J. Field Ornithol., 59(2):135–142

CORRELATES OF NEST-DEFENSE BEHAVIOR OF COMMON TERNS

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Abstract.—Nest-defense behavior was studied at seven Common Tern (*Sterna hirundo*) colonies in southern coastal New Jersey during June and July 1981. Data were collected weekly on numbers of adults, nests, eggs, and young in relation to the frequency and intensity of dive attacks on a human intruder by nesting terns. I explored the relationships between attack behavior and colony size/density, seasonality, and brood survival. The results provide little support for social facilitation since neither colony size (range 30–250 nests) nor density was related to mean attack frequency; however, in larger colonies, fewer birds participated in dive attacks. Although the intensity of attacks was strongly seasonal, patterns were very different among colonies and peak attack rates did not always coincide with peak hatching periods. Defense levels declined late in the season in most colonies regardless of whether brood survival was high or low. Colonies with individuals that attacked early in the season had higher overall nesting success than in colonies where individuals showed little early-season aggression.

CORRELACIONES EN LA DEFENZA DEL NIDO POR PARTE DE *STERNA HIRUNDO*

Resumen.—El comportamiento de defensa del nido fue estudiado en siete colonias de palometa común (*Sterna hirundo*) en la costa sur de Nueva Jersey durante junio y julio de 1981. Se coleccionaron datos semanalmente sobre el número de adultos, nidos, camada de huevos, y juveniles en relación a la frecuencia e intensidad de los ataques en picada hechos por las palometas a un intruso humano. Los resultados brindan poco apoyo a la facilitación social ya que ni el tamaño de la colonia (alcance 30–250 nidos) ni la densidad de nidos están relacionados al promedio de vuelos en picada/minuto; aunque, en colonias más grandes, menos aves participaron en vuelos de picada. A pesar de que la intensidad de ataques fue marcadamente estacional, los patrones fueron muy diferentes entre colonias y los picos de la tasa de ataques no siempre coincidieron con el pico del periodo de eclosionamiento. Los niveles de defensa declinaron tarde en la temporada en la mayor parte de las colonias indistintamente de si la supervivencia de los juveniles fuera alta o baja. Colonias con individuos que atacaban temprano en la temporada tuvieron un éxito de anidamiento más alto que en colonias donde los individuos mostraron poca agresión a comienzos de la temporada.

Parental defense of eggs and nestlings by ground-nesting birds, particularly members of the Laridae, has attracted considerable attention (Becker 1984, Burger 1981, Cullen 1960, Erwin 1979, Kruuk 1964, Lemmetyinen 1971, Simmons 1962, Veen 1977). Most questions have focused on proximate factors underlying defensive behavior, which is costly in terms of risk, time, and energy (Biermann and Robertson 1983). In colonially nesting species, correlations between the frequency and intensity of dive attacks by nesting birds and various parameters, such as colony size and density and phenology, have often been made (see above references). However, recent sociobiological approaches have recast questions of parental behavior within the framework of parental investment (Trivers 1972), i.e., relating behavior to "ultimate" factors such as offspring survival as one measure of fitness (Biermann and Robertson 1981, 1983). In this paper, nest-defense behavior of Common Terns (*Sterna hirundo*) in seven New Jersey colonies is described with respect to colony size and density, seasonal effects, and brood survival.

A priori, several relationships were expected concerning levels of nest-defense aggression: (1) The attack rate, both absolute and relative to the numbers of participants, should be related to the size and/or density of colonies (social facilitation *sensu* Darling 1938). (2) A seasonal pattern of defense behavior resembling a bell-shaped curve should be shown. Although the results vary among species (see below), the majority of studies of terns and other larids suggests that aggression increases through incubation, peaks at or after hatching, and tapers off late in the season.

