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EXPERIMENTAL ASSESSMENT OF THE INFLUENCE OF GULL-BILLED TERNS ON NEST SITE CHOICE OF BLACK SKIMMERS

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Abstract. The hypothesis that members of one species might benefit from nesting with heterospecifics has been proposed to explain the existence of mixed-species breeding colonies. Black Skimmers (*Rhynchops niger*) usually nest in close association with one of several tern species (*Sterna* spp.); benefits of this association might lead skimmers to use different nesting substrates than terns, thus facilitating coexistence. Manipulating availability of substrates, we found that skimmers exclusively nested on substrates normally occupied by terns, indicating that habitat partitioning detected in previous studies was not a result of species-specific preferences. Using arrays of tern, skimmer, and control decoys, we found that skimmers nested more often with conspecifics than with terns. Our re-

sults suggest that the tendency of skimmers to nest in association with terns, but on different substrates, may be more influenced by nesting sequence than from a preference to nest near terns.

Key words: colonial waterbirds, competition, mixed-species colony, nest site selection, *Rhynchops niger*, seabird, *Sterna nilotica*.

Estimación Experimental de la Influencia de *Sterna nilotica* sobre la Selección de Sitios de Nidificación de *Rhynchops niger*

Resumen. La hipótesis que sugiere que miembros de una especie podrían recibir beneficios al anidar con organismos de diferentes especies ha sido propuesta para explicar la tendencia de algunas aves coloniales a formar grupos interespecíficos de nidificación. Individuos de *Rhynchops niger* generalmente anidan en asociación con alguna de las diferentes especies de golondrinas marinas (*Sterna* spp.). Los beneficios de esta asociación podrían hacer que *R. niger* utilice diferentes substratos para anidar que aquellos utilizados por las

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golondrinas lo cual facilitaría su coexistencia. Al manipular la disponibilidad de los sustratos, se encontró que *R. niger* anida en sustratos ocupados normalmente por golondrinas; indicando que la repartición del hábitat observada en estudios previos no es el resultado de preferencias especie-específicas. Encontramos que los rayadores anidaron más comúnmente con miembros de su misma especie que con golondrinas cuando se les dio la opción de elegir entre grupos al utilizar líneas de señuelos. Nuestros resultados sugieren que la tendencia de *R. niger* a anidar en asociación con golondrinas en diferentes sustratos podría estar más influenciada por la secuencia de nidificación, que por la preferencia de anidar en proximidad a las golondrinas marinas.

Mixed species groups are common among colonial birds. Many species may nest with other species primarily for the purpose of protection from predators (Erwin 1979, Burger 1981, 1984). Given that some colonial birds have similar habitat needs, it is also possible that species nest together only because suitable habitat is limited (Burger 1981). If several species use similar habitats with limited nest sites, the presence of multiple species in a colony could result in interspecific competition for nest sites (Burger and Shisler 1978, Quintana and Yorio 1998). Determining whether individuals prefer nesting with heterospecifics or simply require the same habitat is fundamental to understanding the formation of mixed-species colonies.

Subtle differences in habitat requirements of heterospecifics may make habitat partitioning possible. In addition to reducing competition for nest sites, habitat partitioning may allow an area to support a larger colony of heterospecifics than would be possible if the colony were composed of a single species. Because the effectiveness of defense against predators increases with colony size (Burger and Gochfeld 1990), habitat partitioning could benefit all members of a colony that are vulnerable to the same predators.

The Black Skimmer (*Rhynchops niger*) nests in close association with a variety of terns (*Sterna* spp.) throughout its range (Burger and Gochfeld 1990, Gochfeld and Burger 1994). In Louisiana, Black Skimmers often nest with Gull-billed Terns (*S. nilotica*, Leberg et al. 1997, Pius and Leberg 1997, 1998). Leberg et al. (1997) found that Black Skimmers and Gull-billed Terns have different nest site characteristics, suggesting habitat partitioning. Nest sites of Gull-billed Terns had much higher proportions of shell than did the nest sites of skimmers. By experimentally manipulating shell availability, Mallach and Leberg (1999) found that terns occupied substrates with a high content of shell much more frequently than did skimmers, and that skimmers were equally likely to nest on sand-silt substrates as on shell. The apparent lack of preference by skimmers was puzzling, as eggs of both skimmers and terns were more likely to hatch and were better camouflaged when laid on shell than on sand-silt substrates (Mallach and Leberg 1999). This finding, and the tendency of Gull-billed Terns to select nest sites earlier than Black Skimmers, provided the alternative hypothesis that terns may exclude skimmers from nesting on shell, creating the appearance of hab-

itat partitioning. In this paper, we further investigate skimmer nest-site choice and coloniality.

Our first objective was to experimentally assess whether Black Skimmers nested on a different substrate than Gull-billed Terns as a matter of choice, or if apparent habitat partitioning was actually the result of interspecific competition for a preferred substrate. To do this, we experimentally provided both shell and sand-silt substrates to nesting skimmers after terns had established their nests.

