



Nesting Stage and Nest Defense by Common Terns

Author(s): Brian G. Palestis

Source: Waterbirds, 28(1):87-94. 2005.

Published By: The Waterbird Society

DOI: [http://dx.doi.org/10.1675/1524-4695\(2005\)028\[0087:NSANDB\]2.0.CO;2](http://dx.doi.org/10.1675/1524-4695(2005)028[0087:NSANDB]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1675/1524-4695%282005%29028%5B0087%3ANSANDB%5D2.0.CO%3B2>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Nesting Stage and Nest Defense by Common Terns

BRIAN G. PALESTIS

Department of Biological Sciences, Wagner College, Staten Island, New York 10301, USA
Internet: bpalesti@wagner.edu

Abstract.—Several hypotheses predict that nest defense should increase as the nesting cycle progresses, but the predicted pattern of increase differs. Previous studies of nest defense in gulls and terns have given conflicting results. Most of these have treated colonies as a unit, thus breeding asynchrony may have obscured temporal patterns. Common Tern (*Sterna hirundo*) nest defense against Great Black-backed Gulls (*Larus marinus*) was observed during two years, and responses of individuals or pairs of known nesting stage were recorded. Responses of terns to observers were also recorded. Mobbing of gulls did not increase as incubation progressed, contradicting parental investment models, but did increase as chicks aged. Chicks were defended more strongly by parents than were eggs. Responses to Great Black-backed Gulls were more frequent during the second wave of nesting, when the potential for re-nesting would be very low. There was no association between clutch size and nest defense. Aggression by terns to observers was rare during incubation, but became common immediately after hatching and remained frequent until the chicks fledged. The temporal pattern of mobbing in the semi-precocial Common Tern most closely resembles that predicted for species with altricial young. However, interpretation is complicated by the fact that gulls prey more frequently on chicks than eggs. *Received 25 July 2004, accepted 30 August 2004.*

Key words.—Antipredator behavior, breeding phenology, mobbing, parental care, *Sterna hirundo*, Common Tern.

Waterbirds 28(1): 87–94, 2005

Birds are highly flexible in their responses to predators, as interactions with predators involve not only predator recognition but also assessment of risk (McLean and Rhodes 1991). Because mobbing is a potentially costly activity, nest defense should vary with the threat that particular species represent (Patterson *et al.* 1980; Buitron 1983; Curio *et al.* 1983; Clode *et al.* 2000). Even within a single species of nest predator, antipredator responses should vary with the context of the encounter (McLean and Rhodes 1991; Curio 1993). In the present study, the responses of the Common Tern (*Sterna hirundo*) to the Great Black-backed Gull (*Larus marinus*) are compared across stages of the tern nesting cycle.

Avian nest defense often increases in intensity as the breeding season progresses (reviews in Knight and Temple 1986b; Montgomerie and Weatherhead 1988; Redondo 1989; Brunton 1990; McLean and Rhodes 1991), and several hypotheses have been proposed to explain and predict temporal variation in nest defense. Models based on optimal parental investment and offspring reproductive value predict an increase in defense throughout incubation, because the value of offspring increases and the ability to re-nest decreases as offspring age (Barash 1975; Andersson *et al.* 1980;

Montgomerie and Weatherhead 1988). Hypotheses based on either offspring conspicuity and value to predators (Harvey and Greenwood 1978) or feedback between parents and offspring (McLean and Rhodes 1991) predict a constant level of defense during incubation, because eggs do not become more conspicuous with age (until pipping). All three categories of hypotheses predict that, at least in altricial species, parents should defend chicks more strongly than eggs, because chicks are more valuable and more conspicuous than eggs. Most authors have predicted that parental defense of chicks in altricial species should increase as chicks age and then decline at fledging (Barash 1975; Andersson *et al.* 1980; Montgomerie and Weatherhead 1988) or shortly thereafter (McLean and Rhodes 1991). Nest defense in precocial species, on the other hand, should peak shortly after hatching (Barash 1975; Andersson *et al.* 1980; Montgomerie and Weatherhead 1988). These declines in parental nest defense are expected because fledglings can escape predation via flight and precocial chicks can hide from predators, and because predators are less likely to remove an entire brood at once if chicks have dispersed from the nest site. All of these models predict that large clutches or

broods should be defended more strongly than smaller clutches or broods, although very few empirical studies have supported this prediction (Rytkönen 2002).