METHODS

Seven Common Tern colonies in Atlantic and Ocean Counties, New Jersey were visited weekly from the period of egg-laying in late May 1981 until the young fledged in July. Weekly visits were believed to be too infrequent to cause habituation to human intrusion (H. Hays, I. C. T. Nisbet, pers. comm.). The Holgate colony was a barrier beach-dune colony, while the others were located on small (<100 ha) marsh islands in estuarine bays. Colonies were repeatedly censused and either a sample (Holgate and Obes, Table 1) of nests, or all active nests found, were marked with wooden stakes (see Table 1). As part of a related study, clutch sizes were recorded on each visit, and 30-cm high poultry wire enclosures ($n = 3–7$; 10–20 m^2 area) were constructed around groups of nests in different parts of the colony to facilitate monitoring of young until fledging (≥22 d of age) (see Erwin 1979, Erwin and Smith 1985, Nisbet and Drury 1972). Enclosure location was as close to "random" as practical, as long as edge was avoided. There is no evidence that enclosures affect predator access or predation rates. The wire was too low to exclude either avian or mammalian predators.

Colony site histories were incomplete, but as far as could be determined, all colonies had been occupied at least once between 1977 and 1980, therefore none were new colonies (Erwin and Korschgen 1979, G. Inman, pers. comm.). All colonies were virtually free of human disturbance and the Holgate colony was posted and monitored from a distance of >100 m by full-time wardens to insure protection. No evidence of mammals was found in any of the colonies during the study. In three years of work, no other people were seen near any colony during the nesting season.

Adjacent to three enclosures, an observation point was chosen from which to record data on tern defense. Observation points were spaced at least 15 m apart to maximize the likelihood of data independence (tern defense around the nest drops sharply beyond 5 m [Kruuk 1964, Veen 1977]). To preclude a center/edge bias (Coulson 1968, Spurr 1974), all points were located in the interior of each colony. The locations of all active nests within 5 m of each observation point were marked and nest survival was monitored. On five (five colonies) or six (two colonies) weekly visits from early June through early July, a field assistant stood next to each observation point for a 1-min period while I remained at least 25 m from the colony perimeter recording data. Data recording began 30-s after the assistant arrived at the point. On standardized forms, I recorded the maximum number of birds in a column of airspace with a 10-m radius centered above the observation point, the number of dives directed at the assistant, and whether the bird struck the assistant. The order in which points were visited was changed each time. Nest checks were made each visit to confirm the presence and identity (band number) of eggs or young for the enclosed nests. The entire procedure required only about 10 min on each visit.

Distances between adjacent nests within enclosures were measured as an index of colony density. Hatching dates were calculated in each colony using only nests within enclosures. Because of the infrequent visit schedule, hatching dates of first chicks were not always recorded directly, but had to be extrapolated using estimated ages of chicks (Nisbet and Drury 1972). This method is probably accurate to within 2 d, at least for the first 14 d.

To reduce the variance due to daily weather effects on behavior, I attempted to visit all colonies on the same day. Time of day could not always be standardized due to the intensive work schedule, however the majority of visits occurred between 1030 h and 1600 h EDT. No visits were made during rain or strong winds.

RESULTS

Social stimulation.—Colony size was significantly correlated with the mean number of birds overhead ($r = 0.97$, $t = 9.52$, df = 6, $P < 0.01$), but not with either the mean number of dives/min (absolute) or mean number of dives/min/bird overhead ($r = 0.64$, $t = 1.86$, df = 6, $P > 0.10$; $r = -0.19$, $t = -0.42$, df = 6, $P > 0.5$, respectively). Colony density (reciprocal of nearest-neighbor distances) was not significantly correlated with any of the above three behavioral measures ($P > 0.20$ for all). Thus, there is little evidence that either the size of the colony or proximity of neighbors influences the frequency or intensity of attack; however, relatively few birds were involved in attacks in the larger colonies.

Seasonal patterns.—Seasonal patterns of attack indicate that for only three of the seven colonies did peak defense levels correspond with the median hatching date or the visit immediately following it (Table 1, Fig. 1). For three colonies, Parker, Obes, and Holgate, dive attacks began at the first visit, while for Wading Thoro, Boomerang, and Goodluck, no attacks occurred during the first two visits. By the last visit, levels of defense had declined at all colonies except Obes. Direct contact was made by diving terns only at Parker Island. No contacts were made during the first three visits, three were made on visit four (two birds), and increased to six hits (three birds) on the final visit.

Seasonal differences in attack rates were not correlated with differential brood survival among colonies. At Parker Island, where 90% of the nests

TABLE 1. Characteristics of seven Common Tern colonies in southern New Jersey, 1981.

