ASPECTS OF CALIFORNIA LEAST TERN BREEDING
BIOLOGY:
CHICK FEEDING RATES AND THEIR
RELATIONSHIP TO FLEDGING SUCCESS, AND
THE SPATIAL DISTRIBUTION OF NESTS IN A
BREEDING COLONY

By

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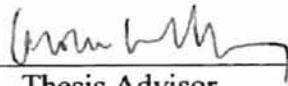
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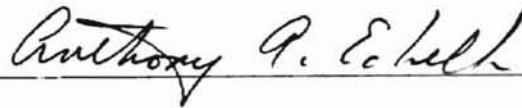
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CHAPTER 1

BACKGROUND:
CALIFORNIA LEAST TERN CONSERVATION

The state and federally listed endangered California Least Tern (*Sterna antillarum brownii*) breeds during the spring and summer along the coast of California, from its border in the south, north to the San Francisco bay area (Fig. 1). Within this range, the number of breeding sites (locations) used by terns each year varies, e.g., ranging from 28 to 38 during the years 1987-1994 (Caffrey 1995b). The number of sites used by breeding pairs in a given year is a function of site-specific characteristics causing terns to either settle or not, abandon once there, or, in some years, establish new sites (Caffrey 1993). The number of breeding pairs present at active sites also varies greatly, both between years at a particular site (e.g., occupancy at Ormond Beach/Edison increased by 314% between the 1994 and 1995 seasons; Caffrey 1997), and among different sites within a single year (in 1994, Venice Beach was used by 345 breeding pairs, while only two pairs nested at Pismo Dunes; Caffrey 1995a).

Since they were afforded protection under the Endangered Species Act in 1970, the statewide number of breeding California Least Terns has been steadily increasing, from a low of 300 pairs in 1970 (Craig 1971), to a high of approximately 4100 pairs in 1998 (Keane 2000). This increase in numbers is primarily attributable to the efforts of the dedicated agencies and individuals working on behalf of the recovery of the species, through habitat enhancement and restoration, and on-site monitoring. The latter involves monitor presence at breeding sites, baseline data collection, verification of predation and other sources of disturbance, and, in some cases, direct intervention to minimize the effects of such disturbances.

Determining and mitigating the sources of mortality and breeding failure are vital to the management and eventual recovery of any endangered species (Clark et al. 1989). Historically, the primary causes of breeding failure for California Least Terns have been both naturally occurring and anthropogenic. Habitat loss and degradation is assumed to be the major cause of the birds' decline to "endangered" status (Caffrey 1995b), and continues to constrain recovery efforts currently. Breeding failure has been documented to result from predation on terns of all ages, human-related sources of disturbance, and adverse environmental conditions, particularly El Niño (Massey 1988, Caffrey 1993). The first two of these threats are to some extent mitigable, and efforts to curb their occurrence and impact have largely been responsible for the terns' continuing increase in numbers (Caffrey 1995b). Yet, it has been the case at different sites in different years that chicks have died in large numbers, their carcasses found on site. These mass die-offs remain unexplained, although food shortage has been suggested as the cause (C. Caffrey pers. comm.); many of these cases have occurred during El Niño events (e.g. Massey et al. 1992). The predicted reoccurrence of El Niño in 1998 prompted our study of the relationship between chick feeding rates and fledging success, in order to lend support to the contention that these mass mortality events are due to chick starvation. In this thesis, Chapter Two examines this relationship for newly hatched California Least Terns at four breeding sites during a severe El Niño event.

California Least Tern recovery efforts would further benefit from a greater understanding of what constitutes an "optimal" breeding site for this subspecies. In

chapter three, we present a detailed spatial analysis of nest site selection at one

historically successful California Least Tern breeding colony (Venice Beach), in order to

test hypotheses regarding nest placement over time in relation to colony center and edge,

nearest-neighbors, and vegetation patches.

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Figure 1. Locations of California Least Tern breeding sites used between 1985 and 1995 (from Caffrey 1995b).

Port Chicago

PGE Pittsburg

NAS Alameda
Oakland Airport

California

Costa Del Sol
Terminal Island
Venice Beach

Seal Beach
Bolsa Chica
Huntington Beach
Newport Slough
Upper Newport Bay
White Beach
Santa Margarita River
Buena Vista Lagoon
Agua Hedionda*
Batiquitos Lagoon
San Elijo Lagoon

Pismo Dunes
Oso Flaco Lake
Guadalupe Dunes
Mussel Rock Dunes
San Antonio Creek
Purisima Point VAFB
Santa Ynez River
Santa Clara River
McGrath Beach
Ormond Beach
Point Mugu

San Dieguito Lagoon
Mission Bay
Naval Training Center
Lindbergh Field
NAS North Island
D Street Fill
Chula Vista Wildlife Reserve
Delta Beach
Saltworks
Tijuana River Mouth

United States
Mexico

Pacific Ocean

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CHAPTER 2

CALIFORNIA LEAST TERN CHICK FEEDING RATES AND THEIR
RELATIONSHIP TO FLEDGING SUCCESS

Abstract: The state- and federally- listed endangered California Least Tern (*Sterna antillarum brownii*) breeds along the coast of California from its border with Mexico in the south, north to the San Francisco Bay area. In past years, El Niño has caused a sharp decrease in the abundance of fish off the California coast, resulting in high mortality and low reproductive success in many seabird species. In 1998 (an El Niño year), four geographically separated Least Tern breeding sites were monitored, and data were collected on fish delivery rates, chick feeding rates, size of fish fed to chicks, size of dropped fish, and the proportion of time chicks were attended by parents. Rank correlation analysis detected a significant relationship between chick feeding rate and fledging success. The site with the highest parental attendance, fish delivery, and chick feeding rates, with significantly higher proportion of small (edible) fish brought to chicks than the other sites had the highest fledgling-to-pair-ratio. Two sites did not differ from each other, having lower than average parental attendance rates, fish delivery rates, and chick feeding rates, and a proportion of small fish delivered to chicks far below reported values. Although the fledgling-to-pair ratio was unavailable for the southern-most site, behavioral observations and the large number of chick carcasses and abandoned eggs found strongly suggest that this site had the poorest fledging success. Correspondingly, it had the lowest parental attendance rates, fish delivery rates, chick feeding rates, and proportion of edible fish brought to chicks of all four sites.

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Introduction

Availability of food for nestlings has been determined to be an important variable limiting the reproductive success of birds [e.g,. Zebra Finches (Lemon and Barth 1992), magpies (Hogstedt 1981), pelicans (Anderson et al. 1982), and gulls (Bukucenski et al. 1998)]. Fledging success has been shown to be highly dependent upon prey abundance for Arctic Terns (*Sterna paradisaea*: Monaghan et al. 1989a and 1989b), Common Terns (*S. hirundo*: Le Croy and Collins 1972, Safina et al. 1988), Roseate Terns (*S. dougallii*: Le Croy and Collins 1972, Ramos 1998), and Royal Terns (*S. maxima*: Uttley et al. 1989). For the endangered California Least Tern, chick mortality has been able to be ascribed, via direct evidence, to predation, unauthorized human presence in tern nesting areas, injury, and disease (Caffrey 1995b). However, several occurrences of chick carcasses being found in large numbers, with no external evidence as to cause of death, had been reported by monitors at various breeding sites within California from 1992-1996 (Caffrey pers. comm.). In part because these cases coincided with El Niño events, many believed that the chicks had starved as a result of a climatically-induced decrease in the availability of prey (small fish).

The types of evidence suggested to indicate that tern prey items were limited include: (1) reduced parental attendance of chicks at the nest (presumably due to the increased time required by parents to find food), compared to "good" conditions when at least one parent always attends the nest or chick (Keane 1987); (2) decreased rates of

adult foraging success (D. Woods, unpubl. data); (3) below average clutch size and/or increased abandonment of nests, which, in other *Sterna* species, have been shown to result from inadequate food supplies (Nisbet 1973); (4) many large fish found discarded at the site, presumably because their large size precludes swallowing by small chicks [dropped fish have been used to indicate feeding habits of California Least Terns (Atwood and Kelly 1984), Interior Least Terns (*S. antillarum albifrons*; Schweitzer and Leslie 1996), and Roseate Terns (Ramos et al. 1998), and relative sizes and numbers of discarded fish may be an index of local abundance]; (5) chick carcasses found with large fish lodged down their throats; and, (6) reduced rates of food delivery by adults to their chicks. Each of the above has been anecdotally reported for California Least Terns at various sites in different years (C. Caffrey pers. comm.), and many of the above were observed by myself while working as a monitor at the Venice Beach site in 1995 and 1996. The systematic, multi-site collection of data regarding evidence for #1, #4, and #6 were the focus of this study.

Past El Niño events have been well documented to have a strongly negative impact upon marine and terrestrial ecosystems throughout the Pacific region, including the California coast (Cruz and Cruz 1990, Polis et al. 1997). The dramatic increase in ocean temperatures which characterizes El Niño events has been shown repeatedly to be accompanied by large reductions in fish abundance, including populations of Northern Anchovies (*Engraulis mordax*), whose numbers reached record lows during the El Niño of 1982-1983 (Barber and Chavez 1983), and upon which breeding California Least Terns depend for their primary source of food (Atwood and Minsky 1983).

The starvation of many seabird hatchlings along the California coast during the 1992 El Niño has been documented by Polis et al. (1997), and similar mass mortality events have been reported by others working in different El Niño affected regions in other years (Ainley et al. 1987, Duffy 1990, Wilson 1991). The 1982-1983 El Niño was documented to result in depressed reproduction at a California Least Tern breeding colony included in the current study (Venice Beach; Massey et al. 1992). Many studies (e.g., those cited above) have shown a strong correlation between El Niño years, reduced fish numbers. and increased seabird mortality. This study is the first to investigate the relationship between chick feeding rates and chick survival for the endangered California Least Tern.

