"OPTIMAL" COLONY SIZE FOR LEAST TERNS: AN INTER-COLONY STUDY OF OPPOSING SELECTIVE PRESSURES BY PREDATORS[1]

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Abstract. I compared breeding success and causes of nesting failure for Least Terns *Sterna antillarum* nesting in 11 colonies ranging from 2 to 606 nests in Connecticut, USA. Although the percentage of nests lost due to predation decreased with increasing colony size, the relationship between colony size and the impact of predators varied with the type of predator. A significant positive correlation was observed between colony size and nest loss due to Black-crowned Night-Herons (*Nycticorax nycticorax*). In contrast, a significant negative correlation was observed between colony size and nest loss due to small mammals, Herring Gulls (*Larus argentatus*), and American Crows (*Corvus brachyrhnchos*). Thus, colonies of approximately 150 nests appear to be large enough for low impacts by small mammals, gulls, and crows, but small enough to be relatively unattractive to Black-crowned Night-Herons. Nest losses and chick mortality were significantly higher during 1988, mainly the result of increased levels of Black-crowned Night-Heron predation on large colonies. Overall, both hatching and fledging success of Least Terns did not increase with increasing colony size, although all colonies with fewer than 10 nests failed completely. Hatching and fledging success did not correlate with increasing nesting synchrony or increasing nest density during either year. However, nesting synchrony showed a significant negative correlation with both hatching success during both years and fledging success during 1988. Thus, less synchronous colonies showed a tendency to be more successful.

Key words: Black-crowned Night-Heron, breeding success, colonial breeding, Least Terns, nesting density, nesting synchrony, predation.

INTRODUCTION

The role of colonial breeding as a selective advantage against predation varies among species. Colonial nesting has been shown to be an advantage in avoiding predators for Bank Swallows *Riparia riparia* (Hoogland and Sherman 1976), Cliff Swallows *Hirundo pyrrhonota* (Brown and Brown 1987), Herring Gulls *Larus argentatus* (Hunt et al. 1986), and Great Black-backed Gulls *L. marinus* (Butler and Trivelpiece 1981). Lower rates of nest predation in larger colonies occur due to one or more of the following: early detection of predators, effective deterrence of predators by group mobbing and defense, swamping predators by synchronizing breeding activities thereby making it difficult for predators to use a superabundant food resource (Wittenberger and Hunt 1985), and because the colony acts as a 'selfish herd' in which peripheral nesters have high predation rates (Coulson 1968, Brown and Brown 1987, Brunton 1997).

Studies examining the antipredator selective advantages of colonial breeding have concentrated on comparing overall levels of nest predation of different sized colonies (Hunt et al. 1986, Brown and Brown 1987). Comparisons of the level of predation by different species of predators on a colony are seldom made (van Vessem and Draulans 1986). The effect each species of predator is likely to have on a colony depends on the size of the predator in relation to the defending species or risk, and the method of approach by the predator (Kruuk 1964, Gochfeld 1984, Brunton 1990, 1997). It is expected that different predator species pose different risks, respond differently to antipredator behavior and thereby have different impacts. Furthermore, not only is the impact of a species of predator likely to vary with colony size but the range of potential predators may also vary with colony size. Hence, the relationship between predation and breeding dispersion is not clear. Danchin and Wagner (1997) suggest that, in selecting a breeding colony, individuals may be assessing

the reproductive success of conspecifics and thereby optimizing their own reproductive success. This assessment is a major component of commodity selection.

Brown et al. (1990) suggest four patterns for the relationship between individual breeding success and colony size: increasing, decreasing, constant, or a peak at intermediate colony sizes. Support for highest success at intermediate colony sizes is rare (Wiklund and Andersson 1980), possibly because few studies have good data on a large range of colony sizes. Currently, the two most common patterns are an increase in breeding success with colony size (Birkhead 1977, Burger and Gochfeld 1990, Brown and Brown 1996) or no relationship (Hoogland and Sherman 1976).

