Development of Common Tern (Sterna hirundo) Sibling Recognition in the Field

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Sibling recognition may be an important factor in the survival of young colonial birds, because it helps chicks to locate their nest sites within colonies. We examined the development of sibling recognition in common tern (*Sterna hirundo*) chicks using choice experiments conducted in the field. Chicks older than 3 days of age showed a significant preference for nestmates over foreign chicks. This preference was quite strong from 5 through at least 12 days of age, and 5- to 12-day-old chicks spent significantly more time near nestmates than did 3- to 4-day-old chicks. These effects of age were expected, because common tern chicks first become mobile enough for brood mixing to occur at approximately 4 days of age, and this mobility continues to increase as chicks age.

Kin recognition

Nestmate recognition

Behavioral development

Laridae

Sibling recognition by gull and tern chicks is adaptive, aiding chicks in discriminating their nest sites from among the many nearby nests in a colony (Burger, 1998a; Noseworthy & Lien, 1976; Palestis & Burger, in press) and helping to maintain family units during movements to new nest sites (Evans, 1970). Most species of gulls and terns (Laridae) are ground-nesting and colonial, and their chicks are semiprecocial. A chick that wanders from the nest site or scatters during disturbance must return to its natal nest to receive parental care and to avoid aggression from adults at neighboring nests, and thus must be able to recognize its own nest site. In addition to the presence of siblings, other potential cues for nest site recognition include parents, neighbors, and vegetation (Burger & Gochfeld, 1990; Noseworthy & Lien, 1976; Palestis & Burger, in press).

In common terns (Sterna hirundo), recognition of siblings is based on discrimination of a combina-

tion of auditory (Burger, Gochfeld, & Boarman, 1988) and probably visual cues (Palestis & Burger, 1999). The mechanism of sibling recognition appears to be prior association at the rearing site (the nest), probably the most common mechanism of kin recognition (Holmes, 1988; Holmes & Sherman, 1983). In other words, the identity of nestmates is learned and these chicks are recognized as "siblings" regardless of actual relatedness. In the laboratory, common tern and herring gull (Larus argentatus) chicks have been shown to discriminate nestmates from other familiar chicks (Burger, 1998a; Burger et al., 1988; Palestis & Burger, 1999). These nestmates were not true siblings, but instead were nonsiblings in artificial sibships created shortly after hatching. Pierotti, Brunton, and Murphy (1988) found that western gull (Larus occidentalis) chicks in the field preferred to associate with familiar chicks, regardless of whether the familiar chicks were actually

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nonsiblings and regardless of whether the unfamiliar chicks were actually siblings. Because nestmates are used as an aid in nest site recognition in both herring gulls (Noseworthy & Lien, 1976) and common terns (Palestis & Burger, in press), the relatedness of nestmates may not matter, although other possible benefits of sibling recognition do exist (Palestis & Burger, 1999, in press).

Palestis and Burger (1999) demonstrated a significant preference in laboratory-reared common tern chicks for nestmates over chicks from neighboring nests at 4 days of age, earlier than previously reported by Burger et al. (1988). In simultaneous choice tests, chicks were more likely to approach nestmates than foreign chicks and spent more time near nestmates than foreign chicks. We conducted the present study in the field, following a protocol similar to our laboratory study (Palestis & Burger, 1999), to determine whether discrimination of nestmates from foreign chicks also occurs in nature. We studied chicks ranging in age from 3 through 12 days, to examine the timing of the development of nestmate discrimination, and to test whether preferences for nestmates vary as chicks age.

Methods

We conducted experiments during the 1999 breeding season, mostly on Pettit Island (39°40'N, 74°11'W), a 0.3-hectare salt marsh island in Manahawkin Bay in New Jersey. Further site description can be found in Burger and Gochfeld (1991). The common terns at Pettit nested relatively densely (median nearest neighbor distance = 1.04 m) on wrack (mats of dead vegetation, largely eelgrass Zostera) and in more scattered locations in smooth cordgrass (Spartina alterniflora) (median nearest neighbor distance = 1.90 m). We marked the position of nest sites with numbered flags and checked for the presence of new eggs and chicks approximately daily. We recorded the contents and fate of each nest (214 nests, including replacement nests, from approximately 190 breeding pairs) on individual index cards. Each egg was individually marked with a nontoxic marker, and all chicks were banded with aluminum bands. Additional details of the census methods, as well as data on nesting success are given in Palestis (2000). Hatching peaked in the colony between June 20 and June 26. The first of several large nocturnal predation events occurred

on the night of June 28, and by July 2 no chicks le than 1 week old and only several widely scatter older chicks (usually without nestmates) remains