Methods

Chicks at four California Least Tern breeding sites were observed to examine the relationships between chick feeding rates and several aspects of breeding biology during the early chick rearing and feeding stage. The four sites spanned the entire breeding range (from north to south) of the species; this allowed for comparison of data collected from sites where reproductive success was expected to be relatively unaffected by El Niño (in the north) with sites where reproductive success was expected to be heavily impacted (in the south; Caffrey pers. comm.). These sites also were chosen because of their large size, in terms of the number of breeding pairs present, and because all four share historically high levels of fledgling production, due, in part, to low rates of predation.

Terns were observed at the following four sites, from north to south: Naval Air

Station Alameda (AL) (hereafter NAS Alameda; Alameda County), Venice Beach (VB)

(Los Angeles County), Huntington Beach (HB) (Orange County), and Mission Bay/

Mariner's Point (MP) (hereafter Mariner's Point; San Diego County) (Chapter 1, Fig. 1).

Data collection involved the observation of chicks from positions outside of the sites

themselves (so as to not disturb the birds), using a 30X power spotting scope and, where

necessary, a portable blind.

Each site was visited for five consecutive days during late May through early July.

Because the timing of breeding events at different sites varies throughout the tern

breeding range, the order in which sites were visited was determined by the timing of tern

nesting activities. Visits coincided with each site's peak hatching period, in order to

maximize the number of young chicks available for observation. Nests containing one or

two hatchlings were each watched for two hours. Across all sites, a total of 120 nests

were observed for 234 hours.

In this study, we control for chick size and age, choosing for observation only

chicks of age one week or less (size and plumage characteristics permit such age

determination; Thompson et al. 1997). To account for daily temporal variation in food

availability, terns at all sites were observed nearly all day (0700 to 1600) for each of the

five days. Nest numbering via marked tongue depressors, placed adjacent to nests by

monitors (see below), and other landmarks near nests made it possible to determine that,

at each site, each nest was observed only once.

Monitors associated with the California Department of Fish and Game California Least Tern Monitoring Program collected nesting data and estimated the number of breeding pairs present and the number of fledglings produced at each site, according to established protocol (Caffrey 1995c); these estimates were used to generate fledgling-to-pair ratios for the four sites. For each observation period, I determined (1) the proportion of time that at least one parent attended the chick or chicks (parental attendance); (2) the total number of fish brought back to the nest, independent of brood size and regardless of whether or not the fish were eaten by chicks (overall fish delivery rate); (3) the number of fish actually eaten by chicks (chick feeding rate); (4) the estimated body length of fish brought to nests (fish size); and (5) the frequency of adult aggressive interactions, such as kleptoparasitism of terns returning to the colony with fish, and aggression toward chicks. At Huntington Beach and Mariner's Point, we also determined the number and sizes of fish found dropped on site by chicks or adults. The length of fish offered by the parents can be reliably estimated by comparison with adult bill length (approximately 2.5 cm; Thompson et al. 1997). Fish in this study were assigned to three size classes: size 1 = a body length of less than 2.5 cm, size 2 = 2.5-5.0 cm, and size 3 = longer than 5.0 cm (*sensu* Atwood and Kelly 1984). During this study, fish longer than 5.0 cm were never observed being successfully swallowed by chicks; therefore, fish in size category three are considered "inedible".

For all sites, feeding rate data were summed over five days, and mean chick feeding rates were compared with chick survival (in the form of fledgling to pair ratios). Analyses of variance (one- and two-way ANOVAs) were performed to compare results at

the four sites during the El Niño year of 1998; Least significant difference (LSD) tests were then performed to identify where significant differences occurred. Spearman Rank Correlation Analysis was used to determine the nature of the relationship between chick feeding rate and fledging success. Nonparametric tests were used when the assumptions of parametric ones were not met. Descriptive statistics are presented as mean ±1 standard error.

Results

Total numbers of breeding pairs present (Keane 2000) and the number of nests I observed at each site were as follows: NAS Alameda = 243 pairs present, 32 nests observed; Venice Beach = 383 pairs, 30 nests; Huntington Beach = 319 pairs, 29 nests; Mariner's Point = 528 pairs, 29 nests.

In 1998, tern chicks across all nests at Huntington Beach were attended by a parent, on average, 94% of the time observed. At the three other sites, mean parental attendance was significantly lower: NAS Alameda = 36.9%, Venice Beach = 48.9%, and Mariner's Point = 50.9% ($F = 12.46$, df = 3, $P = 0.0001$; Fig. 1)

At Huntington Beach, mean overall fish delivery rate was 1.501 ± 0.212 fish/hour. At the three other sites, mean overall fish delivery rate was significantly lower: NAS Alameda = 0.95 ± 0.130 fish/hour, Venice Beach = 0.91 ± 0.134, and Mariner's Point = 0.86 ± 0.126 ($F = 3.75$, df = 3, $P = 0.0130$; Fig. 2).

The size distribution of fish brought to nests at Mariner's Point differed significantly from that at the other sites (Heterogeneity Chi-square; $G_H = 28.21$, df = 3, P< 0.005). At Mariner's Point, 22% of food items brought to chicks were too large for them to swallow, while at NAS Alameda, Venice Beach, and Huntington Beach, fewer than 6% were inedibly large (Fig. 3).

Monitors at Venice Beach and NAS Alameda were unable to regularly collect the fish dropped by adults while feeding chicks; data are thus presented for only two sites. At Mariner's Point, 59 dropped fish, representing eight species, were collected from the ground (Table 1). Fifty-six of these (95%) were too long for chicks to have swallowed (Fig.4), and 13.5% belonged to species that, because of their morphology, are generally considered "inappropriate" for Least Tern consumption (Atwood and Kelly 1984). At Huntington Beach, only six dropped fish representing three species were found on the site (Table 2). All were too long for chicks to have swallowed (Fig. 5) but all represented "suitable" prey species (Atwood and Kelly 1984).

A two-way ANOVA detected no effect of brood size on per-chick feeding rate (F = 0.09, df = 3, P = 0.9629). Therefore, broods of one and two chicks were combined to calculate a mean, per-chick feeding rate at each site. Mean chick feeding rates at NAS Alameda (0.461 ±0.087 fish/chick/hour), Venice Beach (0.538 ±0.104) and Mariner's Point (0.455 ±0.078) were significantly lower than at Huntington Beach, where chicks were fed, on average, 0.958 ±0.122 fish/chick/hour, (F = 5.74, df = 3, P = 0.0011; Fig.6).

At both NAS Alameda and Venice Beach, 1998 fledgling-to-pair ratios (0.37 and 0.52, respectively) were considerably lower than the mean fledgling-to-pair ratios at those sites for 1987 through 1994 (1.39 and 1.00, respectively: Caffrey 1993, 1994, 1995(a); Johnston and Obst 1992; Massey 1988, 1989; Obst and Johnston 1992) (Fig 7). At Huntington Beach, fledging success in 1998 was approximately twice the mean reported for that site for 1987 through 1994 (0.78 vs. 0.37; Fig 7). At Mariner's Point, the evening roost (where fledglings are usually counted) was not located in 1998; an estimate of the number of fledglings produced at that site was therefore unavailable. However, the abundance of chick carcasses found on site suggests chick survival was very low. At the remaining three sites for which fledgling numbers could be estimated, chick feeding rate and fledgling to pair ratio were highly significantly correlated (Spearman Rank Correlation: r= 0.958; Fig.8).

Discussion

The El Niño event of 1997-1998 was unparalleled in its severity (Parades and Zavalaga 1998). The estimated number of California Least Tern fledglings produced statewide in 1997 was approximately 3200 per 4000 pairs (Keane 1998); only 2700 fledglings per 4100 pairs were produced in 1998 (Keane 2000). Decreased productivity of coastal marine fisheries (Love et al. 1998), coupled with increased mortality and decreased reproductive success of many piscivorous Pacific coast seabirds (Parades and Zavalaga 1998) suggests that fish numbers were reduced in the region where California Least Terns breed.

For Lesser Black-backed Gulls, it has been demonstrated experimentally that an inadequate food supply increases chick mortality due both to starvation (decreased chick feeding rates) and predation (because of the prolonged absence of foraging parents from their chicks) (Bukacinski et al. 1998). Decreased prey availability has been demonstrated to negatively affect the reproductive success of Common Terns by increasing the foraging time required by adults for successful prey capture (Courtney and Blokpoel 1980). When parents are foraging for their chicks, and themselves, they cannot also be attending those chicks. The extended absence of adults can leave tern chicks vulnerable to death by exposure (hyper- or hypothermia) and predation (Courtney and Blokpoel 1980, Parades and Zavalaga 1998). Because Least Tern chicks under the age of 12 days cannot thermoregulate effectively (Howell 1959), their survivorship, too, would appear dependent on parental brooding.

My observations provide comparative information on the provisioning and attendance of young California Least Terns. Under "normal" conditions, Least Tern chicks under one week of age are brooded or attended for at least 95% of the day (Johnston 1995, Keane 1987, Thompson et al. 1997). In 1998, only chicks at Huntington Beach were attended at "normal" rates; chicks at NAS Alameda, Venice Beach, and Mariner's Point were not attended more than 51% of the time. Chick mortality at these three sites, apparently the result of starvation, was likely exacerbated by the prolonged absence of parents from nests.

Overall fish delivery rate (fish/nest/hour) was incorporated into the study as an indirect measure of prey availability. Direct measures have been made of the foraging success of Least Terns (Schweitzer 1994, Talent and Hill 1985, Wilson et al. 1993, D. Woods unpubl. data); these can be unreliable indicators of prey abundance, however, because foraging success varies widely as a function of the foragers' age and experience, the chosen foraging habitat, climatic conditions, and interference from competing individuals (Atwood and Minsky 1983, Dunn 1972 and 1973, Hawksley 1957, Shealer and Burger 1993). Absolute measures of local food abundance cannot be determined via fish delivery rates, yet these rates likely reflect the relative foraging success of adults at different sites. Under "normal" conditions, overall fish delivery rates for Least Terns are reported to be approximately two fish per nest per hour (Brubeck et al. 1981, Schweitzer 1994, Thompson et al.1997, Wilson et al. 1993). This value was approached only at Huntington Beach, suggesting that prey items were more scarce at NAS Alameda, Venice Beach, and Mariner's Point.

