

IMPACTS OF PREDATORS: CENTER NESTS ARE LESS SUCCESSFUL THAN EDGE NESTS IN A LARGE NESTING COLONY OF LEAST TERNS¹

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Abstract. The spatial and temporal patterns of breeding success of Least Terns *Sterna antillarum* were studied within a large colony at Sandy Point, Connecticut, an ocean beach on the East Coast of North America. Contrary to the 'selfish herd' hypothesis, nests located in the center of the colony suffered from significantly higher levels of predation and had correspondingly lower hatching and fledging success than nests located at the edge (particularly during 1988). Breeding success dropped from 0.56 chicks per nesting attempt during 1987 to 0.08 chicks per nesting attempt during 1988, primarily due to increased predation by Black-crowned Night-Herons (*Nycticorax nycticorax*). Abandonment levels were proportionally equal for center and edge. Abandonment decreased slightly during 1988 when Black-crowned Night-Heron predation was most intense. Different patterns of predation were observed for the two major predators, Black-crowned Night-Herons and American Crows (*Corvus brachyrhynchos*). Predation by herons included chicks and eggs, began just prior to peak hatching, and was primarily in the center, whereas predation by crows was confined to eggs and was restricted to the edge of the colony. Results from this study suggest that the different impacts of these two predators may be due to the effectiveness of Least Tern antipredator behavior (viz. mobbing). Least Terns appeared not to mob predatory Black-crowned Night-Herons, but the extent of other antipredator behavior is unknown. The high concentration of Least Terns at the Sandy Point makes this colony particularly vulnerable to predators.

Key words: Least Terns, Black-crowned Night-Herons, colonial breeding, predation, selfish herd, nest and chick mortality.

INTRODUCTION

Reduced probability of predation among large breeding colonies is one major hypothesis explaining colonial nesting (Wittenberger and Hunt 1985, Brown and Brown 1987, Wiklund and Andersson 1994). Lower rates of nest predation potentially occur because of early detection of predators, effective deterrence of predators by group mobbing and defense, or predator swamping (Wittenberger and Hunt 1985). Furthermore, predator avoidance may be achieved through the "selfish herd" effect (Hamilton 1971). In a "selfish herd," an individual's survival is determined by the number of its immediate neighbors. Because peripheral nests only have neighbors on one side, the selfish-herd hypothesis predicts that individuals breeding at the edge of a colony should suffer higher losses due to predation than individuals breeding near the

center (Tenaza 1971, Hoogland and Sherman 1976). The main assumption of this hypothesis is that predators are equally likely to approach from any direction. For ground nesting birds, the assumption is that predators are restricted to terrestrial and aerial approaches and will attack whenever possible. There also is a further assumption that individuals compete for central positions. Hamilton's (1971) hypothesis does not assume that individuals show antipredator behavior towards predators (Hoogland and Sherman 1976). The "selfish herd" concept has been extended to predict the center as the optimal location for a nest within a colony (Tenaza 1971). Thus, predators should encounter peripheral nests first, and would be exposed to less severe mobbing on the periphery.

Breeding success may differ between center and edge nests (Coulson 1968, Balda and Bateman 1972, Brown and Brown 1987), but it is not always attributable to predation (Coulson 1968, Bunin and Boates 1994). Location differences may be confounded by factors such as slope, colony accessibility, food supply, nesting density, and quality of birds choosing to nest in

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these areas (Siegel-Causey and Hunt 1981, Fredrick and Collopy 1989, Bunin and Boates 1994). Several studies have failed to find a difference between center and edge (van Vessem and Draulans 1986, Berg et al. 1992).

In this study I investigated the influence of predation on the spatial and temporal patterns of breeding success within a large breeding colony of Least Terns (*Sterna antillarum*). Evidence is presented that predation may be highest in the center of colonies, suggesting that the "selfish herd" model may have restricted application.

