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Author(s): Rebecca M. Whittam and Marty L. Leonard

Source: *The Condor*, 102(2):301-306.

Published By: Cooper Ornithological Society

DOI: [http://dx.doi.org/10.1650/0010-5422\(2000\)102\[0301:COPAOI\]2.0.CO;2](http://dx.doi.org/10.1650/0010-5422(2000)102[0301:COPAOI]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1650/0010-5422%282000%29102%5B0301%3ACOPAOI%5D2.0.CO%3B2>

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CHARACTERISTICS OF PREDATORS AND OFFSPRING INFLUENCE NEST DEFENSE BY ARCTIC AND COMMON TERNS¹

REBECCA M. WHITTAM² AND MARTY L. LEONARD³

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1

Abstract. Nest defense is a critical aspect of parental care that entails both costs and benefits. The purpose of this study was to examine patterns of nest defense in a colony of Arctic and Common Terns (*Sterna paradisaea* and *S. hirundo*, respectively) using observations of natural predators: Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*). Tern nest-defense scores were higher for hunting gulls than for overflying gulls and for gull flights closer to the ground. Defense scores also were significantly higher during the chick stage than during the egg stage. Within the chick stage, response score initially increased with age, but then declined. The results of this study indicate that terns vary their defense in relation to characteristics of predators and offspring that influence the costs and benefits of defense.

Key words: *Arctic Tern, Common Tern, nest defense, predation, Sterna hirundo, Sterna paradisaea.*

INTRODUCTION

The protection of young from predators is a critical aspect of parental care (Barash 1975). Like most types of care, however, defense of young has both costs and benefits. Parents enhance the survival of their offspring, but they also risk injury and death when they attempt to attack or divert predators (Brunton 1986). Generally, the more intense the defensive behavior the greater the benefits to the offspring, but the higher the cost to the parent (Brunton 1990). Thus, the degree to which a parent is willing to intensify defense likely represents a balance between costs and benefits (Montgomerie and Weatherhead 1988).

Variation in the intensity of defense depends on how certain factors alter the cost/benefit ratio of defense (Montgomerie and Weatherhead 1988). For example, parents may vary their defense in relation to the size and behavior of the predator. This is presumably because these characteristics alter the relative risk to both parents and offspring (Brunton 1990, Walters 1990, Burger and Gochfeld 1991). Parents may also vary their response in relation to offspring characteristics such as age (Meilvang et al. 1997). Again, this is presumably because the relative benefits of nest defense vary as the young mature.

Most studies on nest defense in birds have involved field experiments on passerines or shorebirds in which humans or model predators are presented at individual nests (Shields 1984, Dale et al. 1996). Such experiments are useful because they allow hypotheses on parental investment to be tested by examining the parents' response to predators in a controlled manner. However, birds may not respond to human and model predators in the same manner as they do to genuine predators (Burger and Gochfeld 1992), and repeated presentations of model predators can lead to habituation or positive reinforcement (Knight and Temple 1986).

Studying natural predation events is difficult because they are usually widely scattered in space and time (Pettingill 1976, Brown et al. 1998). In seabird colonies, however, multiple predation attempts may be observed in short periods of time (Schauer and Murphy 1996, Whittam and Leonard 1999), thus making them ideal sites at which to observe the response of parents to nest predators under natural conditions.

Colonies of terns are often subject to high levels of predation, especially by gulls (Hatch 1970). Numerous studies have examined the impact of gull predation on tern reproductive success (Whittam and Leonard 1999) and several also have examined the response of terns to both natural and model predators (Erwin 1988, Burger and Gochfeld 1991, Shealer and Burger 1992). Most studies of tern nest defense, however, have been conducted at sites where the risk of predation is either low (Shealer and Burger

¹ Received 5 May 1999. Accepted 24 November 1999.

² Current address: Bird Studies Canada, P.O. Box 160, Port Rowan, Ontario, Canada, NOE 1M0.

³ Corresponding author. E-mail: mleonard@is.dal.ca

1992) or has not been reported (Burger et al. 1993, Palestis and Burger 1997). Nest defense by terns may be better understood by studying natural predation events in colonies under relatively intense predation pressure.

