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Aggression and nest spacing in single and mixed species groups of seabirds

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Abstract When heterospecific seabirds are part of a nesting colony, there may be less opportunity for conspecifics to come in direct contact with each other, resulting in lower intraspecific aggressiveness. To determine if individuals spend less time in aggressive behavior when nesting in conspecific rather than heterospecific groups, we compared the behavior of black skimmers (*Rhynchops niger*) nesting with gull-billed terns (*Sterna nilotica*) in three mixed species subcolonies to those of black skimmers in three single species subcolonies. In contrast to our predictions, black skimmers spent significantly less time in aggressive behaviors when nesting in single species subcolonies than when nesting with heterospecifics. Although skimmers in mixed species subcolonies tended to have more aggressive interactions with skimmers than terns, this may be a function of subcolony composition; the proportions of aggressive interactions with conspecifics were similar to the proportions of conspecifics in each subcolony. However, within the mixed species subcolonies, skimmers that nested nearer to terns were involved in aggressive interactions significantly less than skimmers that nested closer to conspecifics. Also, skimmers nested closer to their nearest neighbor when it was a gull-billed tern than when it was another skimmer. Regardless of which species they nested closest to, skimmers were more aggressive towards other skimmers than to terns within the mixed species subcolonies. Distance to nearest neighbor's nest did not differ significantly between the colony types, and did not seem to influence the duration of aggressive activity in the single species subcolonies. In the mixed species subcolonies, however, the time spent in aggressive behavior increased as the distance to nearest neighbor increased. It appears that of the several benefits that have been proposed of mixed species colonies, reduced time spent in conspecific aggression is not among them. However, within a mixed species colony, an individual can reduce time spent in aggressive interactions by nesting near heterospecifics.

Key words Gull-billed tern · Mixed species subcolonies · Nearest neighbor distance · Nest density · Single species subcolonies

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Introduction

Aggressive behavior during the breeding season is integral to establishing and maintaining territories, protecting mates, nest sites, nest material and young (Hunt and Hunt 1976; Birkhead 1979; Hobson and Sealy 1989). Aggression has been defined as an overt behavior providing some advantage to an individual that harms or threatens to harm another individual, thereby reducing the recipient's future fitness (Wittenberger 1981). Through aggressive interactions, animals may thwart predators, acquire food and mates, and control space (Archer 1988). Although commonly expressed, aggressive interactions seldom lead to injury or death, functioning mainly as a threat (Scott 1958). Nevertheless, aggression remains a cost in terms of time, energy, and risk of injury (Brown 1964). Because competition for nest sites, mates, and food is most intense between conspecifics, the spatial and temporal distribution of conspecifics greatly influences the aggressive behavior of an individual (Tinbergen 1953). Mutual hostility between conspecifics maintains spacing; thus each successful competitor gets part of the available space (Tinbergen 1953).

Breeding colonies of birds range in size from over a million individuals to small groups of a few individuals (Hickey and Craighead 1977). Within a colony, nests may be widely dispersed or densely packed depending on the species, population size, and habitat availability. Advantages of colonial nesting, such as predator defense (Nisbet 1975; Burger and Gochfeld 1990) and informa-

tion about good foraging sites (Ward and Zahavi 1973), increase with colony size. Likewise, certain disadvantages of colonial nesting, such as competition for nest sites, nest material, food, and mates, increase with colony size (Burger 1981). Other common disadvantages of colonial nesting, such as cuckoldry (Møeller and Birkhead 1993) and the rapid spread of diseases, may become more acute when nests are densely packed (Brown and Brown 1986).

With an increase in the density of conspecifics, competition for limited resources becomes intense and aggressive behavior leading to the destruction of neighboring nests becomes common. Such behavior resulting in the reduction in the reproductive success of neighbors may be an important competitive strategy, enhancing the relative contribution of one's own alleles to future generations (Pierotti 1980). In colonies of seabirds, crowding is common (Lack 1968) and thus the frequency of aggressive behavior is expected to be high. Studies of breeding colonies provide evidence that reproductive costs increase with the frequency of aggressive interactions between neighbors (Burger and Gochfeld 1990).