In this study I investigated the breeding success of Least Terns (Sterna antillarum) and the impacts of different species of predators on 11 Least Tern colonies ranging from 2 to more than 606 nests. More than 2,000 nests were followed over two breeding seasons. At each colony I examined the causes and temporal patterns of nest failures, hatching and fledging success, and nesting synchrony and density. There were two major aims of this study. First, quantify, using a logistic regression model, the relationship between colony size and the varying impacts of different predators. Second, describe the relationships between measures of breeding success, such as hatching and fledging success, and both colony size and nesting synchrony.

METHODS

STUDY AREA

Least Terns nest on sandy, ocean beaches on the east and west coasts of North America with smaller numbers nesting on sandy river habitats in the interior. Least Terns vary in colony site tenacity with annual turnover rates varying from 15 to 25% (Burger 1984, Visser and Peterson 1994). This study was carried out from April to August, 1987 and 1988, at 11 colonies located along approximately 80 km of the Connecticut coastline. The colonies varied in size from two nests at Hammonassett Beach to 606 nests at Sandy Point colony. All colonies (with the exception of Menunketesuck Island) had similar site characteristics: sandy ocean beaches with adjacent sheltered, tidal salt marsh areas. Menunketesuck was the only colony located on a small island cut off from the mainland at high tide.

All colonies had one or more observers from sunrise to sunset everyday for the entire nesting phase. Nest checks inside colony boundaries were carried out at least once every 3 days prior to hatching, once every 5 days during the 10 days of peak chick hatching, and then again at least once every 3 days until all chicks had fledged. Larger colonies (Sandy Point, Long Beach, Griswald Point, and Milford Beach) were visited more frequently. All chicks found in the colonies were banded with U.S. Fish and Wildlife metal bands, weighed and measured.

Within each colony, all nests were marked and mapped. For larger colonies, permanent, alphanumeric grids were established prior to the arrival of the birds. These grids made it possible to record, map, and accurately follow the progress of all nests.

Failed nests were assigned to a cause of failure based on either actual observation of predator attacks on the colony or by evidence left at the nest site. Causes of failure could only be accurately assigned during the nest phase which included incubation and the first 5 days after hatching. After this time chicks are mobile and moved to whatever cover was available (Brunton 1997). Black-crowned Night-Herons (Nycticorax nycticorax) and small mammals were attributed as predators when clear tracks were found at the nest scrape and/or depredated eggs showed characteristic punctures (Brunton 1997). The majority of crow and gull attacks on nests were observed directly.

Maximum nesting density was calculated by dividing the maximum number of active nests by the surface area of the colony at that time. Mean date of first egg laying and the standard deviation of the mean and modal of first-egg laying (an estimate of synchrony; Burger 1979) were determined for all colonies except Menunketesuck Island.

Two measures of breeding success were recorded for each colony for both years: hatching success and fledging success. Hatching success was the number of eggs hatched per nest. The number of chicks reaching fledging was more difficult to measure and was calculated by dividing the number of chicks fledged by the total number of eggs laid. Because all chicks were individually banded, it was possible to avoid counting the same chick twice.

TABLE 1. Causes of Least Tern nest losses at all colonies in Connecticut during 1987 and 1988.

Colony	Year	Number of nests	Herons	Crows	Small mammals	Humans	Tides	Aban-don-ment	Unknown	Total failed nests/colony (%)
Sandy Point	1987	545	47	7	0	12	7	46	24	143 (26.2)
	1988	606	279	41	0	0	1	27	30	378 (62.4)
Pleasure Beach	1987	no terns								
	1988	230	107	0	52	0	0	12	13	184 (80.0)
Menunketesuck Is.	1987[a]	194	0	0	0	0	0	6	94	100 (51.6)
	1988	107	22	0	0	0	5	8	13	48 (44.9)
Long Beach	1987	193	15	0	34	1	6	15	34	107 (55.4)
	1988	41	10	0	1	0	1	7	7	30 (73.2)
Short Beach	1987	no terns								
	1988	71	4	0	5	0	0	9	3	21 (29.6)
Milford Point	1987	52	0	0	27	0	0	0	8	35 (67.3)
	1988	21	0	0	14	0	0	1	0	15 (71.4)
Griswald Point	1987	31	0	0	10	0	0	1	5	16 (51.6)
	1988	42	0	0	39	0	0	2	1	42 (100)
Hatchetts Point	1987	8	0	0	1	0	0	1	0	2 (25.0)
	1988	no terns								
Pilots Point	1987	4	0	4	0	0	0	0	0	4 (100)
	1988	4	0	4	0	0	0	0	0	4 (100)
Hammonassett	1987	2	0	2	0	0	0	0	0	2 (100)
	1988	no terns								
Total	1987	1,029	62	13	72	13	13	69	165	407 (39.6)
	1988	1,122	422	45	111	0	7	66	67	718 (64.0)