METHODS

STUDY AREA

Least Terns nest primarily on sandy, ocean beaches on the East Coast and West Coast (*S. a. browni*) of North America. This study was conducted from April to August, 1987 and 1988, at the Sandy Point Least Tern colony, West Haven, Connecticut. This is one of the largest Least Tern colonies with approximately 500 pairs of birds. Least Terns have been nesting at Sandy Point in relatively large numbers for approximately 20 years (Sibley, pers. comm.). The colony is located on a sandspit approximately 1 km long and 200 m wide running parallel to Long Island Sound. The sandspit is bounded on one length by a sheltered tidal salt marsh area, and on the other side by ocean beach. The colony occupies the slightly raised central area of the sandspit and is oval shaped approximately 80 m wide and 200 m long following the shape of the sandspit.

A permanent, alphanumeric grid was established in the colony and consisted of 10×10 m quadrats, with a central marker (brick with the grid coordinates). This grid made it possible to record the presence and location of all nests. Each nest also was marked with a small wooden marker placed 0.5 m from the nest. Nest checks were made by observers entering the colony, and the contents of each nest were noted. Nest checks were conducted every 1 to 3 days before and after peak hatching and every 4 to 5 days during peak hatching (a 10-day period). Nest checks were done concurrently by 3 to 5 observers in different parts of the colony during the cooler parts of the day. The colony was disturbed for a maximum of 30 min. Observers within 2 to 5 m of an active nest were mobbed by the nesting pair. However, birds returned im-

mediately to their nests once the observer moved away. Nest progress was followed until the chicks hatched or the nest failed. Colony checks continued until the last chick had fledged from the colony.

Edge was defined as a band three nests wide around the perimeter of the colony (the maximum distance a fitted convex polygon penetrated into the colony). Edge was thus defined to reflect direct access to nests by predators. All other nests were in the center region. Nesting density was calculated by dividing the number of active nests by the surface area of the center or edge region. The density of nests in the two regions was measured over the course of the study.

The cause of nest failure was listed as predation based on observed predator attacks or evidence of predators at the nest site. Black-crowned Night-Heron (*Nycticorax nycticorax*) predation was deduced from clear tracks at the nest scrape and/or eggs found with large rectangular punctures. Further evidence of heron predation was collected by smoothing the sand around 20 randomly selected nests and identifying tracks the next day; all predated nests ($n = 11$) had heron tracks in and around them. Nests were considered abandoned when obviously unattended (e.g., slightly scattered, cold) or when nests were several days past the expected hatch date. The fertility of abandoned eggs was not assessed.

Hatching success equaled the number of eggs that hatched/total number of eggs laid (renesting was included). Chick fledging success equaled the proportion of chicks fledged/total number of eggs laid. All chicks found in the colony were banded with U.S. Fish and Wildlife metal bands, and weighed. Band numbers of recaptured chicks were recorded and again individuals were weighed. The number of fledged chicks was calculated by looking at the proportion of chicks to reach 14 days old. Average fledging age is 19 days (Brunton, unpubl. data). As all chicks were individually banded, it was possible to avoid counting the same chick twice. Specific causes of chick mortality could not always be assigned accurately.

Maximum Likelihood logistic analysis (ML) was used to test for differences in hatching and fledging success for regions and years. Mantel-Haenszel chi-squared approximation tests (Snedecor and Cochran 1989) were used to compare

TABLE 1. Hatching and fledging success, and causes of nest failure within regions of the colony during 1987 and 1988.

	1987			1988		
	Edge	Center	Total	Edge	Center	Total
Hatching success						
# Eggs hatched/nest						
\bar{x}	1.39	1.28	1.31	0.77	0.80	0.79
SD	0.08	0.07	0.08	0.08	0.07	0.07
Fledging success						
# Chicks hatched/nest						
\bar{x}	0.94	0.41	0.57	0.12	0.01	0.06
SD	0.08	0.09	0.08	0.07	0.09	0.08
95% CI*	0.85–0.95	0.37–0.45	0.55–0.57	0.09–0.17	0.00–0.02	0.04–0.08
(Total # chicks)	(136–152)	(142–174)	(298–310)	(21–42)	(1–9)	(24–49)
Causes of failure						
Hérons	1	46	47	75	204	279
(%)			(32.9)			(73.8)
Crows	7	0	7	39	2	41
(%)			(4.9)			(10.8)
Human	2	10	12	0	0	0
(%)			(8.4)			(0.0)
Tides	7	0	7	1	0	1
(%)			(4.9)			(0.3)
Abandoned	24	22	46	11	16	27
(%)			(32.2)			(7.1)
Unknown	5	19	24	13	17	30
(%)			(16.8)			(7.9)
Total failed nests	46	97	143	139	239	378
(% of each region)	(28.6)	(25.3)	(26.2)	(57.2)	(65.8)	(62.4)
Number of nests	161	384	545	243	363	606

