SPECIES INTERACTIONS IN A MIXED COLONY OF COMMON TERNS (*STERNA HIRUNDO*) AND BLACK SKIMMERS (*RYNCHOPS NIGER*)

BY R. MICHAEL ERWIN*

Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, Massachusetts 01003

Abstract. Black skimmers (*Rynchops niger*) frequently nest among common terns (*Sterna hirundo*) on coastal islands from North Carolina to New York. Behavioural interactions among terns, skimmers, and several potential avian predator species were quantified during the 1973 breeding season at Fisherman Island, Virginia. Common terns were dominant to skimmers, chasing and dive-attacking neighbouring pairs, while skimmers rarely chased terns. Despite agonistic interactions, nesting success of both species was no different whether nearest neighbours were conspecifics or heterospecifics. Common terns chased away potential avian predators much more frequently than did skimmers. Black skimmers, then, appear to derive a 'protective cover' benefit from nesting among the terns. Neither nest-site limitation nor food 'information-sharing' appear to account for the species associations.

Studies of two or more species occurring together in similar habitats have focused chiefly upon competition and niche partitioning (MacArthur 1972; Cody 1974; Morse 1974). Where coexistence persists despite apparently large ecological overlap, interactions between species should exert increases in energetic demands, especially where interspecific territoriality occurs (Orians & Willson 1964; Murray 1971). Such co-occurrences may result when resources are too homogeneous to partition effectively (Orians & Willson 1964).

The recent theoretical and empirical obsession with 'negative' interactions (i.e. competition and predation) may be obscuring the relative importance of such 'positive' associations as mutualisms or commensalisms (Risch & Boucher 1976). The latter are frequently documented only in relatively anecdotal terms; few studies provide any quantitative analysis. In birds, most studies of interspecific breeding associations involve seabirds, where a number of tern and duck species have been reported to nest among aggressive gulls and other terns, thereby gaining protection from predators (Belopol'skii 1957; Koskimies 1957; Lind 1963; Kruuk 1964; Evans 1970). However, this protective advantage may be nullified in cases where nest space or food becomes limiting or where 'protector' species occasionally themselves become predators of nearby individuals (Kruuk 1964).

In this paper, I quantify interactions within a mixed colony of common terns (*Sterna hirundo*) and black skimmers (*Rynchops niger*) in Virginia.

Emphasis is placed on nearest-neighbour interactions and differential responses to potential avian predators. The behavioural data, supplemented by studies of colony association of these species both in the region of the study (Erwin 1975, 1977a, 1977b) and in other mid-Atlantic regions (Soots & Parnell 1975; Gochfeld 1977; Erwin & Korschgen in press), are used to consider the selective basis for the nesting association.

Study Area and Methods

Study Site

From late April through August 1973, observations were made at Fisherman Island National Wildlife Refuge (37°06′, 75°58′), Cape Charles, Northampton County, on the eastern shore of Virginia. On this small, uninhabited barrier island, four subcolonies of common terns and black skimmers were located on sparsely vegetated sandy beach, less than 2 m above mean high tide. Most nests were placed next to small clumps of sea rocket (*Cakile edentula*) or beach grass (*Ammophila breviligulata*). No mammalian predators occur on Fisherman Island (Buckley & Buckley 1972; D. Holland, personal communication), but a number of potential avian predators of eggs and/or chicks nested on the island, including herring gulls (*Larus argentatus*), laughing gulls (*L. atricilla*), great black-backed gulls (*L. marinus*), fish crows (*Corvus ossifragus*), and black-crowned night herons (*Nycticorax nycticorax*).

Behaviour

I selected the largest of the four subcolonies for observations because its location allowed the

*Present address: Migratory Bird and Habitat Research Laboratory, U.S. Fish and Wildlife Service, Laurel, Maryland 20811.

best visibility of the entire colony. In May, an observation blind was erected about 20 m from the edge of the colony. From early May through June, I checked nests and made visual estimates in the colony to determine total breeding numbers of each species. All active nests were marked.

From May 27 through July 8, I made observations from the blind during periods of from 0·5 to 4·0 h throughout the day. Times were randomly selected among days to minimize temporal bias. The observations did not begin until both species had begun egg-laying and terminated when the majority of young were fledged. A total of 38·25 h was spent observing over 15 days.