In the semi-preocial gulls and terns (Laridae), seasonal patterns should be intermediate to those predicted for altricial and precocial species, since their young are mobile but typically remain near the nest site (see Nisbet 2002 for Common Tern). The results of previous studies of larid nest defense have often contradicted one another (see Discussion), and thus no clear pattern has emerged. One weakness of most previous studies of nest defense in larids and other colonial birds (including my own work; Palestis 2000) is that researchers did not examine the responses of individuals or breeding pairs, but instead treated the entire colony as one unit (for a recent exception see Meehan and Nisbet 2002). Because the behavior of many individuals was combined, reproductive asynchrony may have obscured seasonal patterns of nest defense, as not every pair in a colony would be at the same stage of the nesting cycle at a given point in time. Although mobbing may spread among neighbors in a tern colony (Burger and Gochfeld 1991), not all members of a colony or subcolony will respond to the same encounter with a nest predator. For example, Burger and Gochfeld (1991) report that in colonies with 100 to 250 Common Terns, the average number of terns flying up in response to a predator was only 23.4 and was highly variable ($SD \pm 22.0$). Differences in nesting stage may explain some of this variation. This study was conducted to examine temporal changes in nest defense by Common Terns of known nesting stage.

METHODS

Observations of the responses of Common Terns to nest predators were performed at Petit Island ($39^{\circ}40'N$, $74^{\circ}11'W$), a 0.3 ha salt marsh island in Manahawkin Bay in Ocean County, New Jersey. Observations took place from 23 May to 15 August in 2001 and 20 May to 8 August in 2002. The Common Tern colony consisted of approximately 150 breeding pairs in 2001 and 200 in 2002. Laying occurred mainly in two waves, probably due to re-nesting after flooding. In 2001, the first wave lasted 23 May-9 June, and the second lasted 24 June-6 July. In 2002, the two major waves were from 20 May-7 June and 23-27 June.

This study was observational, involving natural encounters with nest predators. Field observations were made from a small boat anchored approximately 20 to 30 m from the island. Most observations were made alone, but occasionally with the help of an assistant. Excluding terns in the center of the island, which were difficult to see from the boat, terns tended to nest along three edges of the island on wrack (mainly dead eelgrass, *Zostera*). A typical observation session consisted of 3 h of observation, one at each of these edges, and typically four such sessions were performed per week at various times of day. Observations totaled 124 h in 2001 and 163 h in 2002.

Whenever a nest predator approached or entered the colony, the responses of the visible individuals were recorded. The variable analyzed was the proportion of encounters that elicited a response, called a "tern flying up". Only encounters with predators that flew directly over or within approximately 20m of the island were included, thus excluding encounters with predators landing or attempting to land on the island, which were rare and more likely to elicit a response from terns (Hatch 1970; Becker 1984; Cavanagh and Griffin 1993). Although the responses of terns to several species of nest predator were recorded, only responses to Great Black-backed Gulls (hereafter, "gulls") are analyzed here, for three reasons: 1) This species was observed frequently (relative to other predators) and consistently throughout the study: on average, approximately 3-4 encounters per hour in both years, with no trend across nesting stages. 2) At Petit Island, terns mob this species more frequently than other species (Palestis and Burger 1997). 3) This was the only species observed preying on tern young, although such events were very rare (only one in the two years of the present study).

Occasionally, terns nesting close to the edge of the island flew toward the observers in the boat. This aggression usually occurred immediately after arrival, when I was preparing to enter the colony, or soon after I left the colony. In addition to responses to gulls, the frequency of aggression by terns toward the observers in the boat is also quantified. Mobbing while observers were on the island was not quantified.

All nest sites that were potentially visible from the boat were marked with numbered tongue depressors. Typically four censuses were performed per week, which included tracking the contents of marked nests and searching for and marking new nests. In 2001, 15 incubating adults were captured in nest traps and uniquely marked in combinations of blue, red and green on their breasts and under their wings using non-toxic markers. Adults were not trapped until they had been incubating for ten days, to prevent nest desertion. No nests were abandoned after trapping, and 89% of eggs hatched at nests where adults were trapped. Most data comes not from marked individuals, but from the behavior of unmarked terns at nest sites that were readily visible from the boat. No color marking was done in 2002.