* Confidence limits for proportions (Fisher and Yates 1963).

the temporal patterns of failures for center versus edge. Nesting densities of center and edge regions were compared using a Mann-Whitney *U*-test. The correlations of nesting density with percentage of nest failures for edge and center were tested using Spearman's rank correlation separately for each year.

RESULTS

HATCHING AND FLEDGING SUCCESS AND NEST LOCATION

A logistic model with "year" and "region within the colony" as main effects was analyzed separately for hatching and fledging success (Table 1). Fledging success was significantly lower in the center compared to the edge during both years (ML $\chi^2_1 = 45.8$, $P < 0.001$, Table 1). Hatching success did not differ between center and edge nests across years (ML $\chi^2_1 = 3.0$, $P > 0.08$, Table 1). Both hatching success and fledging success were significantly lower in 1988

compared with 1987 (hatching success ML $\chi^2_1 = 164.04$, $P < 0.001$; fledging success ML $\chi^2_1 = 126.7$, $P < 0.001$, Table 1). The 95% confidence intervals for the total number of Least Tern chicks fledged at Sandy Point was substantially greater in 1987 (298 to 310) than in 1988 (24 to 49).

THE CAUSES OF NEST FAILURE

The total number of nesting attempts at the Sandy Point colony increased slightly from 1987 (545) to 1988 (606). The major difference between years was in fledging: 62.4% of all nesting attempts failed in 1988, whereas only 26.2% failed in 1987 ($\chi^2_1 = 125.0$, $P < 0.01$, Table 1). The identifiable causes of nest failure are shown in Table 1. The number of failures due to Black-crowned Night-Heron predation increased substantially from 33% in 1987 to 74% in 1988, whereas nest failure due American Crow (*Corvus brachyrhynchos*) predation increased from

5% in 1987 to 11% in 1988. Low numbers of nests were lost during both years due to humans (no losses were directly attributable to observers), tides and unknown factors. Mammal tracks were never sighted within the colony boundaries.

BLACK-CROWNED NIGHT-HERON PREDATION AND NEST LOCATION

Black-crowned Night-Heron predation was the major cause of nest failure for center and edge nests during 1988 (85.4% and 54.0%, respectively, Table 1) and for center nests during 1987 (47.4%, Table 1). Abandonment was the major cause of failure for edge nests during 1987 (24/41, Table 1). Crow predation almost always occurred in the edge region (7/7 in 1987 and 39/41 in 1988, Table 1).

The first sign of Black-crowned Night-Herons during both years was the appearance of tracks in the center of the colony. Because of the impact of Black-crowned Night-Herons during 1987, five evening and night-time observations of the colony were conducted from 17 June to 14 July during 1988. Black-crowned Night-Herons were never observed in or near the colony during daylight hours. Although Black-crowned Night-Herons arrived singly at the colony, the median number of herons observed together in the colony between 20:00 and 22:00 was 3 (range 0 to 4). They always landed in the center of the colony, and we never observed them approaching from the edge, or outside the perimeter of the colony. The length of time spent in the colony was unknown. Reactions to Black-crowned Night-Herons by Least Terns were difficult to assess; despite general confusion (flying and calling by Least Terns), no overt mobbing of Black-crowned Night-Herons was observed.

THE CAUSES OF CHICK MORTALITY

Causes of chick mortality were difficult to determine once chicks reached a week old and left the immediate region of the nest. The major cause of mortality appeared to be Black-crowned Night-Heron predation as tracks were present at 100% of the nests where banded chicks less than one week old had disappeared (27 nests in 1987, 119 nests in 1988). Chicks older than one week moved to the salt marsh area adjacent to the colony where long grasses presumably provided shelter.