[a] Colony not discovered until at least one week after first egg laying date.

STATISTICAL ANALYSES

Results from the two years were pooled where appropriate. The correlations of colony size and hatching success, fledging success, and percentage of nest losses due to herons or small mammals and crows were all tested using Pearson's correlation coefficient. Data were logarithmically transformed to correct for non-normality where appropriate. Logistic regression was used to quantify the relationships between nest losses and colony size by the various types of predators (SAS 1990). Chi-squared tests were used to examine the proportions of nests lost for different levels of synchrony (SD of first-egg laying). Residuals were checked for normality for all parametric tests. A significance level of $P < 0.05$ (two-tailed) was used for all statistical tests.

RESULTS

THE CAUSES OF NESTING FAILURE

It was possible to assign causes of nest failure in the majority of cases at all colonies (Table 1). Over all colonies and both years, 52% of all nests failed (1,125/2,151 nests). The major causes of nest failure for Least Terns were predation by either Black-crowned Night-Herons (43%, 484/1,125 nests) and small mammals (16%). Ameri-can Crows and Herring Gulls accounted for 5% of nest failures, whereas humans and high tides were responsible for <3%. Nest abandonment for all colonies was less than 12%. The number of nests lost to unknown causes was less than 15% for all colonies except Menunketesuck Island. Menunketesuck Island was discovered late in the 1987 breeding season and the rocky substrate made identification by tracks difficult. Levels of overall predation were significantly higher during 1988, with 64% of all nests failing compared to 39% during 1987 ($\chi^2_5 = 129$, $P < 0.01$). This increase in nest failure was primarily due to increased heron predation at the largest colony (Sandy Point). The predominant small mammal predator was the domestic cat (*Felis domestica*). Cats and cat tracks were observed near all colonies throughout the nesting seasons. However, cat tracks were never sighted within the Sandy Point colony boundaries (Brunton 1997). Cats were the main cause of failure at Long Beach (1987), Milford Point (1987, 1988), and Griswald Point (1987, 1988) colonies (Table 1).

PREDATOR TYPE AND THEIR IMPACTS ON COLONIES OF DIFFERENT SIZES

Two categories of predators were identified based on their method of approach (Brunton
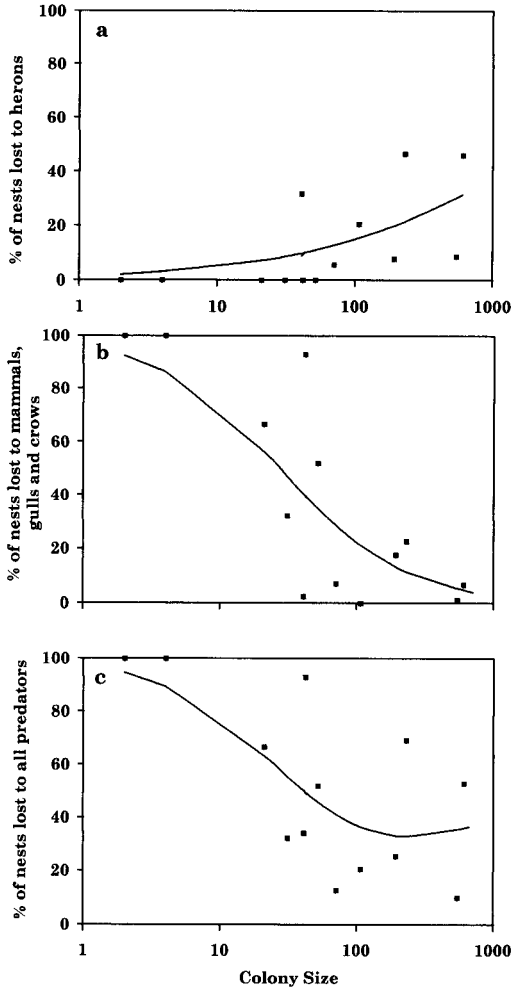
FIGURE 1. The relationships between colony size and nest losses due to (a) herons, (b) mammals, gulls, and crows, and (c) total losses due to predators. Both years combined.

