

# The Effect of Siblings on Nest Site Homing by Common Tern Chicks: A Benefit of Kin Recognition

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**Abstract.**—Studies of kin recognition in birds have rarely tested its adaptive value. We tested whether sibling recognition helps Common Tern (*Sterna hirundo*) chicks find their nests. The ability to discriminate the natal nest from neighboring nests is critical to survival in chicks of ground-nesting, colonial birds, such as the Common Tern. We temporarily moved 70 four-day old chicks 1 m from their nests and compared their ability to return home across the following treatments: siblings in natal nest, no chicks in nest, siblings in neighboring nest, and non-siblings in test chick's nest. With a sibling in the natal nest, test chicks returned within 20 min in 14 of 20 trials. In all other treatments, fewer than half of the chicks returned. When chicks did return, they typically did so within 5 min. Several additional factors may affect nest site homing, such as parental behavior, aggression by neighboring adults, and habitat type. To control for these factors, we restricted the dataset for analysis to 27 nests by excluding chicks led back to the nest by a parent, chicks attacked by neighboring adults, and nests on a rocky beach (most experiments were performed in grassy habitat). In the restricted dataset, seven of nine chicks with siblings in the nest returned. Two of five returned in the empty nest treatment, none of six with siblings at a neighboring nest returned, and one of seven with non-siblings in the nest returned. There was significant variation among treatments in the final distance of test chicks from their nests. Siblings appeared to affect nest site homing, even though parents usually returned quickly to the nest and were least likely to search for displaced chicks if siblings were home. We also tested the ability of singletons to return to the nest, using an identical protocol. Singletons returned to the nest in only two of 14 trials, in none of the six cases when the dataset was restricted. Received 15 September 2000, accepted 24 January 2001.

**Key words.**—Coloniality, Common Tern, kin recognition, nest site recognition, parental care, siblings, *Sterna hirundo*.

Waterbirds 24(2): 175-181, 2001

Since Hamilton's (1964a,b) classic papers on the evolution of altruism via inclusive fitness benefits, there has been much interest and research in kin recognition. However, kin recognition is not necessary for kin selected altruism to evolve (Queller 1992), and kin recognition can be adaptive for reasons other than altruism towards kin, such as inbreeding avoidance (Pusey and Wolf 1996), natal site recognition (Pfennig 1990), and disease avoidance (Pfennig *et al.* 1994). Studies on gulls and terns (Laridae) have demonstrated sibling recognition (Evans 1970; Noseworthy and Lien 1976; Burger *et al.* 1988; Pierotti *et al.* 1988; Burger 1998; Palestis and Burger 1999, in press), but have rarely tested its adaptive functions. Most empirical studies and theoretical discussions of the adaptive value of kin recognition have focused on kin-directed altruism or optimal outbreeding, thus there is little information on how individuals may benefit directly by discriminating kin from non-kin

(Waldman 1988; Blaustein and Porter 1990; Blaustein *et al.* 1991; Sherman *et al.* 1997).

It has been proposed that sibling recognition in colonial birds may help chicks discriminate their natal nests from neighboring nests (Evans 1970; Beecher and Beecher 1983; Palestis and Burger 1999). However, only Noseworthy and Lien (1976) have previously tested this hypothesis, finding evidence for an effect of siblings on nest site homing in Herring Gulls (*Larus argentatus*). This benefit of sibling recognition should be especially important in colonial, semi-precocial, ground-nesting species, like most gulls and terns, because the potential for wandering into a neighboring territory is high. For example, as Common Tern (*Sterna hirundo*) chicks age, they become increasingly likely to run, and run increasingly greater distances, during investigator-induced (and presumably predator-induced) disturbance (Gochfeld 1981). As chicks become more mobile with age, they also occasionally wan-

der from the nest site even in the absence of disturbance (Burger and Gochfeld 1990).

Chicks that are slow to return to their nest sites risk losing food to their siblings. Parental care includes not only feeding, but also shading and brooding, and chicks may need to return to their natal territories to receive this care. Chicks that wander into neighboring territories also risk aggression from neighboring adult conspecifics, which in Common Terns may occasionally be fatal (Quinn *et al.* 1994) and in gulls is often cannibalistic (Parsons 1971). In mixed species colonies, heterospecific neighbors, such as gulls or Black Skimmers (*Rynchops niger*), may also attack and kill wandering tern chicks (Burger and Gochfeld 1991).