TEMPORAL PATTERNS OF NEST FAILURE

The relationship between the number of nest failures and the number of active nests for edge and center was analyzed separately for the two years. During 1987 there was no significant difference between center and edge in the frequencies of failed nests (Mantel-Haenszel $\chi^2_1 = 2.4$, $P > 0.10$, Fig. 1a and 1c). There was a large difference in the temporal patterns of failures between center and edge during 1988 (Mantel-Haenszel $\chi^2_1 = 33.5$, $P < 0.01$, Fig. 1b and 1d). Edge nests showed two peaks of nest losses, one early as nests were being established and the second late in the season. Center nests also showed two peaks of nest losses, one just after hatching commenced (approximately 6 June) and the second late in the season (Fig. 2b and 2d). Center and edge nesting phenology were slightly different with edge nests continuing to be laid later in the season in both years (Fig. 1). Both areas showed a peak in activity in early June, however this peak was higher for the center region (Fig. 1c and 1d).

A significantly different age structure was observed in birds nesting in the center compared with the edge ($\chi^2_2 = 23.3$, $P < 0.01$). Age information was available from 183 center and 100 edge nesting birds recaptured over the two years. Two and three year olds comprised 81% and 15%, respectively, of edge nesting adults, whereas they comprised 52% and 39%, respectively, of center nesting adults. Terns known to be four years or older comprised 9% of center nesting adults and 1% of edge nesting adults.

Temporal patterns of nest failure due to the two major predators, Black-crowned Night-Herons and crows, were examined separately for edge and center for each year (Fig. 2). Crow predation peaked soon after nest laying (20 May), whereas Black-crowned Night-Heron predation always occurred later (Fig. 2). Two peaks were observed in the number of Black-crowned Night-Heron attacks for both center and edge nests during 1988 (Fig. 2b and 2d) and for center nests during 1987 (Fig. 2c). The first peak occurred after chick hatching commenced, and the second in mid-July when all remaining active nests failed.

There were no significant differences between years in nesting densities for the two regions (edge: Mann-Whitney $U = 5$; center: $U = 8$, n_1

