Delayed Nocturnal Occupation of Breeding Colonies by Least Terns (*Sterna antillarum*)

JONATHAN L. ATWOOD
Department of Biology, University of California, Los Angeles, California 90024 USA

Gulls and terns exhibit a variety of behaviors during the nesting period that apparently function primarily to reduce the impact of predators on reproductive success (Cullen 1960, Tinbergen 1967). In this paper I suggest that the use, early in the breeding season, of nocturnal roosting sites that are located away from areas used later in the season for nesting may similarly function to lower predation at Least Tern (*Sterna antillarum*) colonies, and that comparable behavior may characterize other larid species as well.

The nocturnal roosting behavior of Least Terns associated with three nesting colonies in the vicinity of Los Angeles, California (Venice Beach, Long Beach, and Huntington Beach) was studied on 182 dates during 1976–1985. Colony affiliations of birds roosting at localities far from nesting areas were determined from observations of uniquely color-banded adults and juveniles marked with colony and year-cohort band combinations. Nesting chronology and reproductive success at breeding colonies were recorded at 1–7-day intervals as part of the annual monitoring of this endangered population (California Dept. Fish and Game unpubl. data). Supplemental observations of Least Tern roosting behavior were made at California breeding colonies located in Alameda, Santa Barbara, Ventura, and San Diego counties, as well as in Baja California and Colima, Mexico.

Between 1976 and 1985, Least Terns annually arrived in the Los Angeles area on approximately 15 April (California Dept. Fish and Game unpubl. data); the number of birds present in the area, based on counts made at nocturnal roost sites, increased rapidly through the first week of May (Fig. 1). Following their arrival but preceding the initial surge of egg-laying activity that began approximately 10 May (Massey and Atwood 1981, Minsky unpubl. data), the birds invariably roosted at night away from the precise localities where nests were later situated. On 98 nights of observation conducted during this phase of the breeding season at Venice Beach ($n = 19$), Long Beach ($n = 63$), and Huntington Beach ($n = 16$) during 1977–1985, off-colony roost sites were used 100% of the time. Identical use of off-colony roost sites in the early phases of the nesting season also was documented during limited observations at other nesting areas.

Nocturnal avoidance of nesting areas during the early phase of the breeding season was especially dramatic at Venice Beach and Huntington Beach. Birds associated with each of these colonies slept at night on portions of public beaches near the fenced, protected sanctuaries that later in the season were used for both nesting and roosting. Use of these unprotected, off-colony roost sites frequently exposed these individuals to nocturnal disturbances (dogs, foot traffic, vehicular beach patrols) that easily could have been avoided by remaining at night in the nearby fenced sanctuaries.

During the period preceding egg-laying, the number of courting and loafing Least Terns present on the ground in the Venice Beach and Huntington Beach colonies increased prior to and immediately following sunset (Fig. 2). However, these birds then deserted the nesting areas under failing light conditions and flew as individuals, pairs, and small groups to the roost sites used by each colony.

Least Terns were absent from off-colony nocturnal roost sites during daylight hours, with individuals and pairs appearing in flight over these sites 5–10 min before sunset. Synchronized group flight behavior, similar to that exhibited by Sanderlings (*Calidris alba*) and other shorebirds, was often displayed by Least Terns in the vicinity of night roosts before the birds actually landed at the site. I have not observed comparable flight behavior by this species during daylight hours at breeding colonies, foraging areas, or loafing sites. Birds landed first at off-colony roost sites approximately 5 min after sunset, and late-arriving individuals continued to join the roosting flock as much as 20 min after sunset under conditions of nearly total darkness. After the roosting flock settled on the beach, individuals appeared increasingly hesitant to fly as light intensities decreased; birds moved distances of less than 50 m when flushed after dark. Depending largely on subsequent disturbance levels, the roosting terns usually formed a single, relatively compact flock.

Off-colony roost sites used by birds nesting at Venice Beach, Long Beach, and Huntington Beach were situated near the mean high-tide berm on open, sandy beaches. Despite the fact that all of these beaches extended over 2 km in either direction from the roost site, and that other stretches seemed comparable in physical characteristics and disturbance levels to the areas used for roosting, the location of off-colony nocturnal roost sites varied little in their general location throughout each breeding season and from year to year. Roost sites at Venice Beach and Huntington Beach were contiguous with areas used for nesting; approximate distances from the breeding colonies to the roost sites varied from 150 m (Venice Beach) to 450 m (Huntington Beach). In contrast, birds associated with the Long Beach colony, situated on an approximately 0.4-ha landfill bordered by a major highway, a concrete-lined flood control channel, weedy fields, and an active construction site/shop-

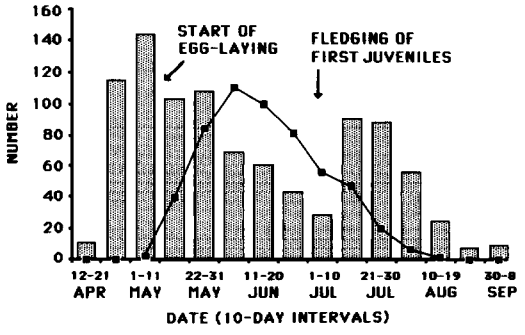

Fig. 1. Chronological relationship between numbers of Least Terns roosting off-colony and numbers of actively nesting individuals present at the Long Beach breeding colony, 1978–1981. The line graph represents the mean number of actively nesting birds (including incubating birds and those with unfledged juveniles); bar graphs represent mean numbers of birds present at the nocturnal roost site.