1997). The first were predators that made aerial approaches directly into the center of the colony. These were Black-crowned Night-Herons which are predators of both eggs and chicks (Brunton 1997) and are strictly nocturnal. The second category of predators approached the colony from the periphery and included small mammals, gulls, and crows. Gulls and crows are diurnal predators, whereas small mammals tend to be nocturnal. The relationship between colony size and level of predation was different for these two predator groups (Fig. 1). Heron predation was most intense for the largest colonies and only occurred in colonies with more than 40

nests. A significant positive correlation was observed between the percentage of nest losses due to Black-crowned Night-Herons and colony size ($r = 0.64$, $P = 0.01$, Fig. 1a). In contrast, a significant negative correlation was observed between the percentage of nest losses due to small mammals, crows, and gulls, and colony size ($r = -0.83$, $P = 0.001$, Fig. 1b). Small colonies appeared to be vulnerable to predation by these predators, whereas large colonies were more vulnerable to predation by herons.

Logistic regression analyses were used to model the relationship between predation by each of the predator groups and the size of the colony. Examination of these two opposing selective pressures (increasing losses due to herons and decreasing losses due to gulls, crows, and small mammals with colony size) lead to the development of a general additive logistic model of the relationship between colony size and predation (Fig. 1c). "Optimal" colony size is predicted from the predation model to be approximately 150 nests (Fig. 1c). Overall, the percentage of nests lost to predation decreased with increasing colony size for colonies less than 150 nests. Increasing heron impact resulted in a greater proportion of nests lost for colonies larger than 150 nests.

VARIATION IN BREEDING SUCCESS, BREEDING SYNCHRONY, AND NESTING DENSITY WITH COLONY SIZE

Hatching success did not increase with increasing colony size (Figs. 2a, b). However, a significant correlation was found between hatching success and colony size during 1987 ($r = 0.88$, $P < 0.05$) but not during 1988 ($r = 0.46$, $P = 0.3$). No significant correlation was found between fledging success and colony size during 1987 ($r = 0.69$, $P = 0.2$) or 1988 ($r = 0.15$, $P = 0.7$).