The purpose of our study was to examine the response of a colony of Arctic Terns (*Sterna paradisaea*) and Common Terns (*S. hirundo*) to natural intrusions by predatory gulls. Predation by Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) is intense at this colony (Whittam and Leonard 1999) and thus provides an ideal opportunity to examine tern nest-defense behavior. In this study we calculate intrusion rates by gulls, and determine how tern defense intensity varies with the species and behavior of the gulls and age of the young. The terns nesting in this colony were not marked, so we could not examine individual responses to predator intrusions. We therefore focus our study on colony-wide responses to predator intrusions.

METHODS

Our study was conducted between May and July 1997 on Country Island, Guysborough County, Nova Scotia, Canada (45°06'N, 61°32'W). The 19-ha island, located 8 km offshore, is surrounded by cobble beach and rocky shoals, and is characterized by organic soils supporting predominantly grasses, herbaceous plants, and small copses of white spruce (*Picea glauca*). In 1997, 170 pairs of Arctic, 51 pairs of Common, and 1 pair of Roseate Terns (*S. dougallii*) bred on the south end of the island on rocky beach and in tall vegetation. Avian predators that also nested on the island included 20 pairs of Great Black-backed Gulls, 120 pairs of Herring Gulls, 2 pairs of American Crows (*Corvus brachyrhynchos*) with 5 unpaired helpers, and 1 pair of Northern Ravens (*C. corvax*). Crows and ravens nested in white spruce trees approximately 300 m from the tern colony, whereas gull nests were spread across the island, some as close as 10 m from the edge of the tern colony. We did not examine tern responses to corvids because these predators are only present in the colony during the egg stage. There were no mammalian predators on the island.

PREDATOR INTRUSIONS AND TERN RESPONSE

We observed the colony from two, 3-m high blinds and one, 12-m high lighthouse to deter-

mine the response of terns to intrusions by gulls. Observation periods ranged from 1 to 3 hr (mean: 2.6 hr) and were conducted from 05:00 to 08:00, 10:00 to 13:00, and 16:00 to 19:00. This resulted in 2.5 ± 0.1 observation periods per day during the 48-day nesting period.

We considered an intrusion to occur when a gull walked or flew to within 30 m of the edge of the tern colony, and to last for as long as the gull was in or over the colony. During each intrusion we noted the species of gull and whether the intrusion resulted in the predation of a tern egg or chick. The frequency of daily intrusions was positively correlated with the frequency of daily predation events during the chick stage ($r_s = 0.55$, $df = 20$, $P = 0.01$), suggesting that intrusions are a reasonable indicator of predation pressure. We use intrusions rather than predation events in our analyses because we have more information on this variable.

To examine intrusion patterns over time, we determined intrusion rates for each species of gull during consecutive 4-day periods throughout the tern breeding season. We chose 4 days as a compromise between daily rates that were relatively variable and weekly rates that obscured more detailed patterns. Intrusion rates were calculated as the number of intrusions divided by the hours of observation during each 4-day period.

We scored the response of terns on a scale of increasing intensity and risk (after Shealer and Burger 1992): 0 = no response; 1 = alarm call (terns give alarm calls, fly up from their nests, but do not approach or flee from the predator); 2 = chase (terns pursue and/or swoop at the predator); 3 = attack (terns strike the predator with their bill or feet). Each intrusion was assigned the maximum score observed during that intrusion (Shealer and Burger 1992). The mean response-score per day was correlated with the mean number of terns responding per day ($r_s = 0.48$, $df = 41$, $P = 0.002$), suggesting that our measure of response was an adequate indicator of the overall response of the colony. We could not differentiate between the responses of Arctic and Common Terns. Earlier work, however, suggests that these species respond in a similar manner to predators (Lemmetyinen 1971).

Two-hundred and eighty unmarked gulls nested on Country Island and another 220 nested within 6 km. In total we observed 1,005 gull intrusions into the colony, which indicates that

individual gulls made multiple intrusions and therefore each intrusion is not an independent event. We have no evidence, however, that specialist gulls were responsible for most intrusions. Nonetheless, we attempt to reduce the probability of a Type I error by averaging response scores for all intrusions for each day. Thus our unit of analysis is the mean tern response-score per day. We only include days with five or more intrusions in our analyses.