I recorded on standard data sheets all occurrences of the following acts within the colony: (1) aerial chases (frequency and duration) of all species involving two or more individuals, (2) dive or 'stoop' attacks (frequency of attacks and number of dives per attack), (3) predation attempts upon either eggs or chicks and the identity of the predator, and (4) departure from the nest resulting from either agonistic or predatory interactions. Chase duration was measured to the nearest second with a stopwatch.

Nesting Success

To test for a species effect on hatching success, nests of both black skimmers and common terns were marked with numbered wooden stakes after clutches were initiated. Because observations revealed that a predominant (91 %) proportion of agonistic interactions involved nearest-neighbour pairs, I marked 40 and 30 nests of common terns and black skimmers, respectively, whose nearest neighbour was a conspecific. Also 30 nests of each species were marked whose nearest neighbour was a heterospecific. Nests were chosen haphazardly throughout the central part of the colony to mitigate any position (edge versus centre) effects that might be important (Kruuk 1964). All nests within 8 m of each nest studied were mapped to test for density differences.

To test for differential fledging success, groups of nests of each species were enclosed with 2·5-cm-mesh poultry wire to prevent the young from scattering during nest-checks. The enclosures were erected after all clutches had been completed to reduce the chance of desertion. Four large (diameter 4 to 6 m) enclosures were set up; one contained 13 common tern nests, another contained 10 black skimmer nests, and the other two each contained five nests of each species. The nest groups were selected so that density differences between groups were minimal. Shortly after each chick hatched, a U.S. Fish and Wildlife Service aluminium band was placed on it to allow individual and nest identification. Nest-checks were made every two to three days throughout the season. The fate of all eggs and chicks was recorded. Because the enclosure was very low (c. 24 cm) and large chicks could occasionally escape, I considered 'missing' chicks more than 18 days old to be fledged. Studies have shown that most mortality among gull and tern chicks occurs in the first seven to ten days (Kadlec et al. 1969; Nisbet & Drury 1972).

Nest Movement Experiment

In a further attempt to compare species interaction effects upon nest success, I manipulated nest placement in another subcolony in order to intensify pair interactions. I marked six nests each of common terns and black skimmers whose nearest neighbour was a conspecific. In each of these nearest-nest pairs, one was moved a distance one-half the original inter-nest distance closer to the other. Similarly, 12 pairs of common tern–black skimmer nearest-neighbour nests were selected. For half of the 12 pairs, common tern nests were moved, while for the other half, black skimmer nests were moved. This design allowed separation of movement, distance reduction, and species effects. Twenty control nests each of common terns and black skimmers were chosen near the experimental nests. For nests that were moved, I attempted to reconstruct the sand nest cup and repositioned the nest material (if any) and eggs as close to the original position as possible. The fate of the clutches in all of the nests was determined by checking nests every two to three days until hatching (or clutch loss). If at least one egg hatched in a given clutch, the clutch was scored as 'hatched'.

Non-parametric statistical analysis was used throughout because of limited sample sizes. Medians, means, and standard deviations are presented in tables to provide clarity and simplicity. Mann–Whitney U (or z if $n \geqslant 30$) and Kruskal–Wallis H values are given with probability levels (Siegel 1956).

Colony Association

In 1977, a thorough survey of seabird colonies was conducted from Maine to Virginia (Erwin & Korschgen, in press). All common tern and

black skimmer colonies in New York, New Jersey, and Virginia were censused during June and classified as either single-species or mixed-species colonies.

Results

Common terns arrived on Fisherman Island during late April and early May, with black skimmers arriving about one week later. The terns established territories and began nest-building throughout the first two weeks in May with egg-laying beginning on May 15. Black skimmers began laying eggs on May 23.

Repeated censusing showed that approximately 100 pairs of common terns, 80 pairs of black skimmers, and 3 pairs of herring gulls nested within the subcolony boundary. All three herring gulls nested on the periphery of the colony. In a dune area west of the tern colony, a colony of two great black-backed gulls and 300 to 400 pairs of herring gulls nested. Also, several hundred pairs of laughing gulls nested within 0·5 km of the tern–skimmer colony. A colony of about 800 pairs of royal terns (*Sterna maxima*) was located within 1 km of the study colony.

Total agonistic interactions involving all the species seen within the colony vicinity are shown in Table I. A disproportionate percentage of the total encounters involved common terns. In the following sections, I will first consider tern–skimmer interactions, then examine relations with the other species.