Colony[a]	Nearest neighbor distance (cm)[b]	Visit no.[c]	No. active nests[d]	No. birds overhead[e] (N_1)	No. dives[f] (N_2)	N_2/N_1
Parker	245 ± 25	1	10	12	39	3.3
(28)		2	10	18	67	3.7
		3	10	22	160	7.3
		4	10	17	143	8.4
		5	9	11	16	1.5
			Mean	16.0	85.0	
Main marsh	183 ± 20	1	6	4	0	0
(33)		2	5	12	123	10.3
		3	5	19	99	5.2
		4	5	21	64	3.0
		5	5	12	35	2.9
			Mean	13.6	64.2	
Boomerang	166 ± 20	1	10	12	0	0
(45)		2	10	7	0	0
		3	9	17	57	3.4
		4	7	23	40	1.7
		5	5	11	16	1.5
			Mean	14.0	22.6	
Obes	160 ± 18	1	21	11	2	0.2
(70)		2	21	8	12	1.5
		3	21	19	51	2.7
		4	20	14	7	0.5
		5	18	20	17	0.9
			Mean	14.4	17.8	
Holgate	164 ± 18	1	6	39	27	0.7
(250)		2	6	55	66	1.2
		3	6	45	179	1.9
		4	5	60	139	2.3
		5	5	87	145	1.7
			Mean	67.2	111.2	
Goodluck	233 ± 25	1	11	3	0	0
(38)		2	9	12	0	0
		3	9	15	0	0
		4	8	33	20	0.6
		5	8	21	39	1.9
		6	7	30	45	1.5
			Mean	19.0	17.3	
Wading Thoro	359 ± 22	1	8	7	0	0
(30)		2	8	6	0	0
		3	8	6	0	0
		4	8	12	18	1.5
		5	7	6	9	1.5
		6	4	4	0	0
			Mean	6.8	4.5	

[a] Total number of active nests (as of May 30) in parentheses.

survived between visits three and five, 79% and 88% declines were found in dive rate per bird and per nest, respectively (Table 1). In contrast, at Boomerang, where only 56% of the nests survived the same time period, more modest declines of 56% and 49% for the two dive rates occurred. At the Goodluck colony, dive rates *increased* during nest attrition, with the highest (absolute) attack rate on the last visit when fewest active nests were present.

DISCUSSION

A strong temporal component in parental defense was noted in all seven colonies, however, the patterns differed substantially among colonies. Two colonies (Main Marsh, Obes) had peak attack rates before the median hatching period, while one (Goodluck) had much higher levels 1.5–2.5 wk after median hatching. These results differed from earlier studies of terns. Fuchs (1977), for instance, found that attack rates of Common Terns declined during the 2 wk before hatching, but he gave no data on attack levels during the chick phase. He also reported for Sandwich Terns (*Sterna sandvicensis*) that attack rates increased during the week following first hatching, then declined. Veen (1977) found a peak in defense at hatching for Sandwich Terns. Ryden (1970) reported an increase in Common Tern defense "after hatching," while Lemmetyinen (1971) and Becker (1984) reported that attack rates of Common Terns increased throughout the breeding season. They were highest right after chick hatching and remained high (or increased [Becker 1984]) throughout the chick stage. Erwin (1979) found no strong seasonal component to intraspecific aggression in Common Terns, although aggression was somewhat higher during the chick phase.

I expected that part of the variation in defense among colonies might be due to defense levels of birds in colonies with many surviving broods being higher than for birds in colonies where most nests failed. One expects stronger parental investment (i.e., more defense) where expectation for future "pay-offs" (offspring) is greater (Biermann and Robertson 1981, 1983). My results did not conform to this simple prediction. Obviously factors other than brood survival must influence defense levels. Although I have no data on average age/experience of individuals in the different colonies, average clutch sizes were significantly different among colonies (Erwin and Smith 1985). Mean clutch sizes may reflect average

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[b] Mean ± 1 SE based on all nests marked on initial visits (column 2), except Holgate ($n = 25$) and Obes ($n = 46$).

[c] Visit schedule 1 = June 2–3; 2 = June 9–10; 3 = June 16; 4 = June 23; 5 = June 30; 6 = July 7.

[d] Number of active nests within 5 m of the three observation points in the colony.