DEFENSE INTENSITY AND PREDATOR CHARACTERISTICS

We compared tern response to intrusions by Herring Gulls and Great Black-backed Gulls to determine whether the response score varied with risk to adult terns. We assumed that Great Black-backed Gulls presented a greater risk to adult terns because they are the larger of the two gull species and are known to be predators of adult terns on Country Island (Whittam 1997, Whittam et al. 1998). At this site, Great Black-backed Gulls capture adult terns on the ground before the terns are able to fly up (R. Whittam, pers. observ.).

We also compared the response of terns to gulls posing differing risks to offspring. Each time a gull approached the colony we noted the intrusion type (hunting flight versus overflight) and the height of the gull above the colony. We used the heights of the blinds and the lighthouse as reference points when recording height, which was accurate to ± 1.5 m. We assumed that hunting flights posed a greater risk to offspring than overflights and that gulls closer to the ground were a greater threat than gulls flying higher above the colony. Intrusions were characterized as hunting flights if the gull flew in a zigzag pattern across or around the colony (Kruuk 1964) and as overflights if the gull flew in a direct line across the colony (Burger and Gochfeld 1991). Hunting flights were lower than overflights (hunting: 3.12 ± 0.13 m, overflights: 5.77 ± 0.20 m), although this feature could not be used to distinguish the two types of flight.

DEFENSE INTENSITY AND OFFSPRING CHARACTERISTICS

We monitored the nests of 166 pairs of Arctic Terns and 51 pairs of Common Terns to determine dates of clutch initiation and hatching. For nests found after initiation, the date of clutch initiation was back-calculated based on a 21-day

incubation period for Common Terns and a 22-day incubation period for Arctic Terns (Cramp 1985). We used this information to divide the breeding season into an egg stage and a chick stage. We considered the egg stage to begin when 75% of nests had at least one egg and to continue until the first chick hatched. The chick stage began when 75% of nests had at least one chick and continued until we left the colony 10 days later. This division resulted in an 8-day period in which we considered the colony to be in the egg stage and a 10-day period in which the colony was in the chick stage.

We examined whether tern response score to overflying gulls varied between the egg and chick stages by comparing the mean tern response-score per day for the two periods. Only 6 of the 10 days that composed the chick stage could be included in this analysis; 3 days were omitted because there were fewer than five overflights on those days, and 1 day was lost because we were unable to conduct observations. We also examined the chick stage in more detail to determine whether tern response to all gull intrusions varied with offspring age as measured by date. To determine changes in defense intensity with age, we examined tern response-score per day to gulls over the 10-day period that constituted the chick stage.

Significance was set at $P \leq 0.05$ (two-tailed) and means were reported \pm SE. We used non-parametric tests throughout.

RESULTS

We had 319 hr of observation and scored tern responses in 99% of intrusions. With one exception, Great Black-backed and Herring Gulls showed similar patterns of intrusion over the breeding season (Fig. 1). In general, intrusion rates were below 2 hr^{-1} in the egg stage and ranged from 0.4 to 2.9 hr^{-1} in the chick stage. Unlike Great Black-backed Gulls, Herring Gulls had a high intrusion rate at the end of the chick stage, averaging 6.8 hr^{-1} (Fig. 1). We observed Herring Gulls take two tern eggs and 34 tern chicks, and Great Black-backed Gulls take seven tern eggs and 19 tern chicks. Herring Gulls had proportionally more successful intrusions (i.e., predation of tern eggs or chicks) than did Great Black-backed Gulls, although this difference was not significant (Herring: 8.1%, Great Black-backed: 4.1%; $\chi^2_1 = 3.5$, $P = 0.06$).

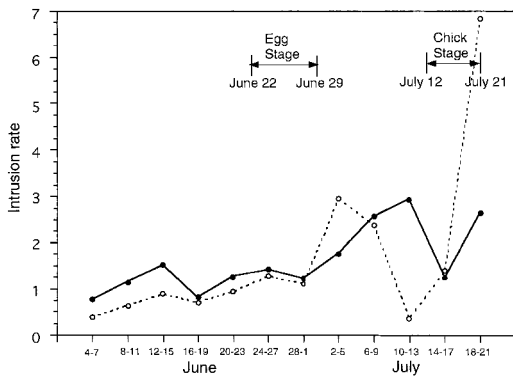


FIGURE 1. Intrusion rate (i.e., intrusions per hr) of Great Black-backed Gulls (filled circles) and Herring Gulls (open circles) during 4-day intervals over the tern breeding season. The egg and chick stages indicated on top of figure are discontinuous because of the manner in which we defined the two breeding stages (see text).