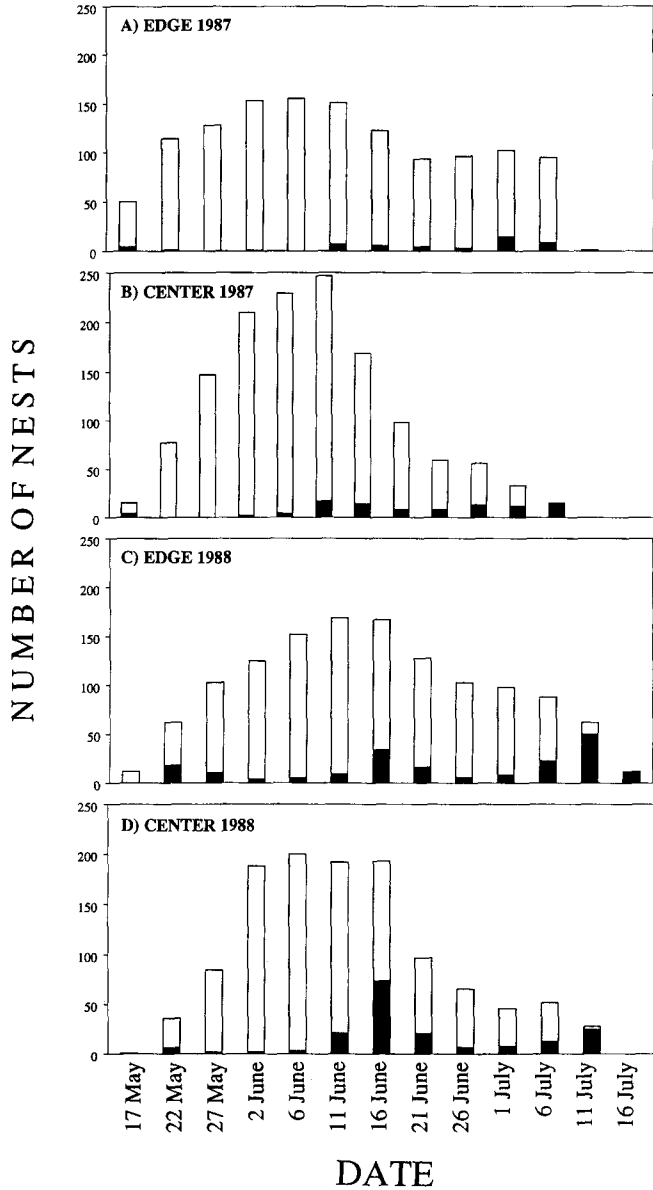


FIGURE 1. The relationship between the number of active nests (open bars) and failed nests (solid bars) in consecutive 5-day intervals throughout the breeding season. Data are shown separately for the edge region: (a) 1987 and (c) 1988, and the center region: (b) 1987 and (d) 1988.

= 12, $n_2 = 12$ in both cases). However, there was a significantly lower nesting density in the edge region compared to the center for both years (1987: Mann-Whitney $U = 52$; 1988: $U = 65$, $n_1 = 12$, $n_2 = 12$ in both years, $P < 0.01$). Edge nests maintained a stable density throughout the nesting season, which may in part be due to the definition of edge. Center region densities

peaked in early June during both years with slightly higher densities observed during 1988. There was no significant correlation between nesting densities and the proportion of nests that failed for either edge or center areas (edge: $r = -0.31$, $P > 0.10$; center: $r = 0.25$, $P > 0.60$), suggesting that other effects such as predation may be more important.

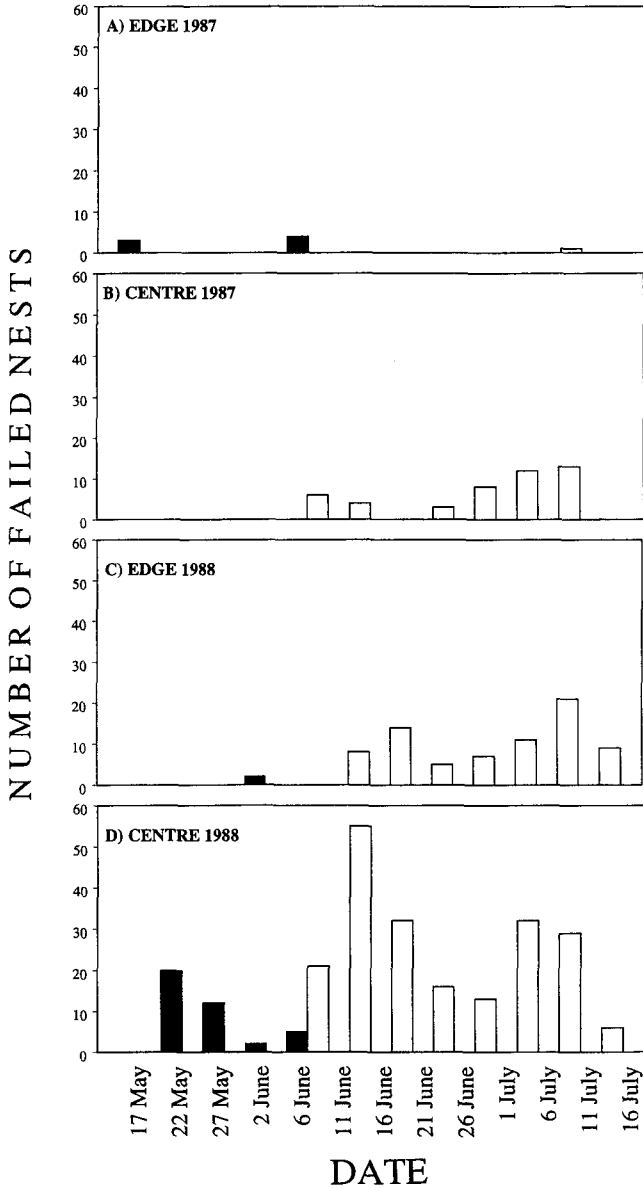


FIGURE 2. The number of nest failures caused by American Crows (solid bars) and Black-crowned Night-Herons (open bars) during consecutive 5-day intervals over the breeding season. Data are shown separately for the edge region: (a) 1987 and (c) 1988, and the center region: (b) 1987 and (d) 1988.