Common Tern chicks learn to recognize the vegetation near their nest sites (Burger and Gochfeld 1990), but social cues from siblings, parents, and neighbors could also contribute to nest site recognition. An effect of siblings on nest site recognition could result both from attraction to siblings and avoidance of non-siblings (Noseworthy and Lien 1976; Burger and Gochfeld 1990). Such social cues may be particularly important if the nest site shifts, as in Ring-billed Gulls (*L. delawarensis*) (Evans 1970). Common Tern chicks have been shown to discriminate nestmates from non-nestmates in the laboratory (Burger *et al.* 1988; Palestis and Burger 1999) and in the field (Palestis and Burger, in press), using both vocal (Burger *et al.* 1988) and visual (Palestis and Burger 1999) cues.

Through a field experiment with Common Tern chicks, we experimentally tested the hypothesis that discrimination of siblings from non-siblings helps chicks find their natal nests in colonies. Other proposed benefits of sibling discrimination among larid chicks include prevention of adoption of unrelated chicks (Holley 1988; but see Pierotti *et al.* 1988), avoidance of aggression from non-siblings (Burger *et al.* 1988; Burger 1998), maintenance of cohesive family groups for efficient provisioning of food and during permanent movements from the nest site (Evans 1970, 1980), and approach toward sibling begging calls to maximize food intake (Burger *et al.* 1988). None of these

proposed benefits are mutually exclusive, with each other or with the hypothesis that sibling recognition aids in nest site homing.

In addition to testing whether siblings are important cues in nest site homing, our experimental manipulations also test the importance of other likely cues. By removing siblings from a nest, we compare homing to an empty nest versus a nest with siblings. By moving siblings to a neighboring nest, attraction to siblings and attraction to the natal nest are directly compared. By replacing the test chicks' siblings with non-siblings, we test for avoidance of non-siblings. This treatment is also necessary to rule out the possibility that a returning chick may simply approach any chick in its nest, rather than approaching siblings *per se*. Additionally, we tested nest site homing in singletons. Singletons would not have developed in the presence of siblings and thus could potentially compensate by relying more strongly on other cues.

#### METHODS

This study took place during the 1998 breeding season on Falkner Island (41°13'N, 72°39'W), part of the Stewart B. McKinney National Wildlife Refuge, located in Long Island Sound in Connecticut, USA. There is a large Common Tern colony (about 3,800 breeding pairs in 1998) on the island. We mapped the location of 97 individually marked Common Tern nest sites, spread over five study plots, that were highly visible from a blind or building. Common Terns were the only species nesting at our plots, although Roseate Terns (*Sterna dougallii*) nest elsewhere on the island. All of our study areas were in sections of the island with frequent human disturbance throughout the breeding season. At our study plots the mean nearest neighbor distance ( $\pm$ SD) between nests was  $0.93 \pm 0.34$  m, although there were only eight cases in which a nest was within 1 m of more than one nest. Of 84 separate trials, 73 were conducted in flat, grassy habitat on the top of the island, and 11 took place on a rocky beach at the edge of the island. Because of the potential for effects of substrate and visibility on nest site homing, we restrict analysis of treatment differences to trials conducted in grassy areas.

We used a total of 84 individually banded Common Tern chicks as test chicks. Of these chicks, 39 were first-hatched (A) chicks, 31 were second-hatched (B) chicks, and 14 chicks with no siblings were also tested (see below). We used no third-hatched (C) chicks. Data from A and B chicks were combined for analysis, as we found no statistically significant differences between them in performance of nest site homing (see Results). We tested each chick only once, both to minimize stress on chicks and to avoid using non-independent data, an error in previous kin recognition studies (Gamboa *et al.* 1991). However, a chick could be used as a test chick in one trial and a stimulus chick in another. We tested chicks when

they reached four days-of-age, the earliest age at which Common Tern chicks are known to be able to discriminate nestmates from neighboring chicks in the laboratory (Palestis and Burger 1999). At this age, Common Tern chicks can also recognize the calls of their parents (Stevenson *et al.* 1970), and have begun to move around their parents' territories, remaining close to the nest unless disturbed (Burger and Gochfeld 1990).