The advantages and disadvantages of coloniality may change when a colony is composed of multiple species. Members of a species may benefit if the heterospecifics in the colony do not require similar resources such as food, nesting sites, and nesting materials (Burger and Gochfeld 1990). A colonial bird in this case has the benefits of membership in a large colony but a lower cost of intraspecific competition than it would experience in a single species colony of the same size (Burger 1981). Because aggression is a major mechanism by which competitors interact (Hammerstein 1981), a decrease in competition for resources is likely to lead to a decrease in aggressive encounters. One of many reasons individuals of a species nest with heterospecifics could be because the time spent in intraspecific aggression is reduced while the advantages of coloniality, such as predator defense, are retained.

Black skimmers (*Rhynchops niger*) are colonial seabirds that nest in colonies on barrier islands, dredge islands and beaches in the summer. On the Atlantic Coast skimmers nest almost exclusively with common terns (*Sterna hirundo*) and with gull-billed terns (*S. nilotica*; Soots and Parnell 1975; Burger and Gochfeld 1990). Black skimmers usually establish nest sites about 7–14 days after the terns have started to nest and are believed to derive some benefits from nesting near terns (Erwin 1977; Burger and Gochfeld 1990). In coastal Louisiana, skimmers tend to nest with gull-billed terns; common terns do not commonly nest in this portion of the Gulf Coast. Unlike the populations along the Atlantic Coast, skimmers in Louisiana are also found nesting in small conspecific groups near the mixed species colonies.

Theoretical models state that one of the benefits of nesting in a heterospecific colony is lowered intraspecific aggression (Burger 1981). We observed skimmer behavior to test the hypothesis that skimmers in the mixed species colonies spend less time involved in aggressive interactions than skimmers nesting in single species groups. Within a mixed species colony, we hypothesized that individuals nesting nearer to heterospecifics are less prone to aggressiveness than those nesting nearer to conspecifics. Because density of a colony may be determined by the levels of aggressiveness displayed between neighbors, we also hypothesized that (1) there are greater internest distances within conspecific groups and (2) there are greater internest distances between conspecific than heterospecific neighbors within a mixed species colony.

Methods

Our study site was located on dredge islands in the Atchafalaya Delta Wildlife Management Area (ADWMA), St. Mary Parish, Louisiana. We studied black skimmers nesting with gull-billed terns on Skimmer Island in the summer of 1994, on Skimmer and Horseshoe islands in the summer of 1995, and on Skimmer and Ibis islands in the summer of 1996. Typically, 2–4 weeks after the mixed species groups formed, skimmers started nesting between 10 m and 40 m away from the heterospecific aggregations in smaller conspecific groups. We refer to the latter as single species subcolonies, and to the former as mixed species subcolonies. Because of the close proximity of the mixed and single species groups, we consider them to be subcolonies (Burger and Gochfeld 1990). We studied single species subcolonies of skimmers that formed on Skimmer and Donna's islands in 1994, and on Horseshoe Island in 1995.

We established a 20×20 m plot near the center of each subcolony. All nests within this plot were marked with a 30-cm piece of PVC pipe and given a specific number. We also measured the distance to the closest conspecific and the closest heterospecific for each marked nest for all subcolonies in 1995 and 1996. The distance to the nearest neighbor's nest was obtained by measuring the distance between the centers of adjacent nest sites. Observations on aggressive interactions were made between mid-May and the end of July in 1994 and 1995. After this time, either offspring had moved away from nests or vegetation had grown high enough to obstruct our observations.

On a daily basis, we randomly selected one to two subcolonies for observations; whether a subcolony was observed in the morning or afternoon was also randomly determined. All observations were made between 0730 and 2000 hours. From an observation tower about 35 m away from the colony, a skimmer nest was randomly selected within the study plot and observed for one hour with a spotting scope. Typically, about four skimmer nests were observed per day per subcolony type. When any of the following behaviors occurred during our observations, we measured its duration, and noted the species that was the focus of the behavior. Ritualized aggressive behaviors observed in skimmers (described by Burger and Gochfeld 1990) are: (1) *bark*, a low-frequency vocalization resembling a dog's bark; (2) *head toss*, a rapid up and down movement of head, usually accompanied by barking; (3) *aggressive upright*, legs and neck are fully extended, raising the body and holding neck high, accompanied by either barking or holding mouth open; (4) *low oblique*, the body and bill is tilted down, the tail and wings up; and (5) *choking*, the bill is pointed down, neck enlarged and the body is jerked forwards. We scored barking episodes only when barking was not part of another display, in order not to exaggerate the frequency and duration of barking. Still, barking was by far the most common of the five ritualized behaviors. We therefore decided to group all five behaviors into a single category, aggressive displays, in our statistical analysis. Besides these behaviors, we also recorded any ground and aerial chases. Chases were also relatively rare so we grouped both aerial and ground chases into one category. Our third category of aggressive behavior was fights with physical contact.