Our second objective was to determine if skimmers were attracted to the presence of heterospecifics in their search for nesting areas. Black Skimmers are so exclusively associated with terns that some observers (Erwin 1977, Burger and Gochfeld 1990) argue that skimmers actively choose to nest in tern colonies. Although the hypothesis that skimmers are attracted to tern colonies is not unreasonable, it is possible that breeding skimmers are simply attracted to active colonies of seabirds, and not strictly terns. Because terns nest earlier than skimmers, they may be the only nesting seabirds present when skimmers initiate nest-site selection. To test the hypothesis that skimmers choose to nest with terns, we arranged decoys of Black Skimmers and Gull-billed Terns into monospecific groups, so that Black Skimmers arriving at the breeding site could choose to nest with either species. Based on past work suggesting a strong association between terns and Black Skimmers, we predicted that Black Skimmers would nest in larger numbers in plots containing Gull-billed Tern decoys than in control plots or plots containing Black Skimmer decoys.

METHODS

Since 1991, Black Skimmers and Gull-billed Terns have nested on 1–3-year-old islands composed of dredged materials in the Atchafalaya Delta, St. Mary's Parish, Louisiana (29°27'N, 91°17'W; Leberg et al. 1997). We studied nesting colonies between early May and mid-August, in 1995 and 1996 (Pius and Leberg 1997, 1998). Work that involved entering the colonies was restricted to <30 min in the early morning or late evening. Observations were made from towers ≥40 m from the colony edge.

The composition and distribution of substrate available to birds in our study area is a function of the source of dredge material used to create islands (Mallach and Leberg 1999). During this study, shell was very rare on the surface of the islands we examined (<2% of the available nest substrates), making it difficult to determine if substrate composition influenced nest choice from an examination of nest sites. To determine if skimmers would choose shell over sand and silt as nesting substrate, we created 30 plots of each of these two substrates. Each plot contained either shell fragments or sand and silt particles spread in a circle of 1 m in diameter. These plots were placed around a large mixed-species colony in the summer of 1996. Because Gull-billed Terns rapidly occupy shell plots early in the nesting season (Mallach and Leberg 1999), we established our substrate plots approximately a month after the first terns had nested, reducing the likelihood of terns occupying the shell sites. Twice a week, we used a spotting scope to determine how

many sand and shell plots were occupied by nesting skimmers.

Because it is difficult to manipulate the composition of seabird colonies, we used decoys to test the hypothesis that skimmers were more likely to nest with heterospecifics than with conspecifics. Seabirds often respond well to decoys (Fancher 1984, Blokpoel et al. 1997), but little published information exists regarding responses of skimmers to decoys. Decoys were cast from molds using a quick-hardening urethane (POR-A-KASTTM, Chattanooga, Tennessee); molds were formed from hand-carved models. Six decoy arrays were established on three islands in the summer of 1995, and four arrays established on two islands in the summer of 1996. Arrays were established about a week after a colony of terns and skimmers was initiated on a dredge-material island. We placed decoy arrays on what we perceived as suitable habitat: bare areas of substrate away from the tidal zone. The decoy arrays were placed no closer than 500 m to other nesting seabirds, reducing the possible influence of the presence of established colonies on the decoy experiment. Birds in naturally formed colonies did not respond when investigators entered the areas around the decoy arrays.

Decoy arrays consisted of three 16-m² square-shaped subplots. The centers of the three subplots were each 10 m from the center of the array plot and were equidistant from each other (~17 m apart). The three decoy treatments were randomly assigned to the three subplots in each array. These treatments consisted of either 16 Black Skimmer decoys, 16 Gull-billed Tern decoys, or 16 pieces of PVC pipes, about 30 cm long and 3.8 cm in diameter. Pipes were chosen as a control because of the possibility that skimmers might treat decoys as structural objects rather than potential colony members.

On a weekly basis, decoy arrays were checked for the presence of skimmers nesting in any of the subplots, and the locations of nests were noted so that they would not be counted twice. The response variable for this experiment was the number of skimmer nests in a subplot; decoy array was the unit of replication. A randomized block ANOVA was used to control for variation in the number of skimmer nests among arrays; each array was treated as a block in this analysis. A Tukey's multiple comparison test was used to evaluate differences in the number of skimmers nesting among treatments using a significance level of $P < 0.05$. Statistical analyses were conducted using SAS (SAS Institute 1999).

RESULTS

When both shell and sand substrates were available for nest sites, Black Skimmers nested on shell more often than on sand. Sixteen of the 30 plots with a shell substrate were occupied by skimmer nests, while all 30 plots with a sand-silt substrate remained unoccupied.