DEFENSE INTENSITY AND PREDATOR CHARACTERISTICS

Daily tern response scores to Herring and Great Black-backed Gulls did not differ significantly (Herring: 2.21 ± 0.10 , Great Black-backed: 2.08 ± 0.09 ; Wilcoxon's signed-rank test, $Z_{22} = 1.51$, $P = 0.13$). For this reason we combine responses by terns to the two species of gulls in further analyses. Tern response scores were significantly higher for hunting gulls than overflying gulls (hunting: 2.90 ± 0.04 , overflying: 1.59 ± 0.09 ; $Z_{22} = 4.19$, $P < 0.001$). This difference was not simply a function of the lower height of hunting flights because response scores were higher for low (3 m or less) hunting flights than low overflights (low hunting: 2.96 ± 0.03 , low overflying: 1.96 ± 0.27 ; $Z_8 = 2.55$, $P = 0.01$). Because 99% of hunting flights were made at heights of 6 m or less, we used overflights to examine the relationship between tern response and gull flight height. Tern response scores were weakly correlated with the height of gull overflights ($r_s = -0.33$, $df = 34$, $P = 0.06$).

DEFENSE INTENSITY AND OFFSPRING CHARACTERISTICS

Tern response score differed significantly between breeding stages (Mann-Whitney U -test: $U = 3.5$, $n_1 = 8$, $n_2 = 6$, $P < 0.01$) with daily response scores to gull overflights higher during the chick stage than during the egg stage (chick stage: 2.11 ± 0.14 , egg stage: 1.64 ± 0.09).

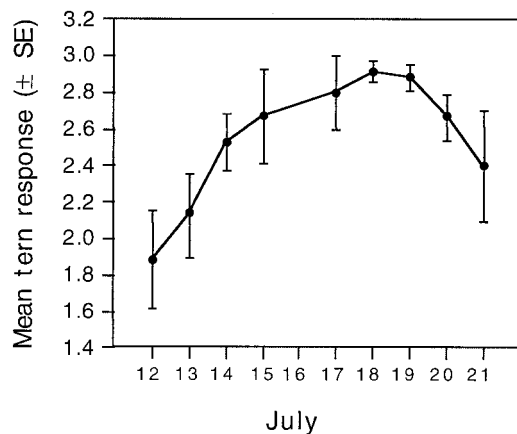


FIGURE 2. Mean daily tern response scores to gulls during the chick stage. No data were collected on 16 July.

Before examining the relationship between tern response and chick age, we first had to determine whether tern response scores varied with intrusion rate over the 10-day chick stage. If so, this could account for changes in tern response independently of chick age. Therefore, we examined the relationship between mean tern response-score per day and the mean number of gull intrusions per day during this stage and found that tern response score did not vary significantly with gull intrusion rate ($r_s = 0.26$, $df = 8$, $P = 0.46$). Given this, we then examined the relationship between mean tern response-score per day and date. Tern response score increased with date for the first seven days of chick-rearing and then declined thereafter (Fig. 2).

DISCUSSION

Arctic and Common Terns responded with similar intensities to Herring and Great Black-backed Gulls. Great Black-backed Gulls are the largest predator at our study site and, unlike Herring Gulls, have been observed to take adult terns (two in 1996, Whittam 1997; one in 1998, Whittam et al. 1998). For this reason, we had anticipated that terns might respond less intensely to this species because they potentially pose a greater risk to adults. A less intense response to Great Black-backed Gulls could minimize the risk of adults being injured or killed. Differences in response to brood predators versus predators that also take adults have been observed in other seabirds (Kruuk 1964, Burger and Gochfeld 1991), as well as passerines (Buitron 1983). This

was not, however, the case at Country Island. Terns at this site may have had a similar response to the two species of gull because predation on adults by Great Black-backed Gulls is relatively rare. In addition, both species prey heavily on chicks, so it might be advantageous to respond with equal strength to both species. Terns respond more strongly to Great Black-backed Gulls in colonies where they pose a greater threat to young than do Herring Gulls (Palestis and Burger 1997). Thus, terns may adjust their response to predators according to local conditions.