Although adult Least Terns can swallow fish that are up to 9.0 cm long (Atwood and Kelley 1984), fish longer than 5.0 cm were never swallowed by chicks under one week of age during the course of this study (Woods pers. obs.). Prey items approximately 2.5 cm. long are appropriate for Least Tern chicks (Atwood and Kelley 1984, Keane 1987, Schweitzer 1994, Wilson et al. 1993). Such items are large enough to provide adequate, high-density sustenance (Harris and Hislop 1978), yet small enough to be easily swallowed. Adult terns ought to "choose" appropriately sized fish for their chicks and, indeed, terns of many species are known to discriminate between potential prey items

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when foraging for chicks, adults (mates), or large fledglings (Wiggins and Morris 1987, Smith 1993, Wilson et al. 1993, Shealer 1998). When food is limited, however, entire classes of prey items (i.e. small larval fish) may be difficult to obtain, and adults foraging under such conditions would be expected to return to their nests with a greater proportion of fish exceeding edible sizes, or those of "inappropriate" species, than those at unimpacted sites.

A very small fraction of the fish offered to tern chicks at NAS Alameda, Venice Beach, and Huntington Beach was composed of inedibly large fish (Fig.3). At these three sites, adult terns were apparently able to select appropriately-sized fish for their chicks (despite the apparent overall scarcity of prey at NAS Alameda and Venice Beach). A much greater proportion of too-large fish were brought to nests at Mariners Point; this likely contributed to the high chick mortality observed there. Small- and medium-sized prey items were presumably locally unavailable, and adult terns at Mariner's Point appeared to be catching and bringing to nests whatever they managed to find, including many fish that were too large or were otherwise unsuitable for chicks (e.g., inappropriate species).

When California Least Tern chicks are offered fish they cannot swallow, the fish usually end up being dropped on the ground. Dropped fish have been used to indicate the feeding habits of California Least Terns (Atwood and Kelley 1984), Common Terns (Palmer 1941, Courtney and Blokpoel 1980), and Roseate Terns (Ramos et al. 1998); the relative sizes and numbers of discarded fish may be an index of local prey availability.

Thus, many more large-bodied and/or unsuitable species of fish would be expected to be dropped at sites where preferred prey items were limited than at sites where such items were available. This contention is supported by the data from Huntington Beach (very few dropped fish/ no inappropriate species) and Mariner's Point (many dropped fish/ many inappropriate species).

Keane (1987) reported that California Least Tern broods of two chicks were fed significantly more often than broods of one, but such was not the case at the sites I observed in 1998; chicks at all four sites were fed at rates independent of brood size. In the literature, "normal" chick feeding rates for California Least Terns are reported to be between 1.1 (Keane 1987) and 2 (Thompson et al. 1997) fish/chick/hour, but in 1998, chicks at three of the four sites under study were fed significantly less frequently (Fig.6). Feeding rates are known to be associated with chick survival for many tern species (Le Croy and Collins 1972, Monaghan et al. 1989a and 1989a, Safina et al. 1988, Ramos 1998, Uttley et al. 1989), and the same appears to be true for California Least Terns; fledging success at the three sites for which data were available was determined to be a function of chick feeding rate. At Mariner's Point, chick carcasses were very abundant, kleptoparasitism of adults returning with fish was frequent (but was never observed at the other three sites), and adults were observed pecking (on one occasion, fatally) neighboring chicks that begged for food. Terns at NAS Alameda, Venice Beach, and, presumably, Mariner's Point, experienced poor reproductive success in 1998, likely as a result of reduced prey availability. At Huntington Beach, where chick feeding rates were well within "normal" ranges, subsequent chick survival was high.

Although the relationship between chick feeding rates and survivorship fits well the initial presumptions of this study, as well as a body of literature, the expected geographic pattern (increasing breeding failure from north to south) was not seen. The degree to which fledging success at NAS Alameda was affected was surprising because terns at this site (and those at other sites in the northern part of the breeding range) have not historically been subject to El Niño's damaging effects (C. Caffrey, pers. comm.). In 1998, the unusually large amount of fresh water runoff into the San Francisco bay from El Niño-related storms, rather than increased ocean temperatures, likely deleteriously affected prey availability there (L. Collins, California Least Tern monitor, Naval Air Station Alameda, pers. comm.). That Huntington Beach, in the center of the breeding range, was seemingly unaffected with regard to food availability was also surprising. Yet, such local variation in fledging success across the state has been repeatedly documented over the years (e.g., Caffrey 1998). In 1998, terns at Huntington Beach were apparently the beneficiaries of some relatively unaffected food source near the site.

Despite these geographic anomalies, the relationships between an apparent food shortage and various aspects of California Least Tern breeding biology were clear: chicks were left unattended and, therefore, vulnerable to predation and adverse weather while both parents foraged for fish that were apparently scarce. As the result of limited food availability, overall fish delivery rates fell, chick feeding rates declined, and inappropriate prey items were brought back to nests and dropped on the ground. The unfortunate consequence for this endangered species was that many chicks failed to fledge, presumably due to starvation during the year of 1998.

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TABLE 1. Numbers and sizes of fish found dropped at two California Least Tern breeding sites in 1998.

Site	Species	n	Percent of Total
Mariner's Point			
	*Jacksmelt (Atherinopsis californiensis)	22	44.1
	*California Barracuda (Sphyraena argentea)	10	16.9
	*Northern Anchovy (Engraulis mordax)	9	915.3
	*Topsmelt (Atherinops affinis)	6	10.2
	Surfperch species (Embiotocidae)	4	6.7
	Sailfin Mollie (Poecilia latipinna)	2	3.3
	Jack Mackerel (Trachurus symmetricus)	1	1.7
	California Needlefish (Strongylura exilis)	1	1.7
Huntington Beach			
	*Northern Anchovy (Engraulis mordax)	3	50.0
	*Jacksmelt (Atherinopsis californiensis)	2	33.0
	*California Barracuda (Sphyraena argentea)	1	17.0

*="appropriate" prey species (Atwood and Kelly 1984)

Figure 1. Proportion of observation period during which at least one parent attended chick(s) at four California Least Tern breeding colonies.

*P=0.001
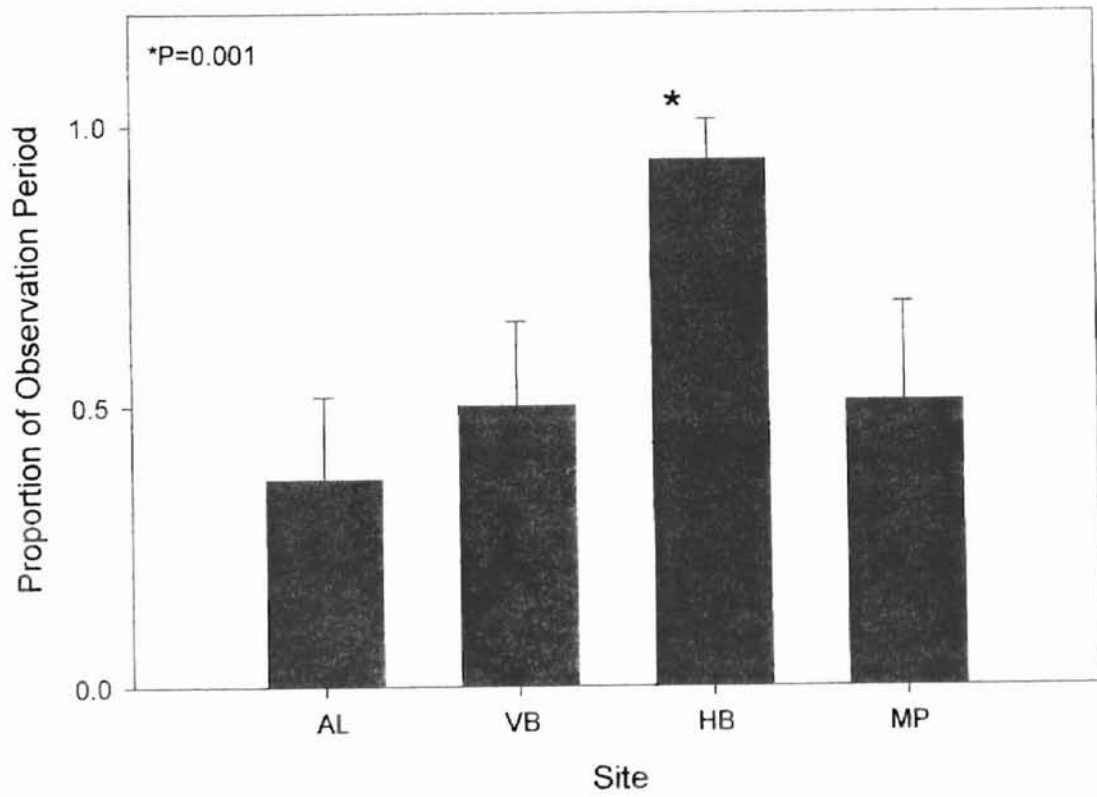
Figure 2. Overall fish delivery rates (fish to nest/hour) at four California Least Tern
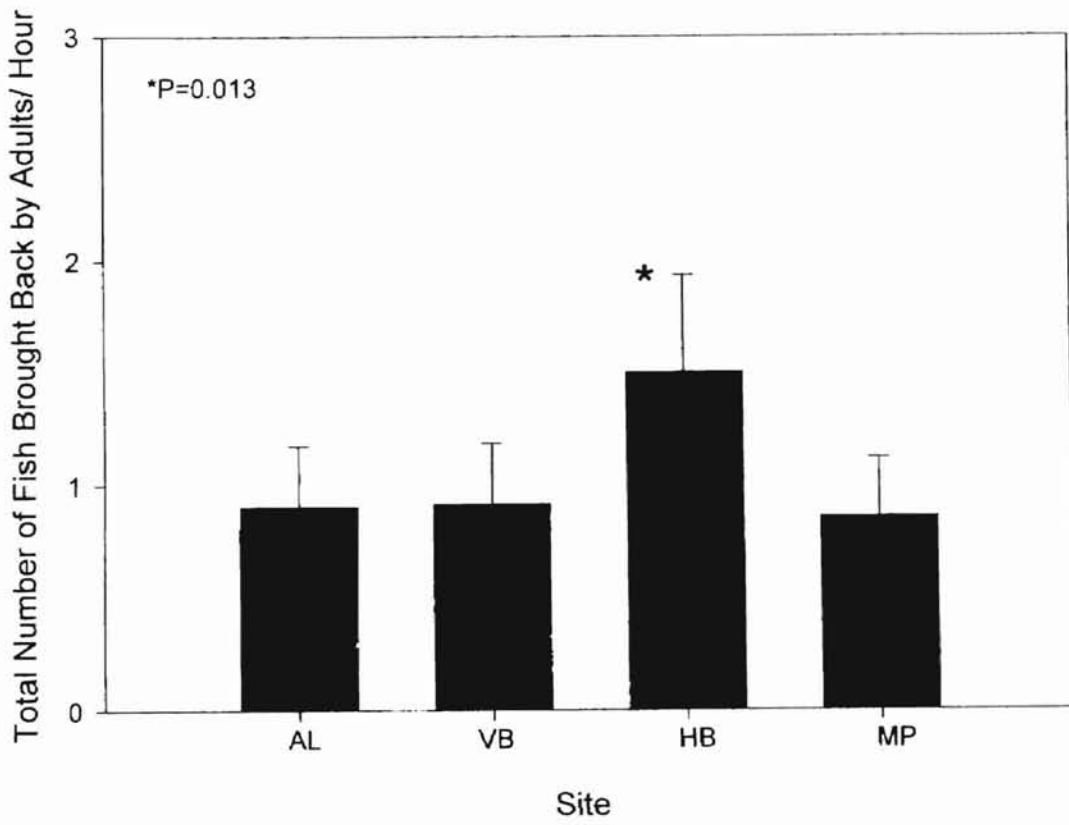
breeding colonies.