The data did not meet the assumptions of normality and homoscedasticity. Hence nonparametric tests were performed using Statistical Analysis System (SAS Institute 1985) and SYSTAT (1992). Mann-Whitney two-tailed tests were used to test the following hypotheses: (1) skimmers in single species subcolonies spend different amounts of time in aggressive behavior than skimmers in the mixed species subcolonies, (2) within mixed species subcolonies, skimmers spend different amounts of time in aggressive interactions when their nearest neighbor is another skimmer than when it is a gull-billed tern, (3) the densities of nests in the single species subcolonies are different than in the heterospecific subcolonies, (4) within mixed species subcolonies, skimmers nest at different distances from their nearest neighbor when it is a heterospecific than when it is a conspecific, and (5) the distance between a skimmer nest and its nearest neighbor is different in the mixed species and single species subcolonies. We used a Wilcoxon paired rank test to test the hypothesis that black skimmers in the mixed species subcolonies direct their aggression in higher proportions towards conspecifics than towards heterospecifics. Because species composition in the mixed species subcolonies was not equal, we also used a Wilcoxon test to evaluate the hypothesis that black skimmers in the mixed species subcolonies direct their aggression in different proportions towards conspecifics than would be expected from the proportion of skimmers in the sample plots. A Kruskal-Wallis test was used to determine if the amount of time black skimmers spend in aggression, in both the single and mixed species subcolonies, differs significantly when their nearest neighbor (irrespective of its species) is either <1 m, 1–2 m, or >2 m away. A Dunn's multiple range test was used to evaluate differences in the time spent in aggressive interactions among the three nearest neighbor distance groups. For each of the nearest neighbor distance groups, we compared the duration of aggressive behavior in skimmers between subcolony types using a Mann-Whitney *U*-test, to determine the effects of colony type on aggression while controlling for the effects of nest density.

Because we selected nests for observation randomly, a few pairs of birds were observed more than once during a breeding season; these we treated as independent observations because of the dynamic nature of nest location, reproductive status, and colony membership. To assess the possibility that this treatment of observations may have influenced the results of our analyses through pseudoreplication, we also conducted all statistical analyses using the mean of multiple observations for the same nest as the dependent variable. Regardless of the method we used to treat multiple observations of aggressive behaviors for a nesting pair, the same null hypotheses were rejected at the 0.05 level.

Results

We made 252 and 184 h of observations of nesting skimmers in the mixed and single species subcolonies, respectively. There was a significant difference between the amount of time that black skimmers spent in overall aggressive behavior ($P < 0.001$) between colony types. We rejected the hypothesis that black skimmers in single species subcolonies spend significantly more time in aggressive behavior than skimmers in mixed species subcolonies. Skimmers in mixed species subcolonies spent more time in aggressive displays ($\overline{x}_{\text{mixed}} = 36$ s; $\overline{x}_{\text{single}} = 12$ s; $P < 0.0001$) and chases ($\overline{x}_{\text{mixed}} = 4$ s; $\overline{x}_{\text{single}} = 2$ s; $P = 0.036$) per observation hour than did skimmers in single species subcolonies (Fig. 1). Aggressive behavior was observed to be mainly expressed through barking (the vocalization of black skimmers), and ground and aerial chases. Fighting occurred on the ground or in the air and was characterized by pecking and interlocking beaks with the opponent; there was no significant difference between the colony types ($\overline{x}_{\text{mixed}} = 1.3$ s/observation h; $\overline{x}_{\text{single}} = 1.2$ s/observation h; $P = 0.076$; Fig. 1).