Because the predation events at Pettit Isla greatly limited the number of chicks available study, we also performed additional experiments Little Mike's Island (39°57'N, 74°05'W) in Barnes Bay, New Jersey. The common tern colony at Litt Mike's has contained between 250 and 500 pa since the early 1990s (Burger, 1998b). Little Mike is a salt marsh island originally formed from dred spoil, is similar in size to Pettit, and is covered by alterniflora and saltmeadow cordgrass (S. patent The terns nest largely on wrack adjacent to ree (Phragmites communis) (median nearest neighb distance = 1.07 m). We could not use any of chicks present on the island when we arrived (I 13) because these young were close to fledging a highly mobile, thus we could not know who the nestmates were. However, there were nests conta ing eggs, due to renesting after flooding. We man these nest sites with numbered flags, and band the chicks after hatching.

We used simultaneous choice experiments to termine the development of nestmate recognit with age and whether preferences remain strong o developed. We performed 21 tests from June through July 3, using a different test chick in e test, across the following test chick ages (in days (n=2), 4 (n=9), 5 (n=4), 6 (n=1), 9 (n=2), (n = 1), 12 (n = 2). Eleven of the test chicks w first-hatched ("A") chicks, and 10 were seco hatched ("B") chicks. Data from A and B chicks h been combined, because we found no evidence any effects of brood order on nestmate discrimi tion (Palestis, 2000). It is important to note that not all cases were nestmates actually siblings. had cross-fostered eggs among nests to test for fects of relatedness. It appeared that relatedness no effect on nestmate discrimination (Palestis, 20 but because the predation event limited our san sizes, we were not able to perform rigorous tes relatedness effects. The analyses of the effect age presented here only include trials present choice between a nestmate and a foreign (n = 18). In other words, tests involving c choosing between two nestmates (a sibling cross-fostered nonsibling) or between two fo chicks (a nonsibling vs. a cross-fostered sibling been excluded.

For each trial we captured a test chick and two stimulus chicks (one nestmate and one foreign chick) by hand. We never used a chick as a test chick more than once, to avoid nonindependent data (Gamboa, Reeve, & Holmes, 1991) and to limit chick stress due to handling. We chose stimulus chicks that were similar in age to each other and, whenever possible, chose chicks from neighboring nests. We tried to use neighboring chicks so that test chicks would have to compare among familiar individuals, and not simply discriminate familiar from strange individuals (see Palestis & Burger, 1999). The median distance between the test chick's nest and the foreign chick's nest was 1.9 m.

After capturing the chicks, we retreated to an edge of the island away from nesting areas. We placed the test chick in an inverted cup in the center of the test arena, a translucent plastic $99.1 \times 40.6 \times 16.5$ cm box, with a stimulus chick at each end of the test arena in transparent plastic boxes. The test chick was 25 cm from each stimulus chick's box, and masking tape on the outside of the arena divided it into four equal sections (each 12.5 cm long). The open ends of the boxes faced upward, allowing airflow and transmission of sound, in addition to visual cues. We avoided placing nestmates consistently on the right or left side of the arena, to control for any direction preferences, but the observer was not blind to the identity of the chicks. After we retreated to a boat in the water several meters from the test box, the adults in the colony quickly settled down, other than occasional diving by single individuals. We then removed the cup remotely with twine and recorded the test chick's movements for 5 min, and recorded the amount of time it spent on each end of the test arena. We defined the ends of the test arena as the sections within 12.5 cm from either stimulus chick's box. After the completion of each 5-min trial, we measured the final distance from the test chick to the stimulus chick boxes, weighed the three chicks, and returned them to their nests.

We selected a 5-min time limit based on our previous laboratory study (Palestis & Burger, 1999). In the laboratory study, in which we used a nearly identical test arena, a trial ended if the test chick spent two consecutive minutes near a stimulus chick. Of 181 choice tests, approximately 70% ended within 3 min, and only four reached 5 min. In the present study, by setting a constant duration for the trials, we were able to use absolute time in

the statistical comparisons, instead of having to use proportions.