Figure 3. Size (body length) distribution of fish brought back to nests by adults at four

California Least Tern breeding colonies. Size 1 = <2.5 cm, size 2 = 2.5-5 cm, size 3

(inedible) = >5 cm.
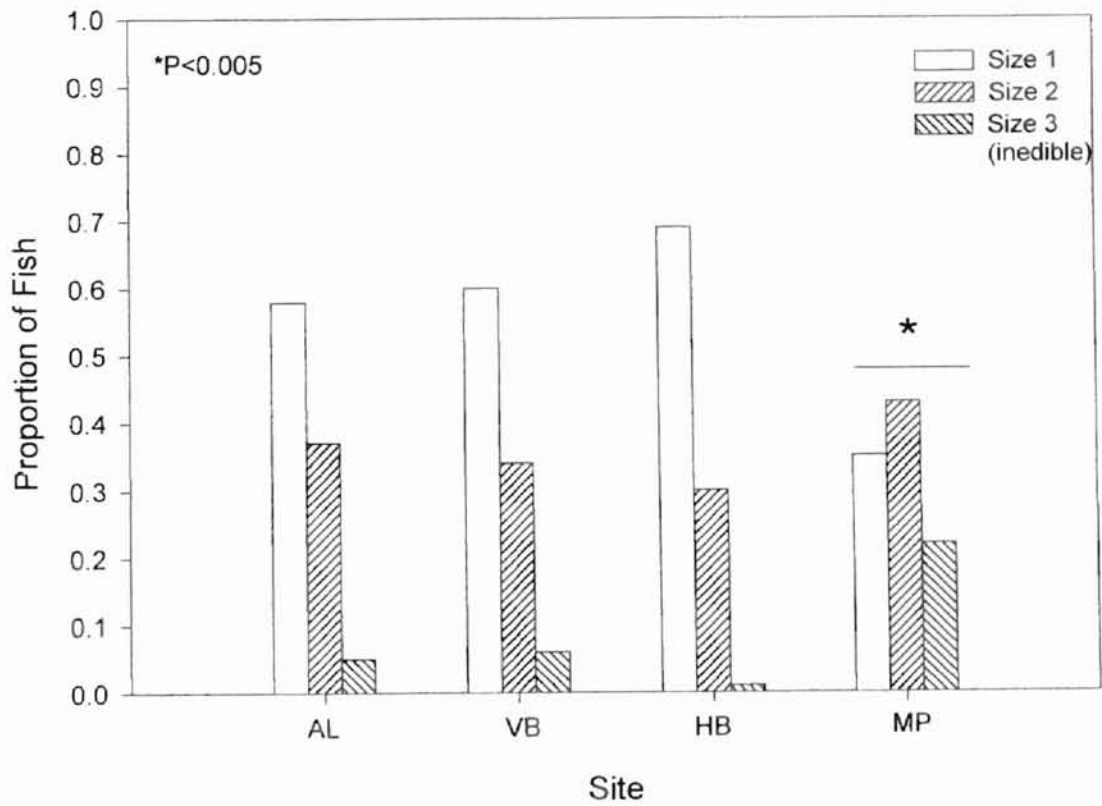
Figure 4. Numbers and sizes of fish found dropped on the ground at California Least

Tern breeding colony Mariner's Point.

Body Length (cm)
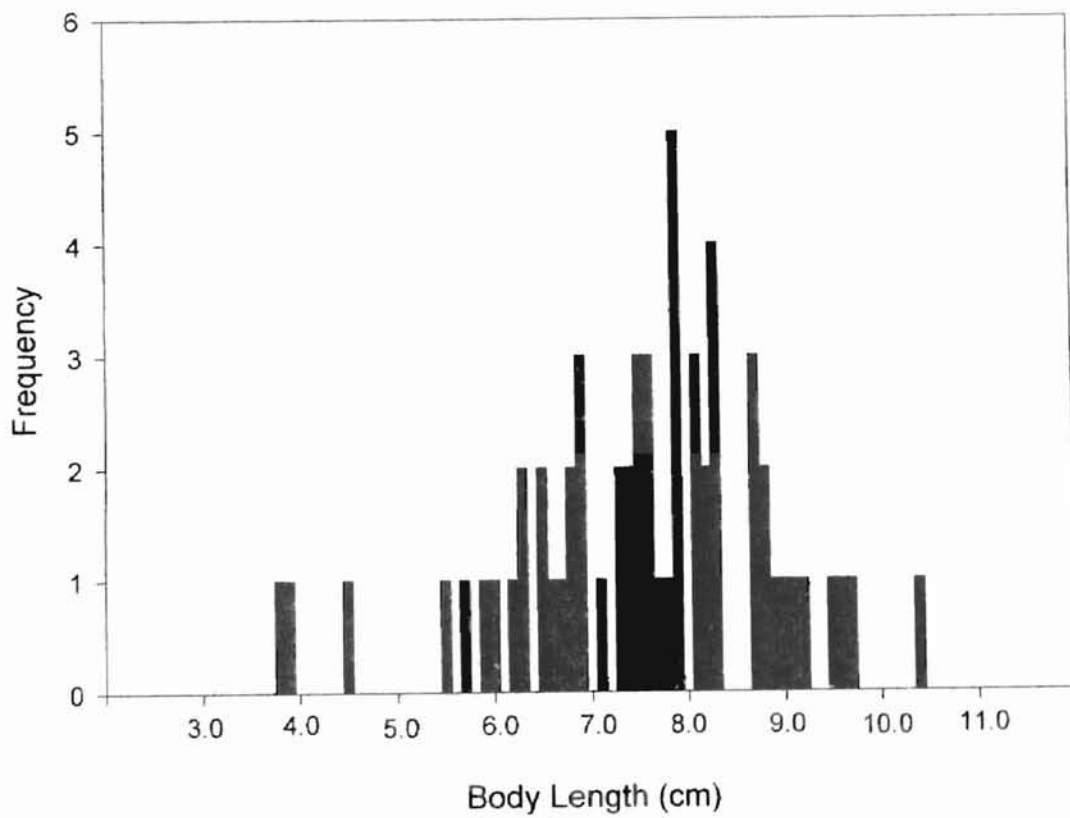
Figure 5. Numbers and sizes of fish found dropped on the ground at California Least

Tern breeding colony Huntington Beach.