DISCUSSION

CENTER VERSUS EDGE: THE IMPACTS OF BLACK-CROWNED NIGHT-HERONS AND AMERICAN CROWS

The major cause of nest loss and chick mortality at Sandy Point during the two years of this study was predation by Black-crowned Night-Herons and crows. Black-crowned Night-Heron

predation was most intense in the central region of the colony and coincided with the beginning of chick hatching and continued until all the eggs had either failed or hatched. Crow predation was limited to edge nests and occurred early in the nesting season. Mammalian predation was notably absent. The second major cause of nest failure for Least Terns was aban-

donment. Among colonial sea/water birds, reported levels of abandonment vary enormously from 7% in Common Terns, *Sterna hirundo* (Nisbet and Welton 1984) to 31% in Ciconiiformes (Frederick and Collopy 1989). High levels of nest abandonment may be due to fluctuations in food availability because central and edge regions had similar proportions of abandoned nests.

It is widely assumed that edge or fringe nesters should have a lower breeding success compared to center nesters (Wittenburger and Hunt 1985). Several authors have reported that edge or fringe nesters show higher levels of failure than more central nesters and that the center advantage increases as colony size increases (Kruuk 1968, Brown and Brown 1987, Spear 1993). Furthermore, several studies have shown preferences by males for establishing territories within the center of colonies (Kittiwake, *Rissa tridactyla*, Coulson 1968; Least Terns, Burger 1988). In the present study birds nesting in the center were older and commenced nesting slightly earlier. However, my study not only fails to support the hypothesis that edge nesters suffer higher levels of predation, but demonstrates that the highest levels of predation occur in the center, giving edge nesters the highest reproductive success. This is because Black-crowned Night-Herons are able to fly into the center of the colony undeterred by Least Terns. The "selfish herd" hypothesis predicts aggregative behavior because edge individuals are at higher risk. Thus, individuals in the densest parts of the aggregation should be safest. The "selfish herd" hypothesis does not assume active antipredator behavior by the individuals in the group. My findings lead to the conclusion that the "selfish herd" hypothesis has limited application. It may only apply when predators are restricted to approach from the edge due to the type of predator, such as mammalian predators, the effectiveness of the antipredator behavior by the prey species, or the physical characteristics of the nesting site, e.g., cliffs and vertical nesting sites, and shape of the colony.

The relationship between the numbers of active nests in the colony and the patterns of predation depended on the type of predator. Black-crowned Night-Herons appear to be attracted to the areas of highest Least Tern nesting activity. This idea is supported by the observation of greater levels of Black-crowned Night-Heron

predation in the central region where nest density was higher. Further, the timing of first attack on the Sandy Point colony by Black-crowned Night-Herons coincided with peak nest density in the center during both years. Hamilton (1971) recognized that although animals in groups reduce the risk of predation per individual, the overall level of predation on the group may increase as predators learn to exploit rich food sources. Clode (1993) hypothesized that at some point, the risk of predation for an individual in a group was greater than for a solitary individual. However, Wittenburger and Hunt (1985) suggest that as a general rule, the proportion of nests lost to predators will decrease with increasing colony size once the colony is large enough to "swamp" all local predators. Goransson et al. (1975) suggested that predators learn to avoid areas where nests are more difficult to find in preference for areas where nests are easier to find. Black-crowned Night-Herons are known chick predators of many colonial sea and wading birds (White Ibises *Eudocimus albus*, Frederick and Collopy 1989; Common Terns, Nisbet and Welton 1984). For precocial or semi-precocial species, chicks are at their most vulnerable to predators just after hatching (Brunton 1990); it is during this period that predation by Black-crowned Night-Herons was most intense. Finally, Black-crowned Night-Herons have only been observed to feed in Least Tern colonies larger than 50 pairs (Collins 1970, Brunton, unpubl. data).