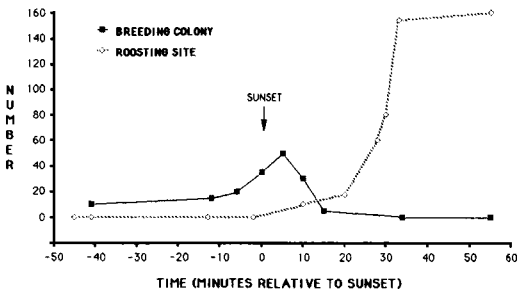

Fig. 2. Nocturnal desertion of Huntington Beach Least Tern breeding colony one day before the beginning of egg-laying.

ping center, slept at night on a stretch of open beach 12 km from the nesting area.

The initial and primary wave of egg-laying activity at Least Tern colonies in California usually is synchronized, with approximately 50% of a season's total nests at a colony initiated during the 15-day period from 7 to 21 May (Minsky unpubl. data). Following this surge of egg-laying activity, which began approximately 4 weeks after the birds' arrival in the vicinity of the breeding colonies, nocturnal roosting gradually shifted from off-colony sites to the nesting areas themselves (Fig. 1). Actively nesting Least Terns, including incubating individuals and birds with unfledged juveniles, slept on the breeding colonies; decreasing numbers of birds, including some nonbreeding first- and second-year birds (Massey and Atwood 1978, 1981) as well as individuals of unknown breeding status, continued to use off-colony roost sites during incubation and the feeding of unfledged juveniles.

During the postfledging period, birds at Venice Beach and Huntington Beach continued to sleep at night on the nesting areas. In contrast, individuals associated with the Long Beach colony usually returned during the postfledging period to the off-colony roost site that had been used prior to egg-laying (Fig. 1). Postfledging roosting behavior may have been influenced by nocturnal predation at the nesting colonies: birds continued to sleep on the nesting colonies in the absence of significant predation, but returned to early-season, off-colony sites when predation at the nesting areas occurred. Unfortunately, the extent and timing of nocturnal predation at the study colonies was inadequately documented to assess this potential relationship.

Based on an approximately 10-week period between the species' arrival in the vicinity of the breeding areas and the fledging of juveniles from the initial, primary surge of nesting activity (Massey 1974, Collins and Atwood unpubl. data), nocturnal use of the colonies occurred only during the last 60–70% of the total time. Although exceptions certainly occur where late-breeding terns are more successful than early-breeding individuals (Massey and Atwood 1981, Nisbet and Welton 1984), in general the likelihood of predators discovering the location of breeding colonies probably increases with the length of time that the sites are occupied. Consequently, a delay of 3–4 weeks in the nocturnal occupation of Least Tern nesting areas would shorten by approximately 40% the period of time that a colony's location would be "advertised" to nocturnal predators, effectively enhancing the probability of successful fledging by juveniles produced in the initial, primary wave of egg-laying.

Among the most evident advantages of coloniality in gulls and terns is the protection afforded eggs and chicks by group defense of the nesting area (Kruuk 1964). Aggressive antipredator behavior is exhibited only during daylight hours, however, and completely different strategies have evolved in response to nocturnal predation (Southern and Southern 1978). Marshall (1942), Nisbet (1975), and Nisbet and Welton (1984) described widespread night desertion by breeding adults at Common Tern (*Sterna hirundo*) colonies disturbed by nocturnal predators, and similar behavior has been reported in Common Black-headed Gulls (*Larus ridibundus;* Kruuk 1964), Mew Gulls (*Larus canus;* Barth 1955), Ring-billed Gulls (*Larus delawarensis*), and Herring Gulls (*Larus argentatus*) (Southern and Southern 1978). Once colonies of these species were located by nocturnal predators, substantial mortality of eggs and chicks (either directly or indirectly due to exposure) frequently resulted.

Little is known of the nocturnal roosting behavior of most larid species, especially during the early period of the breeding season prior to the laying of eggs. However, Common Black-headed Gulls, Herring Gulls (Drent 1967), Franklin's Gulls (*Larus pipixcan;* Burger 1974), Common Terns (Palmer 1941), Cas-

pian Terns (*Hydroprogne tschegrava*; Bergman 1953), Arctic Terns (*Sterna paradisaea*; Cullen 1956), Sandwich Terns (*Sterna sandvicensis*; Veen 1977), and Little Terns (*Sterna albifrons*; Nadler 1976) apparently resemble Least Terns in delaying the nocturnal occupation of their breeding colonies until after the onset of egg-laying and incubation. Tinbergen (1967) hypothesized that off-colony nocturnal roosting prior to egg-laying functioned to reduce predation on adult Common Black-headed Gulls "since the breeding habitat, with its cover, is more dangerous to gulls than are wide open spaces [used for roosting]." Least Terns, however, typically nest and roost in equally open habitats, suggesting that this behavior might also function to lower predation on eggs and juveniles by reducing the period of time that colony locations are subject to discovery by nocturnal predators.

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Development of Formation Flying in Juvenile White Ibises (*Eudocimus albus*)

Daniel R. Petit[1] and Keith L. Bildstein[2]

[1]*Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701 USA, and*
[2]*Department of Biology, Winthrop College, Rock Hill, South Carolina 29733 USA and*
The Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, South Carolina 29208 USA

Nice (1943) described five stages in the development of altricial birds, beginning with hatching and ending with independence. The first three phases, which involve nestling growth and behavioral development, have been well studied (e.g. Ricklefs 1968, Kushlan 1977); the latter two phases, which encompass the fledgling period, have been relatively little studied. This situation is unfortunate as mortality in birds is high at this time (Lack 1968, Recher and Recher 1969). There are few studies of development