Statistical Analysis

Comparison of mobbing by terns throughout the nesting cycle was performed by dividing each pair's breeding stages into weeks (first, second, and third week of incubation, first, second, and third week of chick-rearing, with some data extending into a fourth week). The variable analyzed was the proportion of encounters

with gulls that elicited a response. To allow calculation of meaningful proportions, breeding pairs with fewer than five recorded encounters with gulls in a given week were excluded. Mobbing by parents with fledglings is presented, but is not included in statistical analysis, because the natal nest site and age of fledglings were often unknown and data were only available for fledglings from the first wave of nesting. To avoid pseudoreplication by repeatedly counting the same breeding pairs, each pair was used as only one data point in comparisons across weeks of the nesting cycle, by randomly selecting one week of nesting for each pair (see Fig. 1 for sample sizes). A separate comparison used a within-subjects design, comparing the average values for pairs during incubation to the averages of the same pairs during chick-rearing. Only pairs with a complete sequence (i.e. no missing weeks) were used in this comparison (see Table 1 for sample sizes).

To test for effects of clutch size on nest defense, I randomly selected pairs of nest sites differing in clutch size

by one egg, after matching for location in the colony (same subcolony) and laying date (same day) ($N = 6$ in 2001, 14 in 2002). For each of these matched pairs, one week of nesting was randomly selected for comparison, with the prediction that terns with larger clutches would respond more frequently to encounters with gulls.

Statistical analysis was performed using Statview (SAS Institute 1999). Data on responses to gulls were transformed by an arcsine-square root transformation, as is standard for proportions (Sokal and Rohlf 1995). Effects of nesting week and nesting wave were analyzed simultaneously using a 2-Way ANOVA. Multiple comparisons among nesting weeks were performed using Fisher's PLSD test (SAS Institute 1999; see "least significant difference", Sokal and Rohlf 1995). The within-subjects and clutch size comparisons were performed using the paired t-test. Means are given \pm one SE.

Responses to humans were recorded as the number of times a member of a breeding pair flew towards the observers in the boat per hour. Data are only included from terns that flew toward the observers at least once to avoid an overwhelming number of zero values, since most terns never flew at the observers. Even with this restriction, the distribution could not be transformed to meet the requirements of parametric tests, so only non-parametric tests are used. These data were analyzed using the Kruskal-Wallis test, followed by multiple comparisons using Dunn's procedure (Hochberg and Tamhane 1987; see Fig. 2 for sample sizes). The within-subject comparison was performed using the Wilcoxon signed rank test (see Table 1 for sample sizes).

RESULTS

Responses to Great Black-backed Gulls

Responses of terns to gulls were more frequent during chick-rearing than during incubation. This difference was numerically large in both years (Table 1) and highly significant in 2002, but not significant in 2001 (Table 1). To examine temporal patterns of nest defense in more detail, the nesting cycle of focal pairs of terns was broken up into weeks (first week of incubation, second week of incubation, . . .). There was significant variation among the week-long nesting "stages" in both years (2001: $F_{5,27} = 2.76$, $P < 0.05$; 2002: $F_{6,100} = 3.44$, $P < 0.005$; see Fig. 1). These analyses were controlled for differences between nesting waves (see below) with a 2-Way ANOVA. In both years the frequency of mobbing was low during all three weeks of incubation, was significantly higher by the second week of chick-rearing, and remained high as chicks approached fledging (Fig. 1).