Within the mixed species subcolonies, skimmers spent significantly more time in aggressive displays when their nearest neighbor was a conspecific ($\overline{x} = 46.7$ s/observation h) than when their neighbor was a heterospecific ($\overline{x} = 25.0$ s/observation h; $P = 0.001$; Fig. 2). Time spent in chasing ($\overline{x}_{\text{conspecific}} = 4.3$ s; $\overline{x}_{\text{heterospecific}} = 4.1$ s) and fighting ($\overline{x}_{\text{conspecific}} = 2.2$ s; $\overline{x}_{\text{heterospecific}} = 0.4$ s) per observational hour did not differ significantly for skimmers when their nearest neighbor was either a heterospecific or conspecific ($P_{\text{chase}} = 0.93$; $P_{\text{fight}} = 0.22$; Fig. 2). Aggressive behavior expressed by skimmers in the mixed species subcolonies was directed more frequently towards other skimmers than toward gull-billed terns ($P < 0.001$; Fig. 3). This result may be a function of subcolony composition, as there was no significant difference between the proportion of aggressive acts directed toward skimmers and the proportion of skimmers in the study plots ($P = 0.445$).

Time spent in aggression by skimmers in the mixed species subcolonies was dependent upon the distance to their nearest neighbor's nest ($P = 0.045$). A multiple comparison test revealed that skimmers were less aggressive when neighbors were <1 m away ($\overline{x} = 31.3$ s/observation h) than when they were >1 m away ($\overline{x} = 45.5$ s/observation h; Fig. 4). However, for skimmers in single species subcolonies, there was no significant variation in aggression levels per observation hour among the different classes of distances between nests ($\overline{x}_{<1\text{ m away}} = 13.5$ s; $\overline{x}_{>1\text{ m away}} = 14.4$ s; $P = 0.97$; Fig. 4).

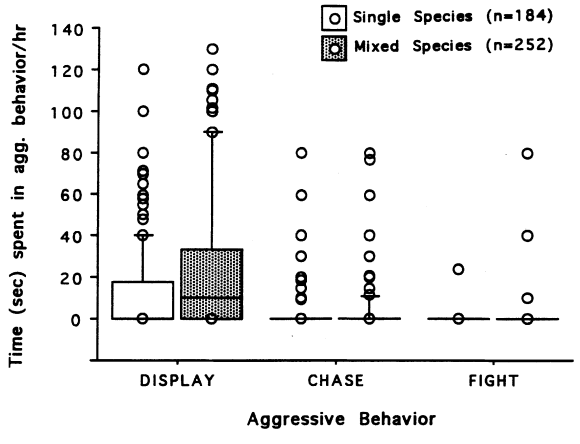

Fig. 1 Box and whisker plots of the amount of time (s) per observation hour spent in aggressive displays, chases, and fights by black skimmers in mixed (*shaded boxes*) and single (*clear boxes*) species subcolonies during the 1994–1995 breeding seasons. *Numbers* in key represent the number of replicate observation hours of randomly chosen pairs of black skimmer in each colony type. We represent our results in box and whisker plots because the data were not normally distributed. The bar within the box represents the median, the box represents the interquartile range (IQR), the whiskers represent 1.5 X IQR, and the *circles* represent more extreme data points

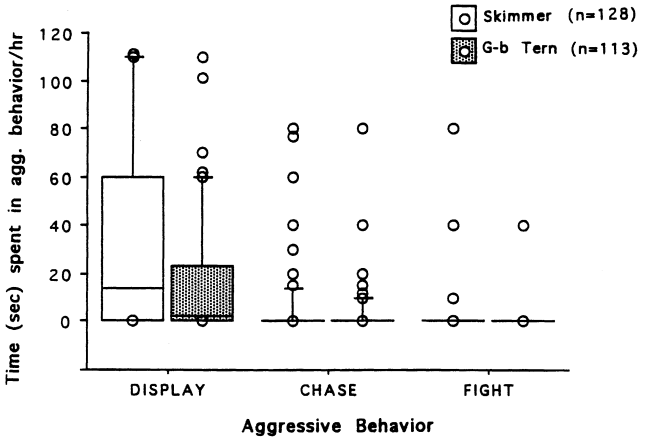

Fig. 2 Box and whisker plots of the amount of time (s) per observation hour spent in aggressive behavior by black skimmers in mixed species subcolonies when their nearest neighbor was either a skimmer (*clear boxes*) or a gull-billed tern (*shaded boxes*) during the 1994–1995 breeding seasons. *Numbers* in legend represent the number of replicate observation hours of randomly chosen pairs of black skimmer in each group