Seabirds did not use 6 of the 10 arrays of decoys; these arrays were omitted from the statistical analysis of colony choice. Two of the arrays not occupied by nesting skimmers were located on an island that seabird colonies had abandoned because it was subject to flooding. There is no obvious explanation for the fail-

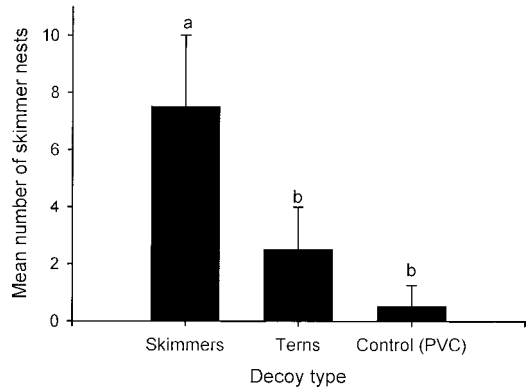


FIGURE 1. The mean (\pm SE) number of skimmer nests established near Black Skimmer decoys, Gull-billed Tern decoys, and PVC pipes, which served as controls, on dredge-material islands in the Atchafalaya Delta, Louisiana. Means are based on four experimental decoy arrays where Black Skimmers nested during 1995 and 1996. Different letters above bars indicate significantly different means ($P < 0.05$).

ure of the remaining four decoy arrays to attract nesting birds.

For the four arrays that attracted skimmers, the null hypothesis that skimmers nested in similar proportions in the skimmer, tern, and control subplots was rejected ($F_{2,6} = 11.4$, $P < 0.01$; Fig. 1). There was no support for the prediction that Black Skimmers preferred to nest with Gull-billed Terns rather than other skimmers. Skimmers nested in higher numbers closer to Black Skimmer decoys than to Gull-billed Tern decoys or PVC. Although there was a tendency for more skimmers to nest among the tern decoys than among the PVC pipes, this difference was not statistically significant.

DISCUSSION

Our study provides experimental evidence that nest site choice in seabird colonies may be affected by the presence of other species. Previous studies suggest that Gull-billed Terns, but not Black Skimmers, choose shell substrates over sand-silt substrates (Leberg et al. 1997, Mallach and Leberg 1999). However, these differences in nesting substrates between species are not strong evidence for habitat partitioning. Our results indicate that when given a choice, skimmers will nest on shell substrates to the complete exclusion of the nearby sand substrates. Given the strong preference that skimmers have demonstrated for shell, it is likely that there is competition for this substrate when it is limited in availability. Terns nest before skimmers in Louisiana (Leberg et al. 1997, Mallach and Leberg 1999), so tern occupancy of limited shell substrates would give the appearance that skimmers and terns were selecting different substrates. Because nest camouflage and hatching success are higher for nests on shell substrates than on sand-silt substrates (Mallach and Leberg 1999), the association between the two species may result in reduced reproductive success of

skimmers. However, if all available shell has been occupied by terns, there might be no additional costs for skimmers choosing to nest with terns rather than in monospecific groups, as either strategy would involve nesting on sand-silt substrates.

In interpreting results of the decoy experiment, we assume variation in the numbers of skimmers nesting next to different decoy types reflects choices that would be made if single-species colonies of skimmers and terns were equally available to birds selecting nest sites. This assumption might be violated if skimmer decoys were more realistic than tern decoys. Human observers noted no difference in the degree of realism between the decoys. If the skimmer decoys were more realistic than the tern decoys, this difference would not fully explain our finding that skimmers tended to nest with conspecifics rather than with terns. Skimmers had the opportunity to nest in large colonies that included terns, but still nested among the skimmer decoys. The choice to nest with decoys rather than in extant colonies was not the result of colonies being so large they had saturated all available habitat. There were large, relatively unoccupied areas near each colony on which skimmers established nests at the same time others were nesting in the decoy arrays.

Our results do not support the hypothesis that Black Skimmers seek to nest in close association with terns (Erwin 1977, Burger and Gochfeld 1990, Pius and Leberg 1997), as skimmers nested in higher proportions next to skimmer decoys than tern decoys. This observation does not preclude the possibility that skimmers in mixed-species colonies benefit from the aggressive responses of terns to predators or from fewer aggressive interactions when nesting close to terns rather than other skimmers (Burger and Gochfeld 1990, Pius and Leberg 1997, 1998).

Given that terns nest prior to skimmers, it is possible that skimmers are simply attracted to the presence of nesting seabirds and not specifically to nesting colonies of terns. Skimmers might nest with other skimmers if monospecific colonies were available. This suggestion is similar to the hypothesis that skimmers use existing colonies as indicators of sites that are safe from predators and tidal action (Burger and Gochfeld 1990). The hypothesis that nesting seabirds are indicators of good nest sites cannot fully explain our results, because it predicts that skimmers would be equally likely to nest among tern and skimmer decoys.

Scale must also be considered in the interpretation of the decoy experiment. It is possible that Black Skimmers prefer to nest close to conspecifics, but at the same time prefer to nest in colonies of skimmers located near terns. Tern decoys were located approximately 17 m from skimmer decoys; perhaps skimmers have a preference to nest with other skimmers as long as they perceive that terns are close enough to participate in anti-predator behavior. The choices made by Black Skimmers in our study might have been different if greater distances had separated our decoy treatments.

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