Nest defense was significantly more frequent during the second wave of nesting in both years. The mean difference between

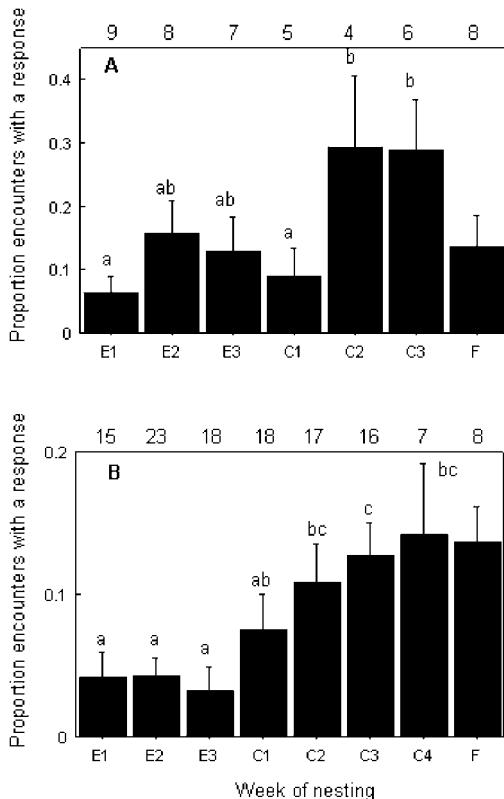


Figure 1. The mean responsiveness of focal terns to gulls is compared across weeks of the nesting cycle (E = eggs, C = chicks, F = fledglings) for 2001 (A) and 2002 (B). There was sufficient data to include parents in their fourth week of chick-rearing in 2002 only. Error bars are \pm SE. Numbers across the top indicate sample size (number of breeding pairs). Letters above bars indicate statistical significance (Fisher's PLSD): bars that do not share a letter are significantly different. These comparisons are controlled for nesting wave. Parents with fledglings are excluded from statistical comparisons.

Table 1. Comparisons of mobbing during incubation and during chick-rearing, directed toward gulls or toward the observers. The same breeding pairs are compared before and after hatching (within-subjects design).

Target	Year	Nesting stage	Mean ^a	N ^b	SE	Statistic ^c	P
Gulls	2001	Incubation	0.08 (8%)	9	0.04	$t = 2.11$	n.s.
		Chick-rearing	0.19				
Gulls	2002	Incubation	0.04	34	0.01	$t = 8.24$	<0.001
		Chick-rearing	0.12				
Obs.	2001	Incubation	0.02 per h	5	0.02	$Z = 2.02$	<0.05
		Chick-rearing	1.33				
Obs.	2002	Incubation	0.04	35	0.01	$Z = 5.16$	<0.001
		Chick-rearing	0.80				

^aMean proportion of encounters with gulls eliciting a response, or mean number of responses to observers per h.

^bNumber of breeding pairs.

^cPaired t-test or Wilcoxon signed rank test (Z) comparing incubation to chick-rearing

nesting waves in the proportion of gull encounters eliciting a response was 0.16 ± 0.05 in 2001 ($F_{1,27} = 8.37$, $P < 0.01$) and 0.07 ± 0.03 in 2002 ($F_{1,100} = 18.6$, $P < 0.0001$). There were no significant interactions between nesting stage and nesting wave (2001: $F_{5,27} = 0.57$, n.s.; 2002: $F_{6,100} = 1.11$, n.s.), as responses to gulls were numerically more frequent in the

second wave across nearly every stage of the breeding cycle in both years.

There was no evidence that terns with larger clutches were more likely to respond to gulls. Combining both years, four comparisons were in the predicted direction and six were in the opposite direction, with ten ties. Overall, pairs with larger clutches responded to approximately the same proportion of encounters with gulls as those with smaller clutches (mean difference = 0.01 ± 0.03 ; paired $t_{19} = 0.58$, n.s.).

Responses to Observers

Responses of terns to observers in the boat were much more frequent during chick-rearing than during incubation. This difference was statistically significant in both years, with responses to observers almost completely absent during incubation (Table 1). The averages presented in Table 1 are higher than for the typical tern, since they only include data from terns that flew at the observers at least once, while the majority of terns never did so. Only the frequency of aggression when observers were in the boat was analyzed quantitatively, but anecdotal evidence also suggests that the intensity of aggression within the colony increased with hatching. For example, although I always