Body Length (cm)
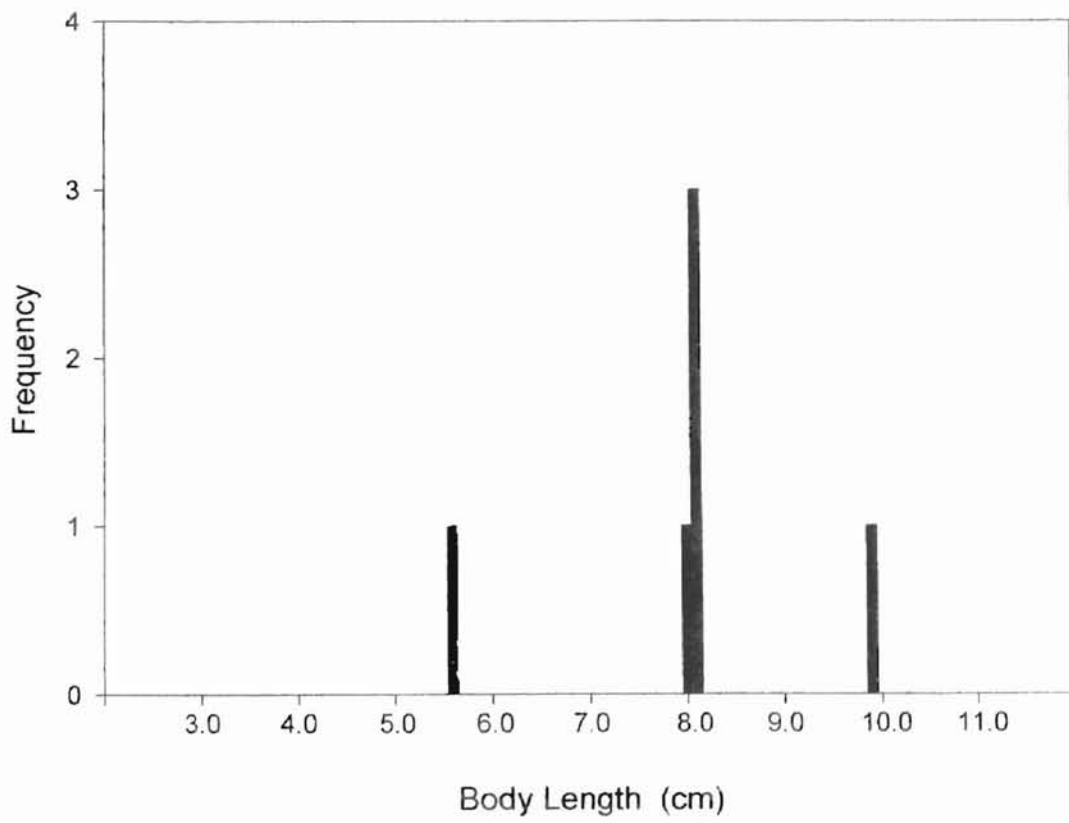
Figure 6. Per-chick feeding rate (fish/hour) at four California Least Tern breeding colonies.

*P=0.001
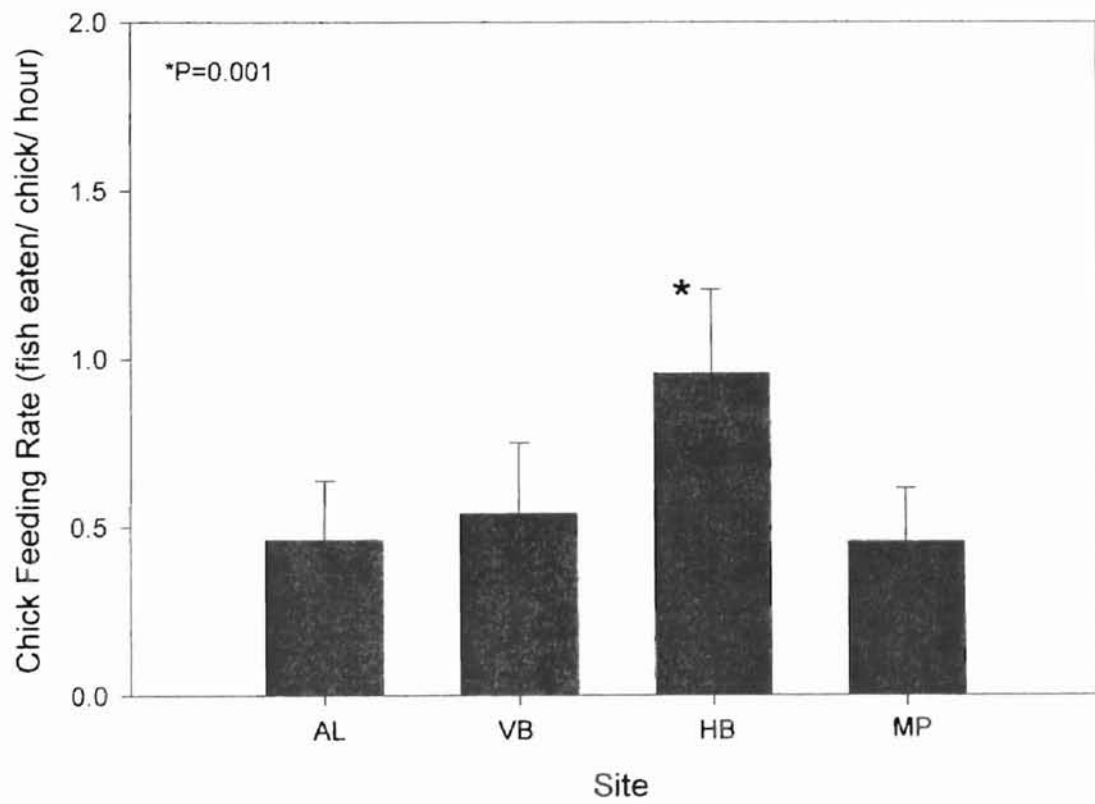
Figure 7. Mean fledging success for 1987 through 1994 versus 1998 for three California Least Tern breeding colonies (fledging success was undeterminable at Mariner's Point in 1998).

Fledgling-to-Pair Ratio

Legend:
- 1987-1994**
- 1998

Site: AL, VB, HB
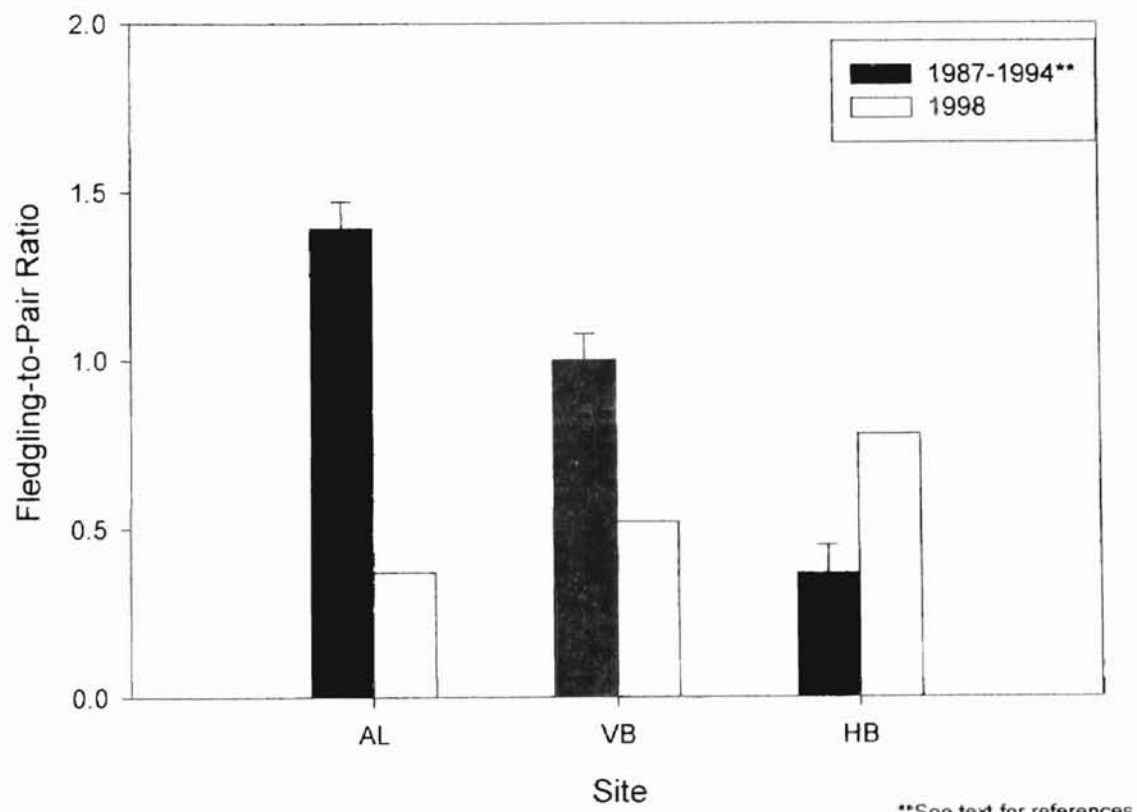
**See text for references

Figure 8. Relationship between per-chick feeding rate and fledging success at three

California Least Tern breeding colonies.
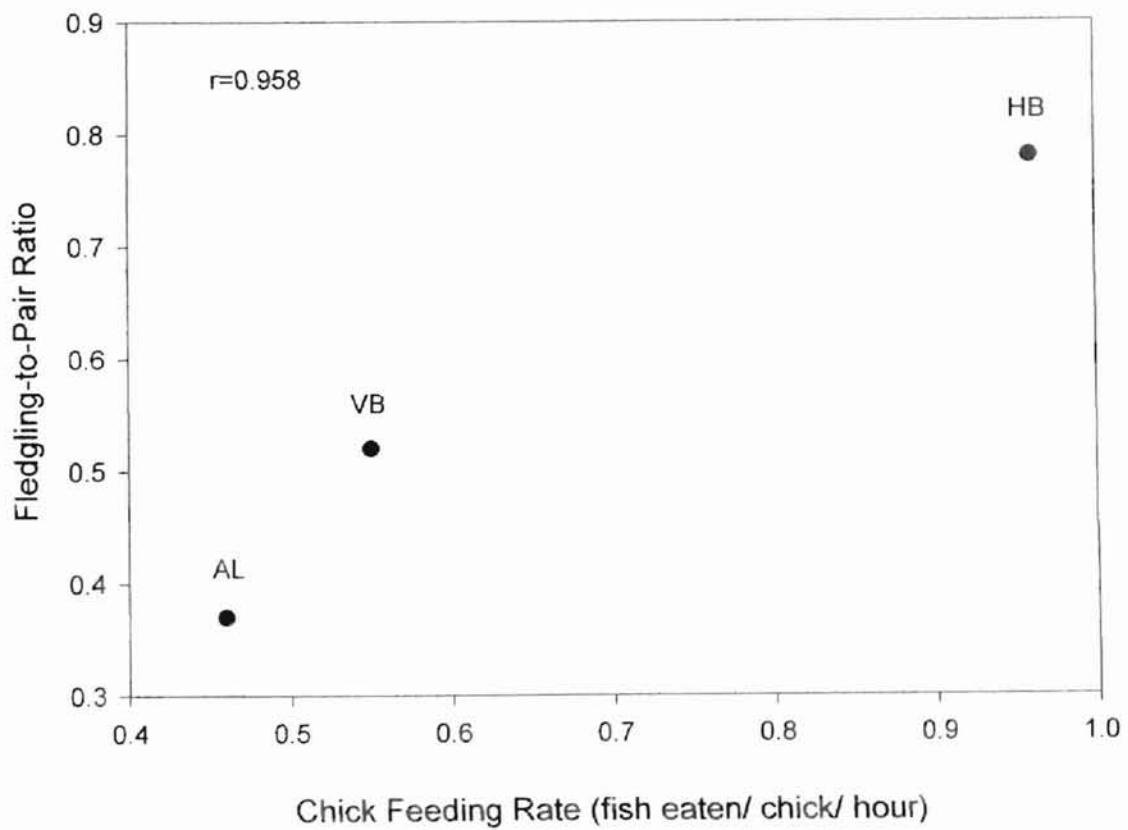
CHAPTER 3