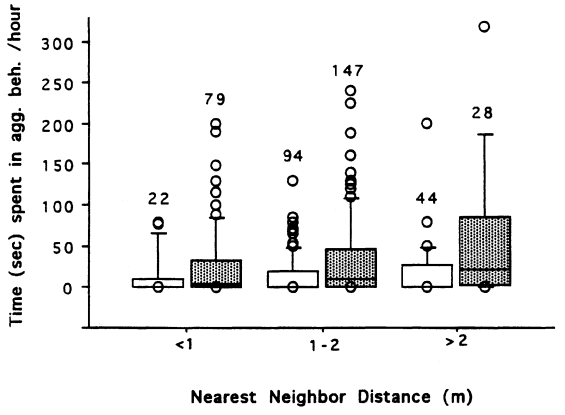

Fig. 4 Box and whisker plots of the amount of time (s) per observation hour black skimmers spent in aggressive behavior when their nearest neighbor was either <1, 1–2, or >2 m away. The *clear bars* represent nesting pairs of black skimmers in the single species subcolonies and the *shaded bars* represent pairs in the mixed species colonies. *Numbers* of replicate observation periods appear above the box plots

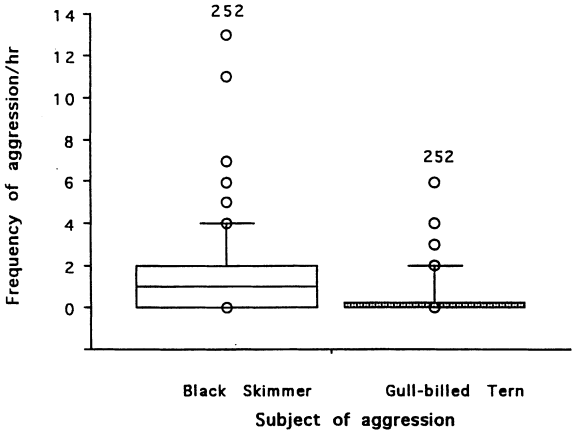

Fig. 3 Box and whisker plots of the number of instances skimmers in mixed species subcolonies were aggressive (per hour of observation) towards skimmers or gull-billed terns during the 1994–1995 breeding seasons. *Numbers* of replicate observation periods appear above the box plots

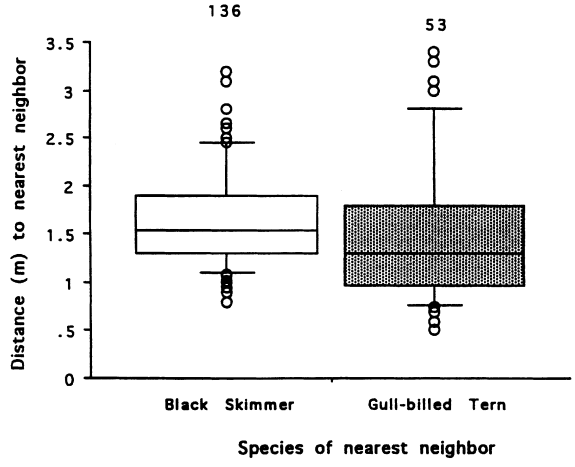

Fig. 5 Box and whisker plots of the distance (m) at which skimmers in mixed species colonies nested from their nearest neighbor when the latter was either a gull-billed tern or a skimmer. *Numbers* of nests surveyed appear above the box plots

When comparisons were made between colony types, black skimmers in the mixed species subcolonies spent more time in aggressive behavior than their counterparts in the single species subcolonies for each of the three nearest neighbor distance classes (<1 m, $P = 0.05$; 1–2 m, $P = 0.001$; >2 m, $P = 0.005$; Fig.4).

For skimmers nesting in the mixed species subcolonies, the distance to the nearest neighbor was significantly less if the neighbor was a tern ($\bar{x} = 1.53$ m; $n = 53$) than if it was a skimmer ($\bar{x} = 1.68$ m; $n = 136$; $P = 0.012$; Fig. 5). There was no significant difference ($P = 0.63$) detected in the distance to the nearest neighbor for black skimmers between mixed species subcolonies ($\bar{x} = 1.64$ m; $n = 189$) and single species subcolonies ($\bar{x} = 1.61$ m; $n = 54$). Mixed species subcolonies were characterized by higher densities ($n = 5$; $\bar{x} = 79$ nests/400 m^2; range 40–133) than the single species subcolonies ($n = 3$; $\bar{x} = 38$ nests/400 m^2; range 14–67). However, there was no significant difference between the densities of the two colony types ($P = 0.124$). The failure to reject this hypothesis is probably because of the small sample sizes.