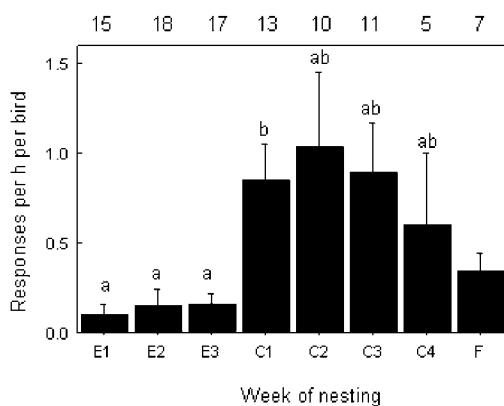


Figure 2. The mean frequency of responses of focal terns to observers is compared across weeks of the nesting cycle (E = eggs, C = chicks, F = fledglings) for both years combined. Data is excluded for terns that never flew at the observers. Error bars are \pm SE. Numbers across the top indicate sample size (number of breeding pairs). Letters above bars indicate statistical significance (nonparametric Dunn's procedure): bars that do not share a letter are significantly different. Parents with fledglings are excluded from statistical comparisons.

wore a hard hat when in the colony, I usually did not need it until chicks were present.

The temporal pattern of aggression toward observers was similar across years. Because of small sample sizes in 2001, data from the two years are pooled. Responses to observers were rare during the three weeks of incubation, but became more frequent immediately after chicks hatched and remained at a similar level throughout most of chick rearing, then appeared to decrease near fledging (Fig. 2). The variation among nesting stages was highly significant (Kruskal-Wallis Test, $H_6 = 25.5$, $P < 0.0005$). Paired comparisons between the first week of chick-rearing and each of the three weeks of incubation were all statistically significant, but no other paired comparisons were significant (Fig. 2).

DISCUSSION

Nest defense by Common Terns against Great Black-backed Gulls was most intense during chick-rearing, as predicted. That nest defense remained at a relatively constant level throughout incubation, rather than steadily increasing, contradicts the parental investment models (Barash 1975; Andersson *et al.* 1980; Montgomerie and Weatherhead 1988) but fits with the conspicuousness (Harvey and Greenwood 1978) and feedback (McLean and Rhodes 1991) hypotheses. However, the increased levels of nest defense in the second nesting wave may support parental investment theory (see below), and would not be predicted by offspring conspicuousness or feedback between parents and offspring.

Nest defense of altricial young should peak at or shortly after fledging, while defense of precocial young should peak shortly after hatching (see Introduction). Common Terns are semi-precocial, and therefore would be predicted to show an intermediate temporal pattern of nest defense. However, the results of the present study closely resemble the predicted pattern for altricial young: nest defense of chicks increased from the first to the second week of chick-rearing and did not drop off at least until fledging. This is perhaps not surprising, because Common Tern chicks remain completely dependent on their parents

after developing mobility, and are even fed by their parents after fledging (Burger 1980; Nisbet 2002). Importantly, the patterns observed were similar in both years of the study.

Previous studies of seasonal patterns of nest defense in gulls and terns have often given conflicting results. The only generally consistent result is that, as in the present study, responses to nest predators or human investigators are more frequent and intense during chick-rearing than during incubation (Lemmetynen 1971, 1972; Veen 1977; Burger 1981; Becker 1984; Kilpi 1987; Burger and Gochfeld 1991; Shealer and Burger 1992; Malickiene and Budrys 1998; Whittam and Leonard 2000), except for responses to species that prey only on eggs (Burger and Gochfeld 1991). Evidence is mixed for other patterns. In some studies, nest defense remained high (Lemmetynen 1971; Malickiene and Budrys 1998) or increased (Becker 1984) throughout the entire chick-rearing period until fledging, similar to the present study. In others, nest defense peaked at or shortly after hatching (Kruuk 1964; Fuchs 1977; Burger 1981; Kilpi 1987; Burger and Gochfeld 1991; Shealer and Burger 1992; Nisbet 2002) or increased through the first week of chick-rearing and then declined (Whittam and Leonard 2000). There are also discrepancies between studies in whether nest defense during incubation increases rapidly just prior to hatching (Burger and Gochfeld 1991) or increases steadily throughout the entire incubation period (Kruuk 1964; Lemmetynen 1971; Burger 1981; Kilpi 1987). Others have found no effect of nesting stage on larid nest defense (Montevecchi 1979) or have found different patterns of temporal variation in nest defense between species at a single colony (Fuchs 1977), between colonies of a single species (Erwin 1988), or between years at a single colony (Palestis 2000).