Examination of first egg-laying dates shows a skewed distribution for large colonies with an early high peak in egg laying. Colonies with fewer than 200 nests showed either an even distribution or a double peaked distribution. Mean egg laying dates varied considerably among colonies (Fig. 2c). Colonies larger than 150 nests had mean egg laying dates prior to May 31, whereas for colonies with fewer than 150 nests mean egg laying dates varied from May 23 to June 16. The standard deviation of first egg laying dates was used to compare the nesting syn-
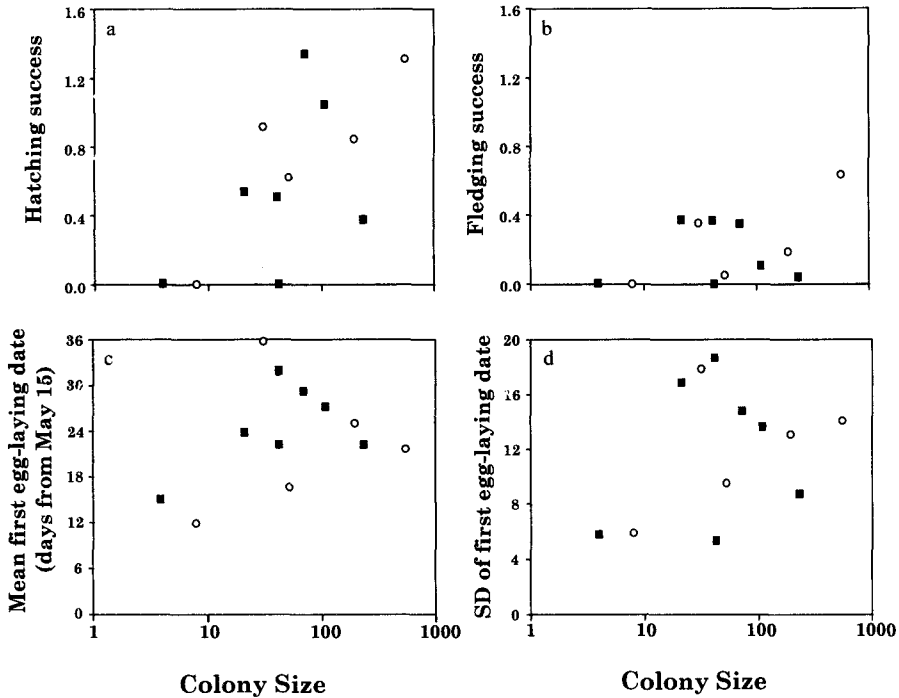
FIGURE 2.   The relationship between colony size and (a) hatching success (number of eggs hatched/total eggs laid), (b) fledging success (number of chicks fledged/total eggs laid), (c) mean first egg-laying date (number of days from 15 May), and (d) nesting synchrony (SD of the first egg-laying date). 1987 (open circles), 1988 (closed squares).

chrony of colonies (Burger 1979). The standard deviations of first egg laying dates (Fig. 2d) did not correlate significantly with colony size (1987, $r = 0.48$, $P = 0.4$; 1988, $r = 0.26$, $P = 0.5$). Thus, smaller colonies were not detectably more synchronous in nest initiation than larger colonies. However, synchrony as measured by standard deviation did show a significant correlation (Fig. 3) with both hatching success during 1987 ($r = 0.81$, $P < 0.05$) and 1988 ($r = 0.65$, $P < 0.05$) and fledging success during 1988 ($r = 0.84$, $P < 0.01$). Thus, less synchronous colonies (larger standard deviation) showed a tendency to be more successful.

The proportion of nests lost to the two categories of predators varied with a nest's degree of within-colony synchrony (herons: $\chi^2_5 = 74.8$, $P < 0.001$; crows and small mammals: $\chi^2_6 = 223.5$, $P < 0.001$, Fig. 4). The early asynchronous classes showed the highest proportion of losses to crows and small mammals, whereas the later asynchronous classes showed the highest proportion of losses to herons.

Maximum nesting density among colonies varied from 0.9 to 16.5 nests 100-m^{-2}. No significant correlation was found between the maximum nesting density and either hatching success ($r = 0.46$, $P = 0.2$) or fledging success ($r = 0.04$, $P = 0.9$). The Menunketesuck Island colony showed the highest maximum nesting density of 16.5 nests 100-m^{-2} in 1987. This colony was unusual because the terns were nesting on a rocky substrate on a tidal island where space was extremely limited.