NEST SITE SELECTION BY CALIFORNIA LEAST TERNS BREEDING AT VENICE
BEACH, CALIFORNIA, IN 1996

Abstract: An abundant literature on nest site selection in Least Terns and other colonially breeding seabird species supports the contentions that breeding pairs should place nests (i) in the center of the breeding colony, (ii) near nests of conspecifics, (iii) away from patches of vegetation, and (iv) away from the colony edge. Nest site location criteria for California Least Terns (*Sterna antillarum brownii*) breeding at Venice Beach, California, in 1996 were examined to determine whether or not these predictions hold for this population. Statistical analyses indicated that nests were established randomly with respect to distance to colony center and distance to nearest neighbor. Ninety-five percent of nests were established more than approximately 2.5 meters from vegetation and seven meters from the colony edge (fence). Variability in nesting patterns among colonies of California Least Terns is well documented; factors other than those examined presumably are influencing nest site selection in these birds.

Introduction

Although colonial breeding is uncommon across all birds (15% of species; Minsky 1987), it is the rule among seabirds (95% of species; Minsky 1987). A large body of literature has developed on the relationship between nest location and reproductive success (e.g., Butler and Trivelpiece 1981: Black-backed Gulls; Schoen and Morris 1984: Herring Gulls; Sherburne 1987: Kittiwakes; Reville 1991: Frigatebirds). Well established within this literature is the generality that, within a colony, pairs nesting in the center experience greater reproductive success than more peripheral pairs (Coulson 1968, Bunin and Boates 1994). Centrally nesting pairs may gain reproductive benefits through increased vigilance ("more eyes on the job") and reduced predation (Hamilton

1971). Local clusters of nests within colonies may experience reduced predation via the same mechanisms at work for the colony as a whole; these include dilution (Foster and Treherne 1981), increased predator vigilance (Bertram 1980, Kenward 1978), and improved defense against predators via mobbing (Birkhead 1977, Whittenberger and Hunt 1985).

Pairs nesting near the colony center also may benefit by avoiding negative characteristics associated with peripheral areas, such as extreme ground slope (Bunin and Boates 1994) or (for terns nesting on public beaches) the frequent flushing of adults from nests by pedestrian traffic (Johnston 1995). The magnitude of the benefits of nesting centrally would vary as a function of nearest neighbor-distance, and would be constrained by associated costs, such as increased conspicuousness of clusters of nests to predators (Andersson and Wicklund 1978), and heightened aggressiveness of adults toward neighbors and their chicks (Baird 1983, Pius and Leberg 1997).

The pattern of enhanced nesting success at the center of a breeding colony does not hold for all colonially breeding species, including California Least Terns (Minsky 1987). No correlation between proximity to the center and reproductive success was found for Least Terns and other colonially nesting species that experience intense predation pressure (van Vessem and Draulans 1986, Berg et al. 1992), and Brunton (1997) found that centrally nesting Least Terns were actually less successful than edge nesters.

California Least Terns reportedly avoid nesting near patches of vegetation (Minsky 1987); vegetation cover at active Least Tern sites across the country is generally low, ranging from 0.2% to 18% (Faanes 1983, Gochfeld 1983, Minsky 1987). Removal by monitors of vegetation at many California breeding sites (including Venice Beach) is thus part of the site preparation protocol thought necessary for attracting Least Terns to those sites (Caffrey 1997). Minsky (1987) posits that the avoidance of vegetation by Least Terns might be caused by the potential for predators to find concealment there. He also reports that California Least Terns avoid nesting near the periphery of colonies, presumably because of the greater disturbance and consequent flushing of adults from nests (Johnston 1995), and the presumed higher potential for depredation (but see Brunton 1997).

California Least Terns begin arriving at the Venice Beach colony in early to late April of each year. Potential breeders continue to arrive for several weeks; nest initiation is thus a protracted phenomenon. The earliest arrivers presumably have the opportunity to choose the "best" nest sites, and thus might be expected to choose central positions. This would then force later-arriving breeders to the periphery. We examined choice of nest site position, as a function of nest initiation date, as well as several other criteria thought to influence nest site selection in colonially nesting species: the tendency to cluster nests within the available space, the tendency to avoid vegetation, and avoidance of colony "edge".

Methods

The site at Venice Beach is an approximately 1.3 hectare fenced enclosure on a public beach in Los Angeles County (see Figure 1, Chapter 1). Condominiums are located approximately 200 meters to the east of the colony and the Pacific Ocean lies 200 meters to the west. Public beach immediately surrounds the site on all sides (see Caffrey 1995 for details). Human disturbance during the breeding season is constant but relatively indirect. The colony is bounded by 8-foot cantilevered chain-link fence that discourages entry by most mammals and prevents Least Tern chicks from escaping to the outside of the colony. Vegetation consisted primarily of sea rocket (*Cakile maritime*).

During the 1996 breeding season at Venice Beach, data were collected on the spatial relationships of Least Tern nests to the geometric center of the colony, neighboring nests, patches of vegetation, and the boundary fence. For each nest, initiation date (date of first egg laid) and date of chick departure were recorded. The location of each nest and the spread of vegetation in the colony were mapped on a ¼-inch-to-one-meter grid. Nest initiation was recorded at least five days per week; vegetation maps were updated weekly. No vegetation was present at the beginning of the breeding season.

A GIS based digital map of the colony was created for each of 17 observation periods (Table 1) using ArcView GIS software. Map coverages included the perimeter fence, X-Y coordinates of all nests, and polygons of vegetation patches. Arcview software allowed for calculations of distances between nests, and from nests to geometric

center of colony, perimeter fence, and vegetation polygons. This software also allowed us to create "buffers" of defined distances from the fence and around each patch of vegetation; we quantified the number of new nests and percent of total nests established within these buffers.

Because Least Tern chicks leave their nest scrape soon after hatching, nest sites selected by early arrivers become available to breeders arriving at least 3 weeks later. As such, the data used to examine the relationship between nest initiation date and proximity to colony center included nests initiated until the first "vacancy" opened up (i.e., the first chicks departed; the end of the third week of nesting). Nest placement with respect to vegetation and perimeter fence was determined for all nests through all 10 weeks of nesting.

Nest placement with respect to colony center was tested by comparing the actual chronological sequence of nest placement to an iterated randomized sequence. Using software developed with Mike Palmer (Botany Department, Oklahoma State University), we performed 1000 iterations of the random nesting sequence; significance of differences between the observed and random sequences were determined via one-tailed t-tests.

The pattern of nest placement with respect to established nesting pairs was elucidated by comparing the observed mean distance to nearest neighbors with the expected mean distance (Clark and Evans 1954). The expected distance to the nearest

neighbor can be calculated very simply for a large population that has a random spatial pattern:

Eq. 1: r_A = Mean distance to nearest neighbor = $\dfrac{\Sigma r_i}{n}$

Eq. 2: ρ = Density of organisms = $\dfrac{\text{Number in study area}}{\text{Size of study area}}$

Eq. 3: r_E = Expected distance to nearest neighbor = $\dfrac{1}{2\sqrt{\rho}}$

The ratio of mean observed to mean expected distances is the Index of Aggregation (R), which was calculated for the new nests in each observation period; R = 0 indicates a clumped distribution, R = 1 indicates a random distribution, and R = 2 indicates even spacing.

The distribution of nests with respect to proximity to patches of vegetation was described for weeks 2 through 10 by calculating the percent of nests occurring within buffers at defined distances from vegetation. Percent vegetation cover of the colony at weeks 1 (minimum) and 10 (maximum) is provided to indicate the range of cover encountered by pairs during the active nesting season. The placement of nests with respect to colony edge (fence) was described similarly; we calculated the percent of nests occurring within buffers at increasing distances from the fence throughout the season.

Results

Once Least Terns began nesting at Venice Beach, the number of new nests increased quickly. By the end of week 3, 186 pairs of terns had begun breeding (Table 1); by the end of the 10-week breeding season, 359 pairs had attempted nesting. Figure 1

depicts actual nest locations, in chronological order, chosen by terns. The first pair to establish a nest chose a location 71.36 m from the center, near the southwest corner of the colony. Placement of the subsequent 185 nests was not statistically different from random with respect to geometric center over the 17 intervals analyzed (Fig. 2, and Table 2: $P=0.643$-0.994, $df=16$).

Beyond a minimum nearest-neighbor distance (1 m for this population in 1996), terns did not place their nests any closer to established conspecifics than would be expected by chance ($R= 0.821$-1.082; Table 3).

Digital colony maps, indicating new nest locations relative to vegetation patches, were created for weeks 2 through 10. The map created for week 2 is presented as an example (Fig. 3). Distances from nests to vegetation were calculated, and tallied for the season (Table 4). Percent colony vegetative cover ranged from 0% (week 1) to 0.852% (week 10). One nest was established in a patch, but few other terns chose to nest near vegetation; only 5% were within 2.5 m, and approximately 90% of pairs nested at least 4 m away. Similarly, terns appeared to avoid the colony edge when selecting nest sites; the minimum distance between any nest and the fence was 0.54 m, yet fewer than 5% of pairs nested within 6 m of the fence (Table 5).