Why do these studies give such inconsistent results? One possible reason is that mobbing was examined at the level of the colony, thus combining responses of many individuals that may not have bred synchronously. For example, in both years of the present study, chicks from the first nesting wave were present at the same time as eggs from the sec-

ond wave. To lessen this problem, breeding pairs of known nesting stage were analyzed. Another complication is that predators vary in the timing of their predation. The Great Black-backed Gull preys more frequently on chicks than eggs (Whittam and Leonard 2000; Nisbet 2002), so perhaps the results of the present study reflect terns adjusting defense to the timing of predation rather than to value or conspicuousness of offspring. However, in the two years of this study, predation by gulls was observed only once in nearly 300 hours of observation, the frequency of encounters with gulls did not vary across nesting stages, and no obvious changes in gull behavior occurred, except that gulls were actually more likely to land on the island when terns were just beginning to nest.

Recently, Meehan and Nisbet (2002) studied individual Common Terns rather than colony responses, but their methodology differed from the present study. They found a positive correlation between offspring age and parents staying at the nest rather than fleeing, at least through early chick-rearing, when presented with a model Peregrine (*Falco peregrinus*), a species that preys on adult terns rather than on young. However, offspring age was confounded with parental laying date and parental quality, because high-quality parents lay early and thus have older young than low-quality parents. Offspring age is not confounded with parental laying date in the present study, because nest defense of pairs was tracked longitudinally as chicks aged, rather than by comparing individuals at one point in time.

In the present study, nest defense was most intense during the second wave of nesting, while Meehan and Nisbet (2002) found nest tenacity to be most intense among terns that nest early in the breeding season. However, their study took place within one nesting wave, and thus did not compare differences between nesting waves. An increase in nest defense from the first to second nesting wave may be expected under parental investment theory, due to differences in re-nesting potential (Barash 1975; Montgomerie and Weatherhead 1988). Second wave parents would probably be less likely to successfully re-lay fol-

lowing the loss of their young than first wave parents. However, fledging success declines as the breeding season progresses (Wendeln *et al.* 2000; Nisbet *et al.* 2002), so it could also be argued that early nests are more valuable and thus should be defended strongly. It is likely that most nests in the second wave at Pettit Island were re-nesting attempts by parents that lost their first nests due to flooding. Since re-nesting birds tend to be high-quality individuals (Wendeln *et al.* 2000), then perhaps the results of Meehan and Nisbet's study and the present study are compatible.

Responses of terns to a natural nest predator, the Great Black-backed Gull, are emphasized here, but responses to human observers were also analyzed. Although responses to gulls and to the observers do not perfectly overlap, the same general conclusions hold: nest defense is most frequent during chick-rearing, and nest defense remains at a low level throughout incubation. It is unlikely that responses to the investigators simply increased over time as terns learned the identity of repeatedly encountered individuals (Knight and Temple 1986a,b). Instead these responses seemed to closely follow changes in the nesting stage of the terns involved. In both years, aggression did not increase significantly as incubation proceeded, then suddenly increased in frequency as chicks hatched. This pattern held even though second wave terns, which may already have been familiar with the observers when laying, were included in the analysis. Why aggression to observers seemed to increase sooner after hatching than did aggression to gulls is unclear. Again interpretation is complicated by temporal differences in the "predator", since the time spent in the colony for censuses increased during the peaks in hatching, though not as dramatically as did mobbing.

In some ways the current study improves upon the methodology of previous studies, but because this was an observational study, many variables could not be controlled. At least four caveats arise that future studies may be able to address. 1) Although encounters with gulls landing or attempting to land on the island were excluded, variation in the behavior of the gulls can influence the responses of terns