We compared the ability of each test chick to return to its natal nest among the following treatments: siblings at home ( $N = 20$ ), empty nest (siblings removed and held in a bag in a blind or building,  $N = 20$ ), siblings at a neighboring nest (natal nest empty,  $N = 15$ , mean distance  $\pm$  SD to neighboring nest =  $0.83 \pm 0.36$  m), and non-sibling from a neighboring nest in the test chick's natal nest (siblings removed and held in a bag in a blind,  $N = 15$ , mean distance to non-sibling's nest =  $0.96 \pm 0.33$  m). Because most nests were either two egg clutches ( $N = 38$ ) or were three egg clutches with early C-chick mortality ( $N = 17$ ), 55 of 70 test chicks had only one sibling at the time of testing. Singletons ( $N = 14$ ) were tested following the same procedure as chicks in the treatments listed above, except that they had no siblings to remove. These chicks included true singletons from one-egg clutches ( $N = 3$ ), chicks from clutches where the remaining eggs failed to hatch ( $N = 5$ ), and chicks whose siblings had died less than one day after hatching ( $N = 6$ ). We alternated among treatments to control for any differences in nest site homing due to time of day or date. To limit thermal stress on the chicks, no experiments were performed during inclement weather, and on hot days all experiments were performed before 09.00 h or after 17.00 h.

During each trial we placed an inverted, transparent plastic box at the test chick's nest and another at a neighboring nest to hold the stimulus chicks in place and prevent aggression toward them. Both visual and auditory cues (and presumably olfactory cues) could be transmitted easily from the boxes. When there were no stimulus chicks to hold in a nest, such as in the empty nest treatment, we also placed the transparent boxes at the natal and neighboring nests, to control for any effects due to the presence of the boxes. We then carried the test chick 1 m from its nest in an opaque cup and inverted the cup to hold the chick in place. At 1 m from the nest, a chick would be in a neighboring territory. The direction that we moved each chick was selected to place the chick approximately equidistant from its nest and a neighboring nest, without placing the chick near a third nest. The release point of the chick was also adjusted if visibility to the observer would have been obstructed. Immediately after retreating to the nearest blind or building, we removed the cup remotely with twine, thus releasing the test chick.

We then recorded the behavior of the chicks and their parents, and any interactions between test chicks and neighboring adults. We recorded the time that the test chick returned to the box at its nest, if within 20 min. Only chicks that actually made physical contact with the box were scored as returning. (The closest chick excluded by this criterion was 0.20 m from the box at the end of the trial.) If the chick had not returned to its nest within 20 min, we ended the trial. Then we left the blind and measured the distance from the location of the test chick at the end of the trial to its nest. We consider the 20 min time limit a reasonable compromise between limiting stress on the chicks and allowing enough time to return home. Those that did return tended to

do so quickly (see Results). At the end of each trial we weighed all manipulated chicks to the nearest 0.5 g, to test whether body size affected homing, and returned them to their natal nests. Although we did not record the time required to set up each trial and to weigh and return chicks after each 20 min trial, it is unlikely that any of the test or stimulus chicks were out of their nests for more than 25 min in total.

In 30 of our 84 trials the test chick was attacked by an adult that approached from a neighboring nest. In most cases the adult simply approached, pecked the chick once, and returned to its nest. If pecking continued ( $N = 8$ ), then the observer put his head out of the blind, causing the adults to fly up briefly, and resumed the trial. No visible injuries to the test chicks resulted from this aggression, but chicks that were attacked were less likely to return than were unharassed chicks (see Results). Therefore, when comparing treatments, we analyze only those trials in which no aggression occurred.

The Rutgers University Institutional Review Board for the Use and Care of Animals approved the experimental protocol (Protocol Number 97-011).

#### Statistical Analysis

Our data on final distance from the nest was highly skewed, with many zero values, thus we use non-parametric tests when comparing the final distance of test chicks from their nests. We compared treatments using the Kruskal-Wallis Test, followed by multiple comparisons using Dunn's method (Hochberg and Tamhane 1987). Dunn's method is based on comparisons of mean ranks among pairs of treatments. Chi-Square values for  $2 \times 2$  contingency tables were calculated using Yates' correction. If any expected values were below five, Fisher's Exact Test was used instead of the Chi-Square Test. Unless otherwise indicated, means are presented  $\pm$  SE.