Definition of Choice

If at the end of a trial the test chick was within 12.5 cm of a stimulus chick's box, then it was scored as having chosen that chick. A test chick located within 12.5 cm of a particular stimulus chick's box would be standing in the 25% of the test arena closest to that stimulus chick, at least 12.5 cm from the center of the arena and at least 37.5 cm from the other stimulus chick. Of the sixteen test chicks scored as having chosen a stimulus chick, only two were at that stimulus chick's end of the arena for less than 2 min when the trial ended, and none for less than 1 min 10 s. The mean (±SD) time spent near the chosen chick was 3 min 30 s (±76 s) out of a maximum of 5 min.

Ethical Note

We did not perform experiments in inclement weather or during the middle of the day, except on overcast days, to limit thermal stress on the chicks and eggs. None of the predation in the colony occurred during the disturbances caused by our activity.

Results

When given a choice between a nestmate and a foreign chick, test chicks chose nestmates more frequently than expected by chance. At the end of the 5-min trials, test chicks were in the end of the arena near their nestmates 12 times, near foreign chicks 4 times, and in the middle of the test arena 2 times $[\chi^2(2) = 18.0, p < 0.0001;$ expected distribution given in Table 1). (See Methods for justification of

Table 1. Observed and Expected Distribution of Test Chick Choices Among Nestmates and Foreign Chicks

	Chose	Remained	Chose
	Nestmate	in Middle	Foreign Chick
Observed	12	2	4
Expected ^a	4.5	9	4.5

 $\chi^2(2) = 18.0, p < 0.0001.$

The expected distribution is based on the size of each section of the test arena. The arena was divided into four equal sections, two of which comprise the middle of the arena.

this definition of "choice".) Two test chicks approached the foreign chick first, but then crossed the arena and chose the nestmate. No test chick chose a foreign chick after first approaching a nestmate. Excluding the two chicks that approached neither stimulus chick, mean ± SE latency to first approach was 13.6 ± 7.2 s, with no significant difference between test chicks that initially approached nestmates $(11.7 \pm 6.7, n = 10)$ and test chicks that initially approached foreign chicks $(16.7 \pm 16.7, n = 6)$ (Mann-Whitney U-test, Z = 0.66, p = 0.51). On average, test chicks (n = 18) spent 146.2 ± 27.2 s in the nestmate's end of the arena and 63 ± 22.9 s in the foreign chick's end of the arena. However, this difference was not statistically significant (Wilcoxon Signed-Rank Test, Z = 1.50, p = 0.13), due to test chick age variation (see below).

Because of our small sample sizes, we had to combine test chicks into two age classes: 3-4 days old (n = 9) and 5-12 days old (n = 9). The effect of age on nestmate discrimination is illustrated in Figure 1. There was no preference for nestmates among 3 to 4 day olds (Wilcoxon Signed-Rank Test, Z = 0.70, p = 0.48, Fig. 1) but a strong and significant preference among 5 to 12 day olds (Z = 2.38, p < 0.05, Fig. 1). Five- to 12-day-old test chicks spent more time near their nestmates than did 3- to 4-day-old chicks (Mann-Whitney *U*-test, Z = 2.19, p < 0.05, Fig. 1). Within 5- to 12-day-old chicks, there was no evidence for a decline in responsiveness or discrimination with age, and only one of nine chicks chose the foreign chick. This preference for nestmates is also significant among 4- to 12-dayold chicks $(156.9 \pm 29.1 \text{ s near nestmates},$ 53.4 ± 20.9 s near foreign chicks; Z = 2.10, p < 0.05,n = 16), but was not significant if 3-day-old chicks were included (see above). Both 3-day-old chicks spent more time near foreign chicks than near nestmates.

Discussion

Sibling recognition, like parent-offspring recognition (Beecher, Beecher, & Hahn, 1981; Burtt, 1977; Davies & Carrick, 1962; Evans, 1970, 1980), should develop before young become mobile enough to allow brood mixing (Beecher & Beecher, 1983; Evans, 1970; Holmes & Sherman, 1982), or entrance into neighboring territories where aggression from neighboring adults can occur (Burger, 1998a). Nestmate