Discussion

Aggressive behavior can lead to serious injuries, especially when it involves stealing of food (Pierotti and Annett 1994). In some cases, chicks are cannibalized by neighboring conspecifics (Burger and Gochfeld 1990; Buckacinska et al. 1996). However, ritualized displays are mainly used in expressing aggression, a strategy

thought to be adaptive (Tinbergen 1953; Piersma and Veen 1988; Burger and Gochfeld 1990; Buckacinska and Buckacinski 1994). In our study, skimmers expressed aggressive behavior mostly through displays rather than chasing and fighting.

Because competition is most intense between conspecifics (Tinbergen 1953), aggressive behavior is expected to be directed more at conspecifics than at heterospecifics. Such behavior is expected especially during the breeding season when competition, cannibalism, and stealing of food increases between conspecifics (Burger and Gochfeld 1990). Individuals must, therefore, spend more time in aggressive displays to ward off conspecifics from coming too close to the nest site (Tinbergen 1953). Hence nesting amidst heterospecifics may mitigate not only the energy and time involved in aggressive behavior but also its risks.

As predicted, skimmers predominantly directed aggressive behavior towards other skimmers. Similar results were reported by Burger and Gochfeld (1990) in their study of common tern-black skimmer colonies in the northeasten United States. However, the proportion of aggressive behavior directed toward skimmers in our study was not different than the proportion of skimmers in the subcolony. Thus it is difficult to argue that skimmers were more aggressive toward conspecifics than toward terns.

Time spent in aggressive behaviors waxes and wanes depending on the value and vulnerability of the resource (Hunt and Hunt 1976) and the degree of threat imposed by neighbors (Hunt et al. 1986; Burger and Gochfeld 1990). When all three are high, the duration of aggressive behaviors is expected to increase. Apart from the energetic costs involved with aggression, the time available for other activities, such as feeding and scanning for predators, decreases (Caraco et al. 1980). Although a theoretical model of mixed species coloniality predicts that aggression is lower when among heterospecifics than conspecifics (Burger 1981), our results show otherwise. Black skimmers spent more time in aggressive behaviors when in mixed species groups than when in single species groups.

In our study, the first black skimmers arriving at the colony selected nest sites between gull-billed tern nests. Successive skimmer nests gradually radiated out as nest sites close to gull-billed tern nests became occupied, and eventually they formed monospecific groups a small distance away from the mixed species subcolony. A study on the nesting habitat of these species found that gull-billed terns are an important component of the nesting habitat of black skimmers (Leberg et al. 1997). The attraction of skimmers for nest sites close to terns suggests that this choice of nest site may be of some advantage for black skimmers. Although nesting in the heterospecific subcolonies did not result in reduced aggression, skimmers in these subcolonies spent less time in aggressive behaviors when they nested nearer heterospecifics than conspecifics.

On several occasions, we observed black skimmers pecking and tossing neighboring chicks that wandered close to their nests, and Burger and Gochfeld (1990) observed skimmers cannibalizing chicks. We did not observe terns being aggressive towards chicks. Thus skimmers may maintain a degree of hostility towards conspecific neighbors in order to reduce the risk of having their chicks injured or even cannibalized. Further, because the breeding period of gull-billed terns precedes that of the skimmers by 1–2 weeks, most of the terns leave the nest site with their chicks shortly after skimmer chicks hatch. For skimmers that nested near the terns, this translates into more space around the nest sites, and hence more room for chicks to wander in without being attacked for trespassing into a neighboring nesting area. Thus it is possible that skimmers have decreased chick mortality as well as the time and energy spent in aggressive displays by nesting closer to gull-billed terns than other skimmers.

Given the reduced levels of aggression observed when they were nesting next to a tern, it is not surprising that skimmers nested significantly closer to their nearest neighbor when it was a gull-billed tern rather than another skimmer. Although skimmers nested only 10 cm further from their nearest neighbor when it was a conspecific, it is possible that this increased area is sufficient to ensure enough space for skimmer chicks to move around without being within pecking distance of the neighboring skimmer. Skimmers were also found to nest closer to the common terns than other skimmers in New York and New Jersey (Burger and Gochfeld 1990).