As noted above, when comparing treatments statistically, we excluded the trials conducted in the rocky habitat and trials in which the test chick was attacked by a neighboring adult. We also exclude trials in which the test chick was led back to the nest by a parent ( $N = 15$ ). The sample size of this restricted dataset (27, plus six singletons) is much smaller than the complete dataset (70, plus 14 singletons). The complete dataset is summarized before analysis of the restricted dataset is given. We then present data on behavior of parents, effects of aggression by neighboring adults, and test chick body mass and brood order, averaging across the complete dataset.

## RESULTS

### Complete Dataset

When siblings were home, test chicks returned to the box at their natal nest within 20 min in 14 of 20 trials, including all five trials in which two siblings were present. In all other treatments fewer than half of the chicks returned within 20 min (Table 1). Only two of 14 singletons returned. Across all treatments, those that did return usually (24 of 36) did so within 5 min. Because four

Table 1. Number of displaced Common Tern chicks returning to their nest within 20 minutes. For each treatment, the restricted data are given below the complete data set.

Treatment	No. returning	No. not returning	Percent returning
Siblings home	14	6	70
	7	2	78
Empty nest	8	12	40
	2	3	40
Siblings at neighbor's nest	5	10	33
	0	6	0
Non-sibling in home	7	8	47
	1	6	14
Singletons	2	12	14
	0	6	0

test chicks took longer than 15 min to return, the mean time to return was above 5 min (5 min 24 s  $\pm$  50 s).

Among the 15 trials when siblings were at a neighboring nest, on three occasions the test chick approached the neighboring nest, eventually returning to its natal nest in two of these trials. Approach toward a neighboring nest occurred in only three of 69 trials in the other treatments (Fisher's Exact Test, n.s.). We observed no reactions of the test chicks to the presence of non-siblings in the nest, although adults pecked at the transparent boxes containing foreign chicks eleven times, but never at empty boxes or boxes containing their own young.

#### Restricted Dataset

The dataset was restricted to exclude chicks that were attacked by neighboring adults, chicks from the rocky beach, and chicks led to the nest by parents (see Methods). In this smaller, more homogenous dataset, seven of nine chicks with siblings in the nest returned. Only three chicks returned in the remaining treatments combined (Table 1). The sample sizes in the restricted dataset are too small to compare the frequency at which chicks returned among treatments using contingency table analysis, due to low expected values. However, the probability of a chick returning when its sibling was present (7 of 9) is significantly greater than when siblings were removed (3 of 18) (Fisher's Exact Test,  $P = 0.004$ ).

To compare among treatments, we analyzed the final distance of test chicks from the nest. Final distance from the nest across treatments was as follows (sample sizes given in Table 1), siblings at home:  $0.16 \pm 0.10$ , empty nest:  $0.40 \pm 0.17$ , siblings in neighboring nest:  $0.92 \pm 0.16$ , non-siblings in the nest:  $0.87 \pm 0.16$  (Kruskal-Wallis Test,  $H_3 = 12.88$ ,  $P < 0.005$ ). Mean final distance from the nest was significantly lower for chicks with siblings at home than for chicks with siblings at a neighboring nest and for chicks with a non-sibling in the nest (Dunn's method,  $P < 0.05$ ). The mean final distance from the nest for singletons ( $1.03 \pm 0.19$  m) was similar to the starting distance (1 m).

#### Parental Behavior

At least one parent returned to the nest site within 20 min in 76 of 84 trials, and did so within 30 s in 51 trials. In seven trials both parents returned. Parents searched for missing chicks in 64 trials. This searching behavior was characterized by an adult calling, flying or walking to a new location near the nest, and calling again. Parents were less likely to search for displaced chicks when siblings were present in the natal nest. When siblings were at home ( $N = 20$ ), parents failed to search for the displaced chick 9 times; this occurred 11 times in all other trials combined ( $N = 64$ ) ( $\chi^2_1 = 5.06$ ,  $P < 0.05$ ). Parents were more likely to feed or brood the test chick away from the nest if siblings were at a neighboring nest (7 of 15 trials ver-

sus 8 of 69 in other treatments;  $\chi^2_1 = 8.08$ ,  $P < 0.005$ ). In 20 trials, a parent appeared to be attempting to lead the displaced chick back toward the nest, landing near the chick, calling, walking or flying closer to the nest and calling again, and repeating this sequence. In 15 of these trials the test chick followed the parent and returned to the nest. Parents attempted to lead only two of 20 chicks with siblings at the nest, compared to 18 of 64 in other treatments, but this distribution does not differ from chance ( $\chi^2_1 = 1.85$ , n.s.). When parents returned with fish, mean final distance of test chicks from the nest was  $0.41 \pm 0.18$  m ( $N = 12$ ), and was  $0.54 \pm 0.07$  m ( $N = 64$ ) when parents returned without fish (Mann-Whitney U Test,  $Z = 1.05$ , n.s.).