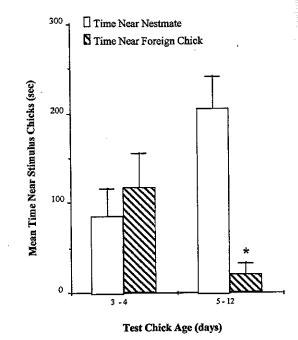


Figure 1. The mean time (seconds) test chicks spent in the sections of the test arena near nestmates (open bars) and foreign chicks (cross-hatched bars) is shown for 3- to 4-day-old chicks (n=9) and for 5- to 12-day-old chicks (n=9). Error bars are \pm SE. The asterisk indicates that 5- to 12-day-old chicks spent significantly more time near nestmates than near foreign chicks (Wilcoxon Signed-Rank Test, Z=2.38, p<0.05). They also spent more time near nestmates than did 3- to 4-day-old chicks (Mann-Whitney U-test, Z=2.19, p<0.05).

recognition facilitates the return of chicks to return to their natal nests, where parental care is available and aggressive neighbors are avoided (Noseworthy & Lien, 1976; Palestis & Burger, in press). We have previously found evidence for sibling recognition among common tern chicks at 4 days of age in the laboratory (Palestis & Burger, 1999). We have also demonstrated that 4 day olds in the field, after being displaced 1 m from the nest, are more likely to return home if siblings are present in the nest (Palestis & Burger, in press). At 4 days of age, chick mobility is typically increasing but is still largely confined to the area near the natal nest (Burger & Gochfeld, 1990). Chicks can also recognize the calls of their parents at this age (Stevenson, Hutchinson, Hutchinson, Bertram, & Thorpe, 1970).

In the present study we found a significant preference for nestmates among pooled 4- to 12-day old (and 5- to 12-day-old) chicks in the field. It is

possible that nestmate discrimination develops earlier than 4 days of age, as we tested only two 3-day-old chicks. Because of small sample sizes we had to pool ages. Overall, 5- to 12-day-old chicks spent more time near nestmates than did 3- to 4-day-old chicks (see Fig. 1). Instead of a fixed age of discrimination there is probably a learning curve among chicks, with some individuals learning the identity of their nestmates faster than others. Alternatively, the cues necessary for discrimination may not be fully developed in young chicks, or young chicks may be able to recognize their nestmates but do not yet discriminate them from foreign chicks.

Our previous work provided evidence that visual cues were important in nestmate recognition (Palestis & Burger, 1999). Most of this evidence came from an extremely low responsiveness, resulting in a loss of the significant preference for nestmates, when test chicks could not see stimulus chicks. However, these visual isolation tests were performed using 8- and 12-day-old chicks, while the highly responsive chicks given access to both auditory and visual cues were 4- and 5-day-old chicks. Thus, we could not conclusively rule out the possibility that what we interpreted as an effect of visual isolation was instead an effect of declining discrimination with age. In the present study, nestmate discrimination remained strong through at least 12 days of age. This is not surprising, as 12-day-old chicks still need to return to the nest site to be fed (Burger, 1980), and thus could still benefit from nestmate recognition. Therefore, the low responsiveness observed in 8- and 12-day-old test chicks in the laboratory (Palestis & Burger, 1999) probably did result from removal of visual contact with stimulus chicks, and not from a decline in discrimination with age. Visual cues may be necessary for the functioning of sibling discrimination in most natural contexts, because common tern chicks surprisingly fail to discriminate contact calls of nestmates from foreign chicks even though they do discriminate among begging calls (Burger et al., 1988). Therefore, although auditory cues have several advantages over visual cues (Beer, 1970; Thorpe, 1968), such as transmission through dense vegetation and reception in all directions, common ern chicks may use begging calls only for discrimination of nestmates from neighbors during feeding vents. As long as a chick that wanders from the est site can still see a nestmate, it should be able to

use that nestmate as a cue in nest site homing (Palestis & Burger, in press), regardless of whether the nestmate is begging or not.

In conclusion, we have confirmed in the field that common tern chicks can discriminate their nestmates from foreign chicks. Discrimination was quite strong between 5 through at least 12 days of age, showing no evidence of a decline with age. Recognition of nestmates is important to the survival of common tern chicks, because they use nestmates as cues for nest site recognition (Palestis & Burger, in press). With the onset of chick mobility in colonial, groundnesting species, nest site recognition becomes important and chicks should thus discriminate nestmates from neighbors.

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Our experimental protocol was approved by the Rutgers University Institutional Review Board for the Use and Care of Animals (amendment to protocol 86-016) and we followed the Guidelines for the Use of Animals in Research, published in *Animal Behaviour*.

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