(Hatch 1970; Becker 1984; Burger and Gochfeld 1991; Cavanagh and Griffin 1993; Whittem and Leonard 2000) and could not be completely controlled for. The frequency of encounters was consistent throughout the breeding season, but biases due to subtle variation in gull behavior cannot be ruled out. 2) A response by one individual to a predator may cause neighbors to respond (Burger and Gochfeld 1991), and thus neighboring individuals are not independent. However, since nesting was asynchronous, such social facilitation would make it less likely that effects of nesting stage would be found. 3) Only terns nesting along the edges of the colony were observed, and these terns may be poorer quality individuals (Coulson 1968). Whether mobbing behavior differs with location in the colony is unknown. 4) Although the entire colony was not treated as a unit, individual breeding pairs were analyzed as a unit and the sex of the individuals observed was not known. However, Meehan and Nisbet (2002) found no evidence for a sex difference in Common Tern nest tenacity. Interestingly, in studies of sex differences in other aspects of larid parental care, the total parental investment by males appears to be equal to or greater than investment by females (reviewed in Fasola and Saino 1995), contradicting the predictions of parental investment theory for monogamous species (Trivers 1972). Whether this pattern holds true for mobbing of nest predators is unknown and warrants further study.

ACKNOWLEDGEMENTS

Funding for this work was provided by the Megerle family. Larry Kusar and Richard Buzby kindly gave me permission to work at Petit Island. I thank Chomee Yoon and Robert Liberto for field assistance and Brett Sandercock and John Coulson for comments on the paper. Nest traps were borrowed from Joanna Burger, who first introduced me to the terns of Petit Island. This study was performed under the appropriate state and federal permits.

LITERATURE CITED

- Andersson, M., C. G. Wiklund and H. Rundgren. 1980. Parental defence of offspring: a model and an example. *Animal Behaviour* 28: 536-542.
- Barash, D. P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the Alpine Accentor. *Wilson Bulletin* 87: 367-373.
- Becker, P. H. 1984. Wie richtet eine Flußseeschwalbenkolonie (*Sterna hirundo*) ihr Abwehrverhalten auf den Feinddruck durch Silbermöwen (*Larus argentatus*) ein? *Zeitschrift für Tierpsychologie* 66: 265-288.
- Brunton, D. H. 1990. The effects of nesting stage, sex, and type of predator on parental defense by Killdeer (*Charadrius vociferous*): testing models of avian parental defense. *Behavioral Ecology and Sociobiology* 26: 181-190.
- Buitron, D. 1983. Variability in the responses of Black-billed Magpies to natural predators. *Behaviour* 87: 209-236.
- Burger, J. 1980. The transition to independence and postfledging care in seabirds. In *Behavior of Marine Animals*, Vol. 4: Marine Birds (J. Burger, B. L. Olla and H. E. Winn, Eds.). Plenum Press, New York.
- Burger, J. 1981. Effects of human disturbance on colonial species, particularly gulls. *Colonial Waterbirds* 4: 28-36.
- Burger, J. and M. Gochfeld. 1991. *The Common Tern: Its Breeding Biology and Social Behavior*. Columbia University Press, New York.
- Cavanagh, P. M. and C. R. Griffin. 1993. Responses of nesting Common Terns and Laughing Gulls to flyovers by large gulls. *Wilson Bulletin* 105: 333-338.
- Clode, D., J. D. S. Birks and D. W. MacDonald. 2000. The influence of risk and vulnerability on predator mobbing by terns (*Sterna spp.*) and gulls (*Larus spp.*). *Journal of Zoology (London)* 252: 53-59.
- Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edge of a colony. *Nature* 217: 478-479.
- Curio, E. 1993. Proximate and developmental aspects of antipredator behavior. *Advances in the Study of Behavior* 22: 135-238.
- Curio, E., G. Klump and K. Regelmann. 1983. An anti-predator response in the Great Tit (*Parus major*): is it tuned to predator risk? *Oecologia* 60: 83-88.
- Erwin, R. M. 1988. Correlates of nest-defense behavior of Common Terns. *Journal of Field Ornithology* 59: 135-142.
- Fasola, M. and N. Saino. 1995. Sex-biased parental-care allocation in three tern species (Laridae, Aves). *Canadian Journal of Zoology* 73: 1461-1467.
- Fuchs, E. 1977. Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed Gulls *Larus ridibundus* with special reference to the Sandwich Tern *Sterna sandvicensis*. *Ornis Scandinavica* 8: 17-32.
- Harvey, P. H. and P. J. Greenwood. 1978. Anti-predator defence strategies: some evolutionary problems. In *Behavioural Ecology: An Evolutionary Approach*. Vol. 1 (J. R. Krebs and N. B. Davies, Eds.). Blackwell Science, Oxford.
- Hatch, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. *Auk* 87: 244-254.
- Hochberg, Y. and A. C. Tamhane. 1987. *Multiple Comparisons Procedures*. John Wiley & Sons, New York.
- Kilpi, M. 1987. Do herring gulls (*Larus argentatus*) invest more in offspring defence as the breeding season advances? *Ornis Fennica* 64: 16-20.
- Knight, R. L. and S. A. Temple. 1986a. Methodological problems in the study of avian nest defense. *Animal Behaviour* 34: 561-566.
- Knight, R. L. and S. A. Temple. 1986b. Why does intensity of avian nest defense increase during the nesting cycle? *Auk* 103: 318-327.
- Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). *Behaviour Supplement* 11: 1-129.