#### Effect of Neighboring Adults

In 30 of the 84 trials, the test chick was attacked by a neighboring adult. Sixteen of these attacks occurred after the chick began moving, 14 before the chick first moved. On three occasions, the adult pecked briefly, then briefly tucked the chick under its wing as if brooding, then pecked it again. Twenty-two of the 30 attacks lasted only a few seconds, and if they continued we interrupted them (see Methods). Averaging across all treatments, chicks that were pecked by neighboring adults were significantly farther from their nests (mean =  $0.74 \pm 0.09$  m,  $N = 30$ ) after 20 min than were non-pecked chicks ( $0.43 \pm 0.07$  m,  $N = 54$ ) (Mann-Whitney U Test,  $Z = 2.82$ ,  $P < 0.005$ ). Pecked chicks were also less likely to return to the nest (7 of 30) than were other chicks (29 of 54) ( $\chi^2_1 = 6.08$ ,  $P < 0.05$ ). Of the eight chicks with siblings at home that were pecked, four returned to the natal nest. Excluding one chick led back to the nest by a parent, only two of 21 pecked chicks returned to the nest in all other treatments combined (Fisher's Exact Test,  $P = 0.034$ ).

#### Mass and Brood Order

Across treatments, A-chicks ( $N = 39$ ) averaged a final distance from the nest of  $0.46 \pm 0.09$  m, while B-chicks ( $N = 31$ ) averaged  $0.50 \pm 0.09$  m (Mann-Whitney U Test,  $Z = 0.50$ , n.s.). A-chicks returned in 21 of 39 trials, while

B-chicks returned in 13 of 31 trials ( $\chi^2_1 = 0.56$ , n.s.). Body mass varied among four-day-old A-chicks ( $31.4 \pm 1.4$ ), four-day-old B-chicks ( $25.8 \pm 1.5$ ) and four-day-old singletons ( $31.5 \pm 2.7$  g,  $N = 14$ ) (ANOVA,  $F_{2, 81} = 3.92$ ,  $P < 0.05$ ). Multiple comparisons tests (Fisher's PLSD) revealed significant differences ( $P < 0.05$ ) between A- and B-chicks and between singletons and B-chicks, but not between singletons and A-chicks. Final distance of test chicks from the nest was not correlated with body mass (Spearman Rank Correlation,  $N = 84$ ,  $N$  corrected for ties = 64;  $r_s = 0.074$ ;  $Z = 0.67$ , n.s.).

#### DISCUSSION

The present study provides evidence that Common Tern chicks, displaced from their nests into a neighboring territory, are better able to locate and return to their natal nests when siblings are present in the nest. Combining treatments involving removal of siblings, chicks were more likely to return if one or two siblings were present in the nest than if siblings were removed. Singletons were unlikely to return to the nest. However, we could not compare the proportion returning among treatments due to small sample sizes. Individual treatments (excluding singletons) were compared using the final distance of the test chick from the nest. Final distance from the nest was significantly smaller for chicks with siblings at home than for chicks with siblings at a neighboring nest and for chicks with a non-sibling in the nest.

Caution in interpreting these results is warranted, because this experiment was conducted under natural conditions and several factors were not controlled. The age of the test chicks was held constant and biases due to time of day or date were also avoided. By restricting the dataset we also controlled for habitat differences, aggression by neighboring adults, and leadership by parents, but the resulting sample sizes were small. Uncontrolled factors that could potentially influence nest site homing include brood size, brood order, the number of parents returning, additional aspects of parental behavior, and the number of neighboring nests nearby. Future studies should attempt to control these vari-

ables. For example, parents could be trapped and experiments could be limited to a single brood size. On the other hand, with large enough samples it may be possible to test the importance of some of these factors.