A different pattern of predation was observed for crows. Crow predation occurred early in the nesting period when numbers of active nests are low and was restricted to the edges of the colony. The reduced impact of crows later in the season is most likely the result of increasing nesting activity and thus higher levels of nest defense by Least Terns. Increasing levels of nest defense during the breeding season against crows has been observed in Common and Arctic Terns, *Sterna paradisaea* (Lemmetyinen 1971) and Black-Headed Gulls, *Larus ridibundus* (Kruuk 1964). Northwestern Crows, *Corvus caurinus*, have been shown to avoid areas of highest nesting density in colonies of Double-crested Cormorants, *Phalacrocorax auritus* and Pelagic Cormorants, *P. pelagicus* (Siegel-Causey and Hunt, 1981).

The different impacts of these two predators may be due to the effectiveness of Least Tern

antipredator behavior (viz. mobbing). Black-crowned Night-Herons are nocturnal predators, and although Least Terns did leave their nests during heron visits to the colony, mobbing was not observed. Nisbet and Welton (1984) described nocturnal desertion for 6.5 to 8 hours by Common Terns when subject to predation by Great Horned Owls (*Bubo virginianus*). Southern et al. (1982) also describe a lack of antipredator behavior toward nocturnal predators by breeding gulls. Similar lack of response seems likely for Least Terns towards Black-crowned Night-Herons as these predators are large enough to pose a threat to adult Least Terns. Conversely, crow predation is diurnal and Least Terns are effective at mobbing and deterring crows from the colony. Crows were never observed to fly into the colony, the usual approach was to walk into the colony from the perimeter. Mammalian predators were never observed within the colony at Sandy Point during the period of this study. Predation by rats, domestic cats and dogs is common at other smaller East Coast Least Tern colonies (Burger 1984, Brunton, unpubl. data). The most likely explanations for low levels of mammalian predation at Sandy Point may be the physical location with approximately 80% of the colony surrounded by water, and the urban nature of the surrounding environment. Frederick and Collopy (1989) suggested that mammalian predation is lower for many colonial waterbirds that nest in locations surrounded by water.

CONSERVATION OF LEAST TERNS: THE POTENTIAL IMPACT OF HERONS

Least Tern preference for sandy ocean beaches brings them into conflict with people, both directly from human-induced nest losses, and less directly from use of these beaches by people and hence loss of suitable habitat. Protective measures in the form of sign-posting and removing vehicle access have been in place at Sandy Point since 1985. The Connecticut coastline has a very small amount of suitable tern nesting habitat with only a small fraction of it protected for wildlife (Brunton 1988). Burger (1984) suggested that loss of habitat appears to cause a decrease in the number of Least Tern colonies but an increase in colony size. This seems a likely explanation for the high concentration of terns at the Sandy Point colony. Sandy Point is the largest Least Tern colony in Connecticut, with

over half of Connecticut's nesting pairs. Burger (1984) predicted that this trend towards large, stable colonies is potentially detrimental to the overall productivity of this species if large colonies suffer heavy losses due to flooding or predators. Large colonies may be more vulnerable to predation because they are more stable and act as a concentration of prey which attracts predators. This appears to have happened at the Sandy Point Least Tern colony, where during 1988 the colony failed, with less than 0.08 chicks fledging per pair because of intense predation by Black-crowned Night-Herons.

The Black-crowned Night-Heron population has been steadily increasing over the last 20 years (Sibley, unpubl. data) as the result of active conservation and management strategies by the Connecticut Audubon Society, Nature Conservancy, and the Department of Wildlife. Black-crowned Night-Herons also nest in colonies and may travel considerable distances to forage (Frederick and Collopy 1989). Two Black-crowned Night-Heron colonies of 400 and 100 pairs are located within 50 km of Sandy Point on Chimon Island and Fishers Island (Sibley, unpubl. data). Thus, the longer term impact of Black-crowned Night-Heron predation on the Least Tern population in Connecticut is likely to be negative. Although data were limited to a few nighttime observations, the number of Black-crowned Night-Herons foraging in the Least Tern colony may be as low as four. Increasing numbers of Black-crowned Night-Herons and human-induced reductions in marsh and wetlands habitat typically used by foraging herons are likely to increase the level of this heron-tern interaction. Protective measures aimed at deterring herons should be undertaken at large and stable Least Tern colonies such as Sandy Point.

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