- Lemmettyinen, R. 1971. Nest defense behaviour of Common and Arctic Terns and its effect on the success achieved by predators. *Ornis Fennica* 48: 13-24.
- Lemmettyinen, R. 1972. Nest defence behaviour in the Arctic tern *Sterna paradisaea* towards stuffed nest predators on Spitsbergen. Reports of the Kevo Subarctic Research Station 9: 28-31.
- Malickiene, D. and R. R. Budrys. 1998. Reproduction stages and colony defense pattern in the Black-headed Gull *Larus ridibundus*. In Proceedings of the 22nd International Ornithological Congress (N. J. Adams and R. H. Slotow, Eds.). *Ostrich* 69: 258.
- McLean, I. G. and G. Rhodes. 1991. Enemy recognition and response in birds. *Current Ornithology* 8: 173-211.
- Meehan, T. D. and I. C. T. Nisbet. 2002. Nest attentiveness in Common Terns threatened by a model predator. *Waterbirds* 25: 278-284.
- Montevecchi, W. A. 1979. Predator-prey interactions between ravens and kittiwakes. *Zeitschrift für Tierpsychologie* 49: 136-141.
- Montgomerie, R. D. and P. J. Weatherhead. 1988. Risks and rewards of nest defense by birds. *Quarterly Review of Biology* 63: 167-187.
- Nisbet, I. C. T. 2002. Common Tern (*Sterna hirundo*). In *The Birds of North America*, No. 618 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia.
- Nisbet, I. C. T., V. Apanius and M. S. Friar. 2002. Breeding performance of very old Common Terns. *Journal of Field Ornithology* 73: 117-124.
- Palestis, B. G. 2000. Common Tern (*Sterna hirundo*) Recognition Systems: Recognition of Siblings, Nest Sites and Nest Predators. Unpublished Ph.D. Dissertation. Rutgers, the State University of New Jersey, New Brunswick.
- Palestis, B. G. and J. Burger. 1997. Recognition of nest predator species and individuals by Common Terns. *American Zoologist* 37: 31A (Abstract).
- Patterson, T. L., L. Petrinovich and D. K. James. 1980. Reproductive value and appropriateness of response to predators by White-crowned Sparrows. *Behavioral Ecology and Sociobiology* 7: 227-231.
- Redondo, T. 1989. Avian nest defense: theoretical models and evidence. *Behaviour* 111: 161-195.
- Rytkönen, S. 2002. Nest defence in Great Tits *Parus major*: support for parental investment theory. *Behavioral Ecology and Sociobiology* 52: 379-384.
- SAS Institute. 1999. Statview. Version 5.0.1. Cary, NC.
- Shealer, D. A. and J. Burger. 1992. Differential responses of tropical roseate terns to aerial intruders throughout the nesting cycle. *Condor* 94: 712-719.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry*. 3rd ed. W.H. Freeman, New York.
- Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man, 1871-1971* (B. Campbell, Ed.). Aldine, Chicago.
- Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). *Behaviour Supplement* 20: 1-193.
- Wendeln, H., P. H. Becker and J. González-Solís. 2000. Parental care of replacement clutches in Common Terns (*Sterna hirundo*). *Behavioral Ecology and Sociobiology* 47: 382-392.
- Whittam, R. M. and M. L. Leonard. 2000. Characteristics of predators and offspring influence nest defense by Arctic and Common Terns. *Condor* 102: 301-306.