Terns appeared to vary their response to gulls in relation to the risk to their young. They responded more strongly to gulls in hunting flights than overflights and to gulls that passed closer to the ground. The type of flight, however, appeared to be a stronger cue than height because even at low heights, hunting flights elicited a stronger response than overflights. Other studies on terns also have shown an increase in response with a decrease in predator height and a stronger response to hunting flights than overflights (Hatch 1970, Cavanagh and Griffin 1993).

Tern defense intensity also varied with nesting stage, with more intense responses in the chick stage than in the egg stage. This response was not a result of differences in the frequency of hunting versus overflights in the two stages because we controlled for the type of flight when examining this problem. An increase in defense between egg and chick stages may be due to either an increase in the vulnerability of offspring after hatching (i.e., gulls take more chicks than eggs at this site) or to an increase in offspring reproductive value when eggs hatch (Montgomerie and Weatherhead 1988). We are unable to separate these factors.

Within the chick stage, defense intensity increased with date, until the last 3 days of this stage when it declined. This result suggests that chick age may affect parental defense. An earlier study on Common and Arctic Terns also showed an increase in response to predators with offspring age (Lemmetynen 1971). In general, however, parental defense intensity in species with precocial young is expected to peak at hatching then decrease through to fledging (Brunton 1990). Indeed, such a pattern has been found for some populations of Roseate Terns (Burger et al. 1993). The pattern is presumably a function of the decreasing vulnerability of

chicks as they mature and become capable of hiding or escaping predators (Hudson and Newborn 1990). We have no information on the vulnerability of chicks in our population, although we did observe gulls taking older chicks (Whittam 1997, Whittam et al. 1998), suggesting that even mobile chicks are subject to predation. The decrease in defense intensity late in the chick stage may be due to a decrease in the number of adult terns participating in defense. Such a drop may occur because as chicks increase in size both parents are required to forage and therefore more adults are away from the colony. Alternatively, parents may abandon the colony as chicks are depredated or die of other causes (Shealer and Burger 1992).

Methodological problems associated with nest defense studies, such as habituation or positive reinforcement to nonthreatening predators or predator models (Viñuela et al. 1995), were presumably not a problem in our study. Terns in our population did not vary their response to gulls according to gull intrusion rate, suggesting that they did not habituate to these predators. Similarly, terns responded to 71% of overflights despite the low probability of predation associated with these flights (Whittam 1997). This may have been because overflights were combined in an unpredictable manner with hunting flights (R. Whittam, unpubl. data). Failure to respond quickly to a gull may be fatal to adults and offspring, especially at this site where predation rates by gulls are relatively high (i.e., average of 1.5 chicks depredated per hr in 1996, and 0.4 chicks depredated per hr in 1997; Whittam 1997). Therefore, it may benefit terns to maintain a high level of defense against all types of intrusions, even if it means disrupting nesting behavior or foraging.

Our study had several limitations. For instance, we were unable to examine the behavior of individual terns, which prevented us from determining whether factors such as parental age and sex, or the quantity and quality of offspring affected defense (Montgomerie and Weatherhead 1988, Viñuela et al. 1995). Similarly, the results of this study reflect the response of a single colony of terns and thus limit our ability to generalize these results.

Gull predation is the major source of chick mortality at this colony (Whittam and Leonard 1999). Given such high predation pressure, there should be selection for anti-predator behavior.

Indeed, Arctic and Common Terns at this site maintained a high level of defense against gulls, especially during the chick-rearing period. Despite these defenses, terns on Country Island had poor breeding success in 1997 (i.e., minimum of 0.53 fledglings per nest for Arctic Terns, and 0 fledglings per nest for Common Terns), suggesting that their defenses are not adequate protection against predation by highly adaptable, generalist predators such as gulls.

ACKNOWLEDGMENTS

We thank Darla Saunders for help with field work, and Sherman Boates, Andy Horn, Ian McLaren, Pamela Mills, Ian Nisbet, David Shealer, Jeff Spendelow, Hal Whitehead, and Martin Willison for help with various aspects of the research. We thank the Manthorne family for support during the field season. We thank Michael Gochfeld, Andy Horn, Pippa Sheppard, Hal Whitehead, and an anonymous reviewer for their comments on previous drafts of this paper. Financial support was provided by an NSERC PGS-A award to R.M.W., and an Endangered Species Recovery Fund grant from World Wildlife Fund Canada to M.L.L. The Nova Scotia Department of Natural Resources and the Canadian Coast Guard provided logistical support.

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