[e] Based on maximum number of birds at each point during 1-min periods; three points combined.

[f] Based on totals for 1-min periods at three observation points.

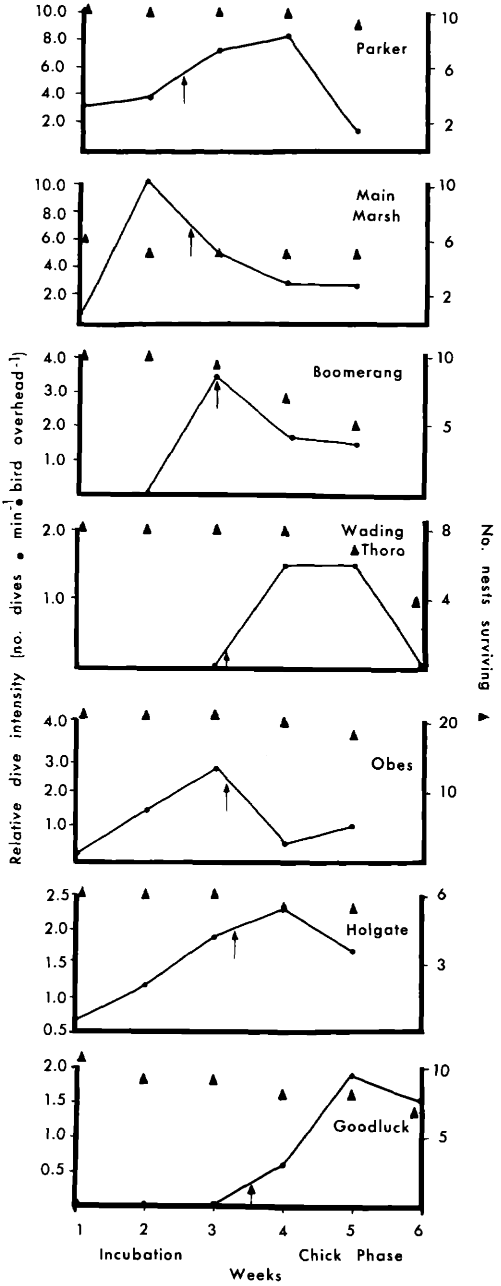

FIGURE 1. Seasonal changes in relative dive-attack intensity and nest survival in seven Common Tern colonies in New Jersey, 1981. Arrows indicate median hatching dates of first chicks in the brood.

age differences of individuals among colonies (Ryder 1980). However, tests relating mean clutch size to per-capita dive attack rate were not significant ($r = 0.38$, df = 6, $P > 0.4$).

It is noteworthy that birds in the two colonies with the largest overall colony success (Holgate = 1.41 young/nest; Parker = 1.36 young/nest [Erwin and Smith 1985]) defended their nests with dive attacks even during the first visit. A comparison of reproductive success in colonies where dive attacks occurred on every visit (Parker, Holgate, and Obes with 1.02 young/nest) with colonies where no attacks occurred during the first two visits (Goodluck = 1.00 young/nest; Wading = 0.54; Boomerang = 0.64) showed a significant difference (Mann-Whitney $U = 0$, $n = 6$, $P < 0.05$). Thus, aggressive behavior of birds early in the season may indicate the level of parental care (Nisbet 1973), which may influence subsequent nesting success.

That colony size did correlate with the numbers of birds overhead, but not with either attack rate, indicates little support for any "Darling Effect" via social facilitation. Nonetheless, the relative decline in numbers of birds attacking in larger colonies represents one advantage of living in colonies (Hooglund and Sherman 1976, Kruuk 1964). Thus there may be an energetic (and safety) advantage for individuals in relatively larger colonies.

ACKNOWLEDGMENTS

I thank M. Agricola and H. Obrecht for field assistance and their bravery under attack, B. Dowell for statistical and graphics support, and M. Kreamer and J. Armstrong for typing. Gaylord Inman, former manager of Forsythe (Brigantine) National Wildlife Refuge kindly permitted studies on two refuge colonies. Comments on earlier drafts were provided by E. H. Burtt Jr., S. Derrickson, M. Howe, and anonymous reviewers.

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Received 4 Mar. 1987; accepted 5 Sep. 1987.