching success, and poorer fledging success have been demonstrated in Sandwich Terns (Veen 1977), Kittiwakes (Coulson and White 1958), and Arctic Terns (Coulson and Horobin 1976) breeding for the first time, as compared with older, experienced breeders. Common Terns ranging from 3 to 7 yr old showed progressively larger clutch size with increasing age, with 3- to 5-yr-old birds having lower hatching success than 6- to 7-yr-olds (Hays 1978). The smaller clutch size and increased rate of abandonment during incubation, plus the tentative nature of the parental behavior of 2-yr-old Least Terns, suggested that their first nesting attempts were more in the nature of a trial run than a real contribution to the breeding season. The results, however, belied this assumption. Fledging success from the second wave of nesting in Anaheim Bay in 1980 was in the same range as the overall seasonal success at several other colonies. Observation of the behavior of 2-yr-old parents showed that, although their initial behavior was often uncertain, by the 2nd posthatching day they were able to properly feed, guard, and brood their chicks. Fledging success of chicks of 2-yr-old parents was surprisingly high (Table 4).

Not every group of late nesting birds has been as successful as the one at Anaheim



Bay in 1980. We have frequently observed failure of second wave nesting in the past, with chances of success apparently diminishing as the season advances. The final nesting pairs of the season have rarely been successful. Conditions at Anaheim Bay in 1980 appeared optimal for a successful second wave, and the number of pairs nesting late was threefold greater than the number in the initial wave. Such an occurrence has been rare in our experience. The large percentage of 2-yr-old birds may have been a significant factor in the high success rate. These birds were making their first attempts of the season, and their nesting drive had not been vitiated by a prolonged breeding period caused by an initial failure. Second waves that are less successful may have a larger component of renesting terns.

These new data on the composition of the second nesting wave have implications for censusing. Since 1978, the California Least Tern census has been based on the number of pairs nesting in the first wave, taken usually just before hatching has begun, plus a variable number of late nesters, determined on the basis of local conditions. In future years, with the help of year-coded banding, we should be able to determine with much greater accuracy how many terns in the second wave are to be added to the season's census figures, rather than considered as renesting birds that had been previously counted.

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