DISCUSSION

"OPTIMAL" COLONY SIZE: OPPOSING PREDATOR PRESSURES

Empirical evidence from Least Terns supports the idea of an "optimal" peak in reproductive success at intermediate colony sizes. Brown and Brown (1996) suggest that, although few good data exist with an adequate range of colony sizes (>6), highest success of intermediate colony sizes may occur in only a few species. Evidence of such an optimal peak implies maximizing reproductive success under specific constraints (Pulliam and Caraco 1984). For Least Terns these
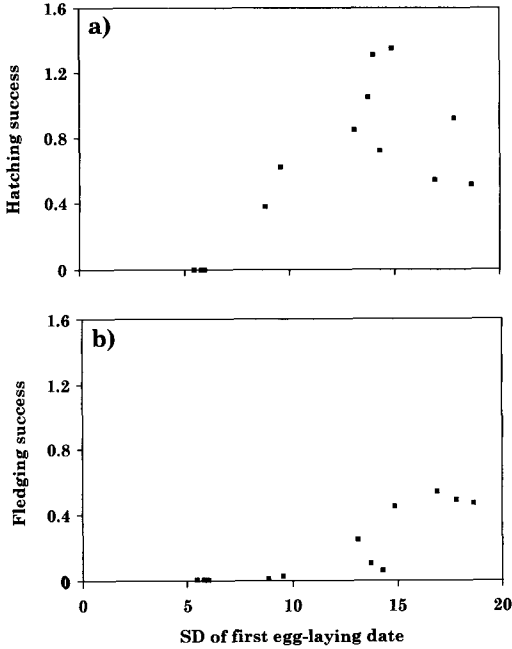
FIGURE 3.   The relationship between colony nesting synchrony (SD of first egg-laying date) and (a) hatching success (number of eggs hatched/total eggs laid) and (b) fledging success (number of chicks fledged/total eggs laid). Both years combined.

The impact of each group of predators varies with colony size. Levels of predation by small mammals, gulls, and crows decreased as colony size increased and was negligible for colonies larger than 500 nests; these predators appear to be deterred from colonies larger than 100 nests (Jackson and Key 1992). By contrast, herons appear to be attracted to colonies with more than 40 nests, and the percentage of nests lost due to herons increases with colony size. Previous studies have shown that antipredator defense is seldom directed towards herons either because of their large size (length 71 cm, wingspan 107 cm compared to Least Terns, length 23 cm, wingspan 51 cm) or their nocturnal approach (Nisbet and Welton 1984, Frederick and Collopy 1989, Brunton 1997). Herons appear to switch from their usual food resources to make use of the abundance of food in the large tern colonies (Collins 1970). Black-crowned Night-Herons are also colonial nesting birds and their gregarious feeding habits mean that more that one heron is likely to be feeding in a colony simultaneously.

Although the proportion of nests lost declined with colony size, fledging success did not significantly increase with colony size. Least Terns nesting in large colonies have a reproductive advantage up until the chicks leave the nest scrape at around 5 days old. However, predation continues well after this stage. Frederick and Collopy (1989) found that predation by Black-crowned Night-Herons on Common Tern (*Ster-*

constraints appear to be primarily due to predators. "Optimal" colony size is predicted from the predation model to be approximately 150 nests.
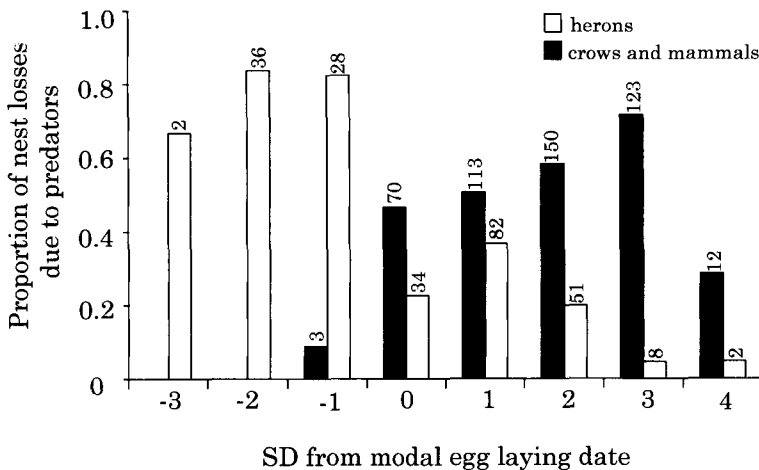

FIGURE 4.   A comparison of the proportion of nests lost to the different types of predators with different degrees of within-colony egg laying synchrony (standard deviations from modal laying date). Total nests of each class (sample size) are shown above bars. Data from all colonies were combined.

na hirundo) nestlings was generally limited to chicks less than 1 week old. Given that Least Tern chicks are at least one-third smaller than Common Terns, heron predation of tern chicks is likely to continue until the chicks are at least 2 weeks old. Although chick predation was difficult to quantify, presumably these high losses are a result of continued heron predation. Colonies with fewer than 10 nests failed completely due to a single predator.