Discussion

Although nest location within a colony may not always correlate with reproductive success (vanVessem and Draulans 1986, Berg et al. 1992, Brunton 1997),

there are well-established theoretical reasons why California Least Terns "should" respond to certain spatial cues when selecting a nest site. Survival and reproductive success are often directly related to an individual's spatial position in the colony, as a function of the number and position of immediate neighbors and an individual's relative distance to the group's periphery (Hamilton 1971). Thus, the central clustering of nests observed at many seabird colonies presumably reflects the cumulative effect of the attempts of individuals to position themselves in the center, where they would be surrounded by conspecifics and as far as possible from the periphery. For colonial nesters that experience intense predator pressure, nesting amidst clusters of conspecifics might reduce predation risk by enhancing early detection and deterrence of predators via mobbing (Burger 1981, Foster and Treherne 1981, Bertram 1980, Kenward 1978).

In this context, it was somewhat surprising that the terns at Venice Beach apparently selected nest sites independent of proximity to colony center or nearest-neighbors. It may be that other characteristics associated with the site's microhabitat are important to breeding pairs selecting nesting locations; nesting substrate size (Thompson and Slack 1982, Palacios and Mellink 1996) and type (Thompson and Slack 1982, Gochfeld 1983, Burger and Gochfeld 1990), the presence of landmarks (e.g. debris; Minsky 1987), and the relative elevation of the site (Burger and Gochfield 1990a) have all been shown to influence choice of nest locations in Least Terns.

Although tern chicks reportedly use low growing vegetation for cover from the elements and predators (Thompson et al. 1997), past studies on California Least Terns

have demonstrated that pairs avoid nesting near vegetation (Minsky 1987) and choose to nest at breeding sites characterized overall by only 0.2-5% vegetation cover (Minsky 1987). In 1996 at Venice Beach, only 4 nests were established within 0.5 m of vegetation (although one was established in the center of a patch), and 95% of pairs nested at least 2.5 meters from the closest vegetation. Although this result could be an artifact resulting from the very low percent vegetation cover (less than 1% at its maximum coverage), it more likely reflects avoidance of vegetation by nesting terns. This, too, was somewhat surprising, as the small, sparse patches of vegetation which developed at Venice Beach seemed unlikely to be able to effectively conceal terrestrial predators, but might have offered chicks cover from avian predators or thermal relief during hot periods.

Indirect human disturbance reportedly decreases the time that California Least Terns spend brooding their nests, relative to pairs nesting in undisturbed areas (Johnston 1995). Disturbance resulting in the flushing of adults from nests exposes eggs and chicks to the elements and predators (Burger 1982). At Venice Beach, beachgoers had access to the tern colony perimeter fence on all 4 sides, and despite the "please keep away" signs, walked close to and even set their belongings right against it. Ninety-five percent of tern nests were established 6 to 7 m from the fence, with 90% being at least 9 m away, indicating that pairs were selecting nest sites so as to minimize the potential for disturbance from outside the colony. A similar avoidance of edge was documented at this same site during the 1982-1984 breeding seasons (Minsky 1987).

For the endangered California Least Tern, an understanding of nest site selection criteria is vital for the appropriate design of areas to be protected in the future, and the maintenance and enhancement of existing sites. Terns at Venice Beach in 1996 appeared to be avoiding nesting near both the perimeter fence and existent vegetation. Protected breeding sites should thus continue to be cleared of vegetation prior to the tern's arrival, and fenced sites need to be large enough to allow pairs to establish nests at least several meters in from the colony boundary. Pairs of terns at Venice Beach did not cluster together, nor did they choose central positions, contrary to many of the findings for colonial seabirds. Possibly microhabitat variables, such as substrate characteristics, were important determinants for choice of nest location, yet the site as a whole seemed extremely homogeneous with respect to substrate. Rather, it may be that the small size of the Venice Beach site nullifies any predicted advantage otherwise accrued to individuals as a function of position within a colony.

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Table 1: A: Number and duration of observation periods during weeks 1 through 3 of the California Least Tern breeding season at Venice Beach. Time interval indicates number of days since previous observation period. Observation period 1 corresponds to 28 April 1996 (Julian date 121). B: Number of new nests established in weeks 4-10. Time interval, in days, set to approximately one week.

A:

Observation Period	Time Interval	# New Nests	Total # Nests
1	1	1	1
2	2	7	8
3	3	20	28
4	1	15	43
5	1	11	54
6	2	16	70
7	1	7	77
8	2	19	96
9	1	10	106
10	1	11	117
11	1	13	130
12	2	34	164
13	1	4	168
14	2	2	170
15	1	3	173
16	2	6	179
17	1	7	186

B:

Observation Period	Time Interval	# New Nests	Total # Nests
22	6	74	260
27	6	30	290
32	6	34	324
36	7	31	355
41	6	2	357
48	9	2	359

Table 2: Mean distances from nests (per observation period) to colony center and significance of differences from a random distribution. Observation period 1 corresponds to 28 April 1996 (Julian date 121).

Observation Period	# New Nests	Mean Distance to Center (m).	P
1	1	71.36	0.987
2	7	48.1	0.81
3	20	47.48	0.937
4	15	46.4	0.926
5	11	45.64	0.909
6	16	45.6	0.945
7	7	46.22	0.989
8	19	45.65	0.986
9	10	44.96	0.959
10	11	44.41	0.935
11	13	44.04	0.994
12	34	43.25	0.664
13	4	43.25	0.664
14	2	43.33	0.778
15	3	43.42	0.851
16	6	43.16	0.643
17	7	43.07	0.648

Table 3: Observed mean nearest-neighbor distances relative to expected mean nearest-neighbor distances. Z-scores are indicated. Observation period 1 corresponds to 28 April 1996 (Julian date 121).

Observation Period	Total # Nests	# New Nests	R	Z	Apparent Distribution
1	1	1			
2	8	7	1.08	-1.44	random
3	28	20	0.89	-1.11	random
4	43	15	0.82	2.44	toward clumped
5	54	11	0.87	-1.78	random
6	70	16	0.93	-1.13	random
7	77	7	0.89	-1.84	random
8	96	19	0.94	-1.15	random
9	106	10	0.95	-0.98	random
10	117	11	0.94	-1.31	random
11	130	13	0.94	-1.38	random
12	164	34	0.94	-1.39	random
13	168	4	0.93	-1.66	random
14	170	2	0.92	-1.88	random
15	173	3	0.931	-1.73	random
16	179	6	0.952	-1.22	random
17	186	7	0.942	-1.51	random

Table 4: Number of nests and percent of total nests established within defined distances to vegetation.

Buffer Size: Distance to Vegetation(m)	# New Nests Initiated within Buffer Distance	% of Total Nests (n=359)
0.0	1	0.279
0.5	4	1.11
1.0	5	1.39
1.5	9	2.51
2.0	13	3.62
2.5	18	5.01
3.0	28	7.80
3.5	35	9.75
4.0	39	10.86
4.5	46	12.81
5.0	54	15.04
> 5.0	305	84.96

Table 5: Number of nests and percent of total nests established within defined distances to colony perimeter fence.

Buffer Size: Distance to Fence (m)	# Nests Initiated within Buffer Distance	% of Total Nests (n=359)
0.5	0	
1.0	3	0.80
1.5	7	1.95
2.0	9	2.51
2.5	9	2.51
3.0	9	2.51
3.5	11	3.06
4.0	13	3.62
4.5	15	4.18
5.0	16	4.46
6.0	17	4.74
7.0	20	5.57
8.0	29	8.29
9.0	33	9.19
10.0	42	11.67