The apparent effect of the presence of siblings was observed even though parents usually returned to their nests quickly, and were least likely to search and call for missing chicks when siblings were present. Therefore, although Common Tern chicks can recognize the calls of their parents (Stevenson *et al.* 1970) and parents can clearly help lost chicks to return home by leading them toward the nest, the effect of the presence of siblings may be at least as important as parental behavior in aiding nest site homing by chicks. Recognition of the nest site itself is also important in nest site homing. In 15 trials in which siblings were at a neighboring nest, the test chick approached its siblings only three times, twice eventually reaching the correct nest. Therefore siblings are not a particularly strong cue when they are present in the wrong nest. Whether avoidance of non-siblings also contributes to nest site homing is unclear (but see Noseworthy and Lien 1976).

We found that chicks pecked by neighboring adults, although apparently suffering no injuries, performed poorly in the nest site homing experiment. Across all treatments, only seven of 30 pecked chicks returned to the nest. While an effect of aggression on return to the nest is not surprising, it does demonstrate that attacks by neighboring adults can be costly even when they are non-lethal and apparently harmless. Chicks that were pecked either fled, often ending up farther from home than before, or crouched down motionless, thus delaying return home. Aggression by neighboring adults is a cost of coloniality not only because it can potentially cause injury or death directly (Parsons 1971; Quinn *et al.* 1994), but also because it can cause wandering chicks to remain separated from their parents, thus losing feeding, brooding and shading by parents. Similarly, Howell (1978) observed Gray Gull (*L. modestus*) chicks in a desert die of heat stress after attacks by adults prevented them from reaching shade.

Tern chicks compete strongly over food, and last-hatched chicks are at a competitive disadvantage and suffer high mortality (e.g., Nisbet and Cohen 1975; Bollinger *et al.* 1990; Bollinger 1994; Burger *et al.* 1996; Nisbet *et al.* 1998). In Common Terns, last-hatched chicks (C-chicks) grow faster and survive more frequently when older chicks are experimentally removed (Bollinger *et al.* 1990). Counterintuitively, chicks (especially A and B) survive best when their siblings survive, presumably due to differences in parental quality (Bollinger 1994). Perhaps A and B-chicks also benefit when their siblings survive because they may use siblings as cues in nest site recognition. Interestingly, sibling recognition should be least beneficial to the already disadvantaged C-chicks, because, by the time C-chicks develop mobility, A and B-chicks would be becoming less strongly attached to their nest sites. Newly mobile A and B-chicks, in contrast, would have a reliable cue for nest site recognition in the immobile C-chick, predictably located at the nest site.

We have interpreted our results to mean that lost chicks can use vocal and visual cues from siblings to help locate the nest site. However, an alternative interpretation is that instead of siblings in the nest being a cue to the location of the nest site, they are an indication that it is safe to return to the nest. Our experimental procedure caused a disturbance similar to that caused by a predator, and the absence of an individual's mobile siblings from the nest may indicate that the predator is still in the vicinity of the nest site and siblings are still hiding. This mechanism seems to be faulty, however, because if each chick followed the decision rule of delaying return home after a disturbance until its siblings had returned, then no chick would return even long after the predator had left the area. It is more likely that chicks "know" that it is safe to return to the nest when parents and neighboring adults have stopped giving alarm calls and mobbing calls. This alternative explanation still requires chicks to recognize their siblings, and to use them as cues when returning to the nest site. The difference is in whether these cues are used to guide the direction or the timing of nest site homing. We feel that the best

explanation of our results is that Common Tern chicks use their siblings as cues to help locate the nest site when disoriented, whether after a predator-induced (or investigator-induced) disturbance or after wandering from the nest in the absence of disturbance.

## ACKNOWLEDGMENTS

We thank the Stewart B. McKinney National Wildlife Refuge for permission to perform this study on Falkner Island (U.S. Fish and Wildlife Service, special use permit no. 53546-8-03-62578). We also thank Jeff Spendlow and the Connecticut Audubon Society for logistical support, Henry John-Alder, Terry McGuire and Bob Trivers for advice during the planning stage and discussion of earlier versions of the manuscript, and Jeremy Hatch, David Pfennig, John Coulson, and the anonymous reviewers for comments on previous versions of the manuscript. Much of the banding of chicks and marking of nests was performed by the staff of the Falkner Island Tern Project. Funding was provided by CRESPP (Department of Energy, AI #DE-FC01-95EW55084) and a Marion Johnson Fellowship from Rutgers, the State University of New Jersey to B.G.P.

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