The estimates of nest predation from tracks/egg damage probably underestimates nest failure due to predation. Abandonment of nests also may be linked to predation, particularly by herons. Peak levels of abandonment coincided with peak levels of predation by herons at Sandy Point during both years. However, high levels of abandonment also may be related to fluctuations in food availability (Frederick and Collopy 1990).

Hunt et al. (1986) found that reproductive performance in five species of seabirds was lower at colonies that supported large populations. They suggested that chicks from larger colonies had higher postfledging mortality. Birkhead and Furness (1985) suggest this negative relationship may be the result of intraspecific food competition near colonies. For Least Terns, predation rather than chick starvation or abandonment was the primary cause of nest failure, which suggests that food may not be limiting for Least Terns on the Connecticut coast.

BREEDING SYNCHRONY AND PREDATOR SWAMPING

Many hypotheses concerning the advantages of colonial nesting predict an increase in breeding success with increased breeding synchrony. These include social foraging (Emlen and Demong 1975), selfish herd, increased predator detection and deterrence, and predator swamping. Data from this study address the predator swamping hypothesis. Predator swamping was first suggested to be the result of increased breeding synchrony by Darling (1938); since then, numerous studies have addressed this question (see Wittenberger and Hunt 1985 for a review). Evidence both for and against this hypothesis has been found (Emlen and Demong 1975, Burger 1979, 1988). Evidence from my study of Least Terns does not support the predator swamping hypothesis. Indeed, the trend across the colonies was for breeding success to

decrease with synchrony. The major assumptions of the swamping hypothesis are that the maximum number of predators in an area is fixed and these predators take a relatively constant biomass of prey throughout the breeding season (Burger 1979). Thus, relative predation rates should be lowest during the peak activity level of the nesting cycle because more chicks and eggs are available. Many predators are opportunistic foragers and may switch to food sources that are locally abundant (Brunton 1997). Furthermore, predators such as herons and gulls are colonial nesters themselves and, if the time of chick hatching for these species coincides with tern hatching, there will be a large corresponding increase in prey taken (Yorio and Quintana 1997). The overlap should be most marked in higher latitudes which have short breeding seasons (Young 1994). The result is an increase in predation rate due to both food switching and greater food requirements by predators. Hence, the relative biomass taken by a predator is not constant and will be, to some degree, density-dependent.

IMPLICATIONS FOR CONSERVATION MANAGEMENT

Clearly the impacts of the different predators on different colony sizes has major implications for management of Least Terns. In areas where Black-crowned Night-Herons are abundant, smaller Least Tern colonies should be more productive than larger colonies. Conversely, where heron populations are low or absent, larger Least Tern colonies will be most productive. The Connecticut coastline has been highly modified by humans. Increases in "pest" species such as domestic cats, rats (*Rattus* sp.), raccoons (*Procyon lotor*), crows, and gulls have increased predation pressure on ground nesting species such as Least Terns. Physical modifications and human use of beaches during the tern breeding period has reduced the available nesting habitat for terns and other species such as Piping Plovers (*Charadrius melodus*). Historically, Least Tern colonies have been ephemeral and small (<50 nests) (Burger 1984). My results indicate that the overall productivity of this species in Connecticut will depend not only on the distribution of suitable habitat but on the composition of the predator community. Of particular importance is the abundance and distribution of the Black-crowned Night-Herons. Given that the trend for

large, stable Least Tern colonies continues (Burger 1984), the impact of Black-crowned Night-Herons is likely to be negative.

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