It is possible that a species, preference and requirement of nesting microhabitat may influence nest density such that a densely packed area may be a function of habitat features rather than the presence of individuals of another species. Gull-billed terns and black skimmers do use different nesting material; nest sites of gull-billed terns have a higher proportion of shell than nest sites of skimmers (Leberg et al. 1997). However, during the three years of this study there was no shell on the islands, presenting an apparently homogenous substrate of sand for individuals of both species to choose nest sites (Pius-Balakrishnan 1996).

Although due to small sample sizes our statistical comparison was not powerful enough to detect any difference in density among subcolony types, the density of black skimmers nesting in single species subcolonies was typically less than the density of nests in the mixed species subcolonies. Yet skimmers in the single species subcolonies did not have significantly larger inter-nest distances than Skimmers in the mixed species subcolonies. Given that aggression is often expressed due to the establishment and the maintenance of territories (Tinbergen 1953), it is puzzling why skimmers in the single species subcolonies did not increase inter-nest distances in response to available unoccupied space. skimmers, like other colonial birds, must maintain inter-nest distances that strike a balance between the need for social facilitation (Darling 1938), predator defense, and nest defense on one hand, and competition on the other.

There was no indication that aggression levels in skimmers increased with proximity to the neighboring nest. Instead, skimmer pairs that nested within 1 m of their neighbors spent less time in aggressive behavior than skimmer pairs with neighbors more than 1m away. This tendency among skimmers with close neighbors to be less aggressive was marked in the mixed species subcolonies and displayed to a lesser degree in the single species subcolonies. To explore this unexpected result we examined, *a posteriori*, an alternate hypothesis that the group of skimmers that nested within 1 m of their closest neighbor's nest predominantly had terns as their nearest neighbor, while those nesting at greater distances predominantly had skimmers as their nearest neighbors. The percentage of skimmers with gull-billed terns as their nearest neighbors decreased as inter-nest distance increased (69%, 38%, and 29% for inter-nest distances of <1 m, 1–2 m, and >2 m, respectively). This difference was significant (G-test of independence; $P < 0.001$). Because closest neighbors tended to be gull-billed terns, aggressiveness increased with distance in the mixed species subcolonies.

Comparisons between the two colony types were not on the same temporal scale, because the single species subcolonies were formed two weeks after the mixed species subcolonies. By comparing both types of colonies throughout the incubation and hatching stages, we avoided possible biases that might result if aggressive responses change due to a bird's stage of reproduction. However, the skimmers in the two types of colonies may have differed in age, breeding experience, and energetic fitness. It is unknown whether or not these differences existed and if they influenced the results of the comparisons between the colony types. Other factors such as rate of predation, kind of predators, availability of food, and distance to food may have also had an affect on aggression levels, territory sizes, or both. Thus caution should be used in interpreting the results.

With these potential problems in mind, our results do not support the hypothesis that black skimmers spend less time in aggressive behavior when in mixed species colonies than in single species colonies as predicted by Burger (1981). Skimmers in the single species subcolonies were less aggressive than skimmers in the mixed species subcolonies despite nesting at similar inter-nest distances. We offer two hypotheses for this observation. First, because the mixed species subcolonies were denser than the single species subcolonies, a pair of skimmers in the mixed subcolonies had more close neighbors than its counterparts in the single species subcolonies. With more close neighbors, the time spent in aggressive interactions between neighbors should increase. Secondly, although aggressive interactions between neighbors prevail, it is common for territory holders to become accustomed to their neighbors and reserve stronger hostility towards intruders (Washer and Wiley 1980; Krebs 1982). If mixed species subcolonies are "hot spots" that continue to attract late arriving skimmers (Nelson 1970), then skimmers with established nests would be aggressive towards these intruders that attempt to nest, or displace an existing nest, in the mixed species subcolony.

Many studies suggest that the main advantage derived by a species nesting with heterospecifics is protection from predators (Erwin 1977; Burger 1984; Young and Titman 1986; Burger and Gochfeld 1990). This advantage, derived through lowered predation in mixed species colonies than in single species colonies, may be the reason for the evolution and the maintenance of mixed species colonies in seabirds. If an increase in aggression is associated with mixed species colonies (because of high densities), the antipredator benefit must out weigh this cost, and nesting next to a heterospecific may make nesting in a mixed species colony more tolerable. Our data suggest a modification to the theoretical prediction of Burger (1981) that one benefit birds derive nesting in heterospecific colonies is reduced aggression. Rather, they nest in a mixed species colony for other reasons such as protection from predators, and nest next to heterospecifics to reduce time spent in aggression.

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