Figure 1. Sequence of California Least Tern nest establishment during the 1996 breeding season at Venice Beach.
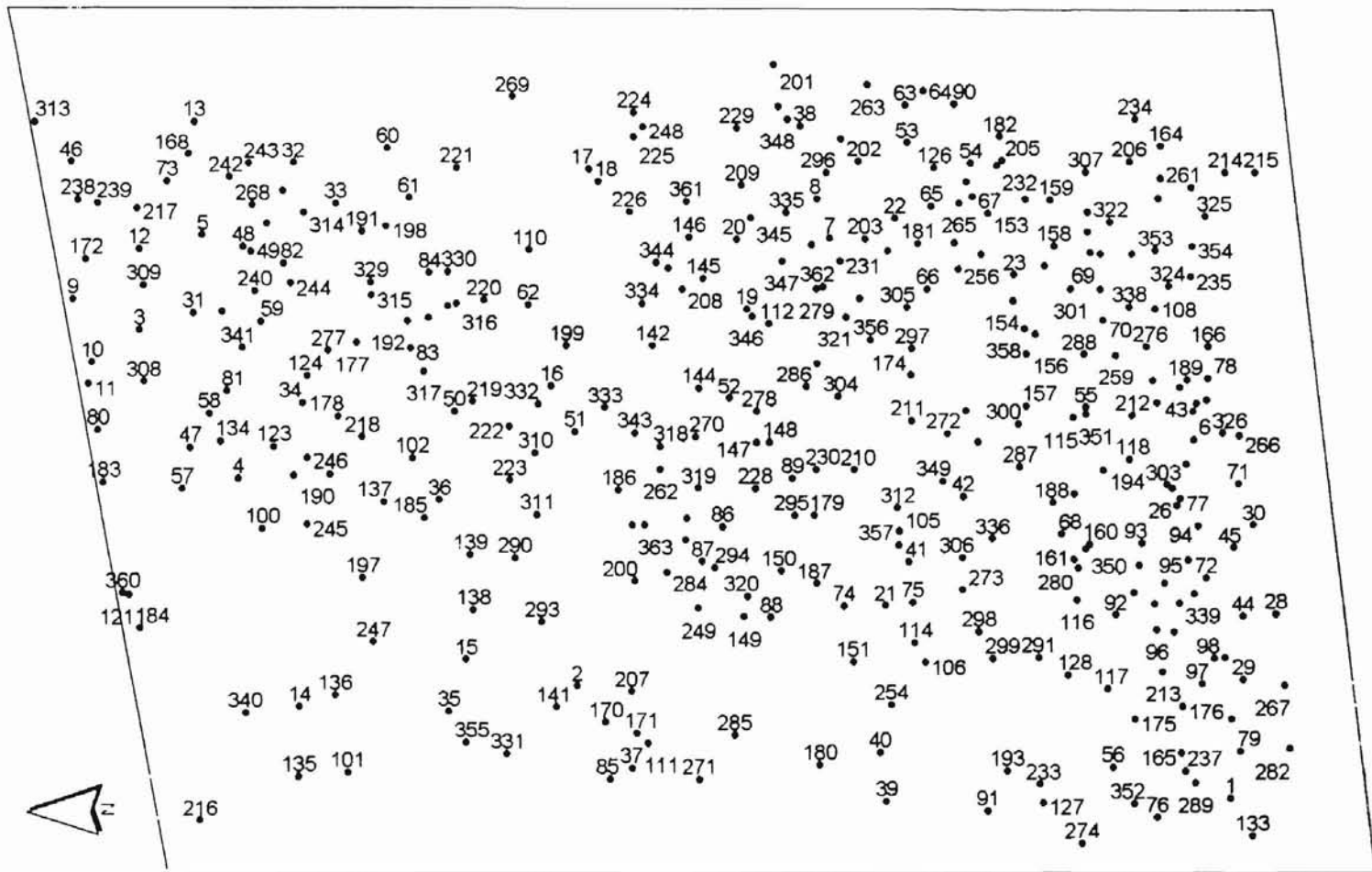
Figure 2. Observed (●) and random (■) sequences of California Least Tern nest establishment, relative to distance to colony center, during weeks 1 through 3 of the 1996 breeding season. 95% lower confidence limit of random sequence shown. The dashed line indicates the predicted distribution, if earlier arrivers are choosing central locations.
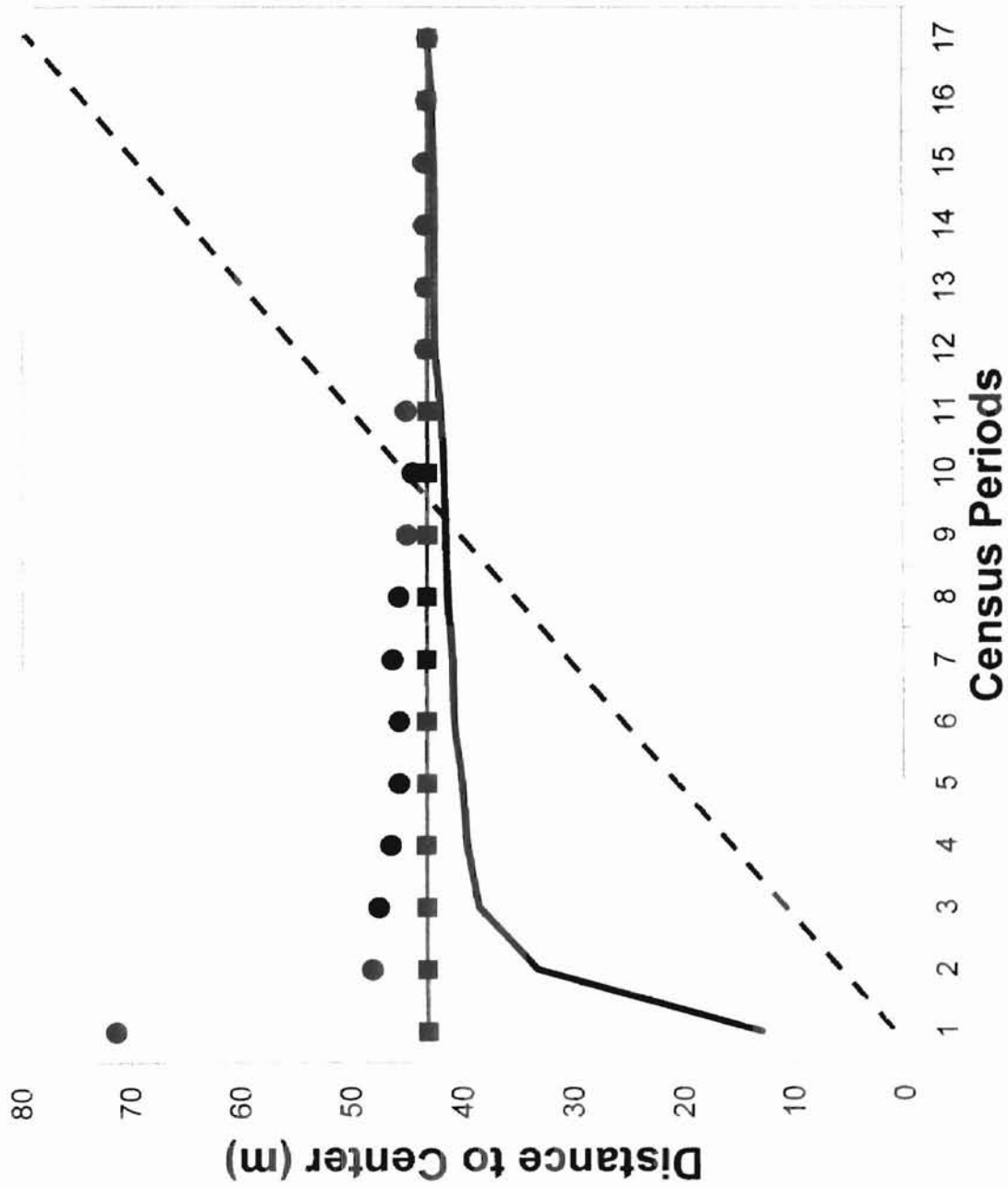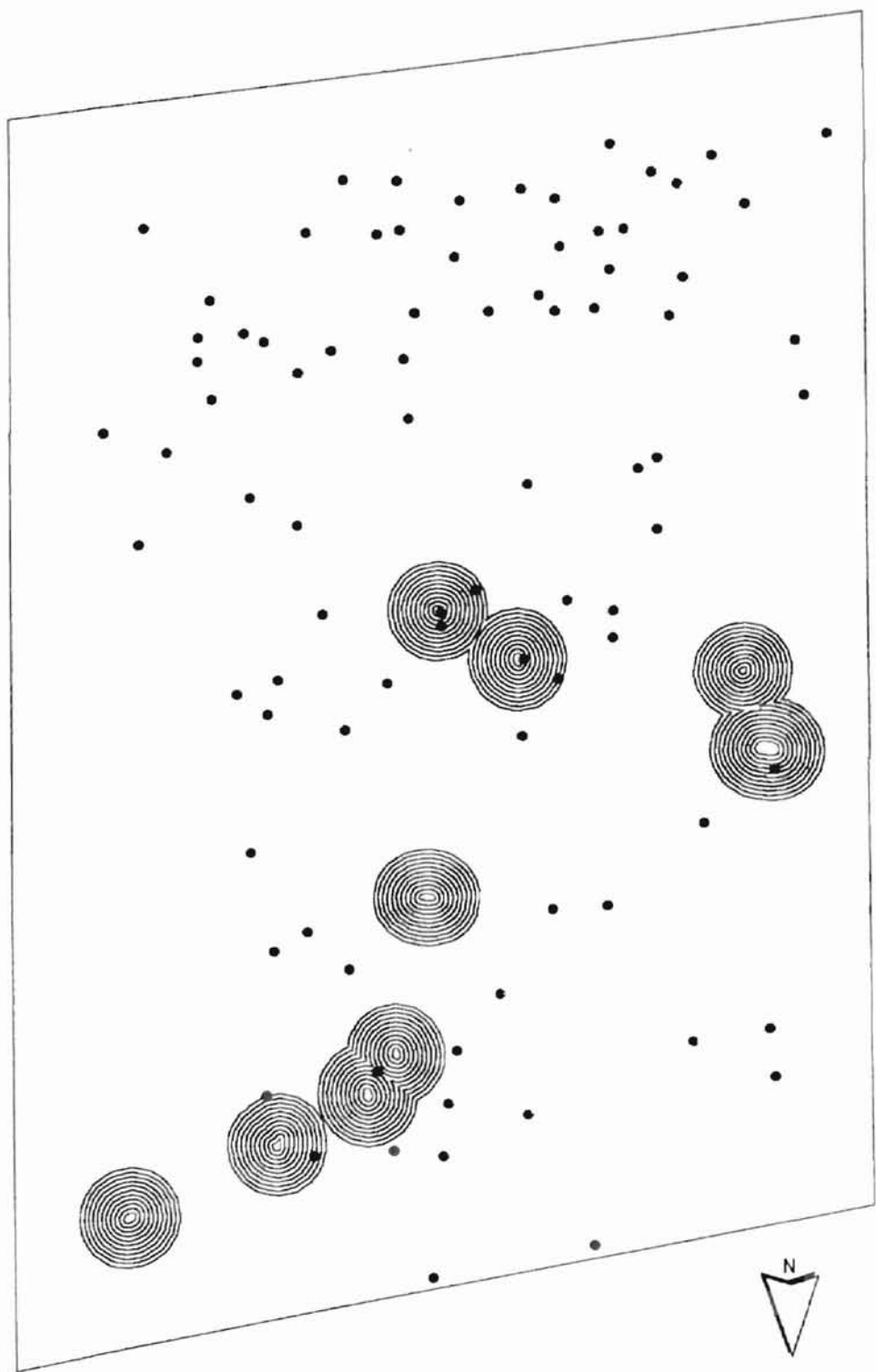
Distance to Center (m)

Census Periods

Figure 3. Locations of nests relative to vegetation, with incremental "buffers" of 0.5 m distances indicated, during week 2 of the 1996 breeding season. Similar maps were created for weeks 3 through 9.

VITA

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Master of Science

Thesis: ASPECTS OF CALIFORNIA LEAST TERN BREEDING BIOLOGY: CHICK
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