Common Tern–Black Skimmer Interactions

In agonistic encounters, a strong asymmetry is apparent between common terns and black skimmers (Table I). Common terns frequently dive-attack black skimmers that are standing or incubating, while the latter have never been reported to dive-attack during hostile encounters (Wolk 1959; Sears et al. 1976). On eight occasions, the dive-attacks were of sufficient intensity to drive skimmers from their own territories.

Chase duration (Table I) is significantly longer when heterospecifics are involved than when conspecifics are chasing each other for both species ($Z = 2·70$, $P = 0·007$ (common tern); $Z = 2·10$, $P = 0·036$ (black skimmer)). The pattern of chase frequency, however, is different for the two species. Common terns chase skimmers much more frequently than is expected on the basis of relative species proportions (Hailman 1975), while black skimmers most frequently chase other skimmers ($2 \times 2 \chi^2$ contingency test; $\chi^2 = 102·6, P < 0·001$). Common terns, then, appear to be socially dominant to skimmers.

Because observations spanned a large part of the nesting period, I examined seasonal (nesting phase) effects on behavioural interactions: incubation phase (May 17–June 5), peak hatching phase (June 6–16), and chick phase (June 17–July 8) (Table II). Common terns showed no seasonal change in the per-hour frequency of intraspecific chases ($H = 4·92$, $P > 0·05$) but reduced their chases of skimmers late in the season ($H = 6·97$, $P < 0·05$). The

Table I. Total Agonistic Interactions in Mixed Common Tern–Black Skimmer Colony, May–July 1973*

Aggressor	Type		Common tern	Black skimmer	Royal tern	Herring gull	Laughing gull	Fish crow
					Species aggressed against			
Common tern	Chase	Frequency	22	79	17	12	15	2
		Mean duration (s)	2·7 ± 2	3·9 ± 2	3·0 ± 2	4·7 ± 3	5·9 ± 5	5·5**
		Median	2	3	2	3·5	4	5·5
	Dive attack	Frequency	0	90	0	62	0	0
		Mean intensity (dives/attack)	–	7·2 ± 9	–	12·0 ± 26	–	–
		Median		4		4		
Black skimmer	Chase	Frequency	5	26	0	1	3	0
		Mean duration (s)	4·0 ± 1	2·9 ± 2	–	3·0**	8·7**	–
		Median	4	2			4	

*Duration and intensities are expressed as means ± 1 standard deviation (rounded to nearest whole number).
**No standard deviation due to insufficient sample size.

Table II. Seasonal Changes in Chase Frequency and Duration between Common Terns (CT) and Black Skimmers (BS)*

Species			Period		
Chaser	Chased		Incubation	Hatching	Chick
CT	CT	Mean no. chases/h	0.42 ± 0.20	0.50 ± 0.22	0.52 ± 0.18
		Median	0.5	0.3	0.7
		Mean duration(s)	2.3 ± 3	3.3 ± 1	2.6 ± 1
		Median	1	3	3
		n	8	7	7
CT	BS	Mean no. chases/h	2.25 ± 1.30	2.47 ± 0.95	1.37 ± 0.55
		Median	2.1	2.7	0.8
		Mean duration(s)	4.7 ± 3	3.4 ± 2	3.7 ± 2
		Median	4	3	2
		n	27	29	23
BS	BS	Mean no. chases/h	0.92 ± 0.41	0.60 ± 0.08	0.65 ± 0.10
		Median	0.3	0.7	0.5
		Mean duration(s)	2.7 ± 1	2.7 ± 1	3.3 ± 3
		Median	2	2	2.5
		n	11	6	9

*Results from four days (10.5 h) during incubation, five days (10.5 h) during peak hatching, and six days (17.25 h) during the chick phase. Means $\pm$ 1 standard deviation are given.

duration of intraspecific common tern chases was lowest during incubation and highest during the hatching phase ($H = 6.90$, $P < 0.05$). No statistically significant change occurred in tern–skimmer chase duration ($H = 0.12$, $P > 0.05$). Black skimmers showed no seasonal change in intraspecific chases either in frequency ($H = 5.35$, $P > 0.05$) or duration ($H = 0.04$, $P > 0.05$). There were insufficient data to analyse seasonal changes in chases directed at common terns.

Nesting success data indicated that a nearest-neighbouring species effect is slight. Common tern clutches were equally successful in hatching whether the nearest neighbour was another tern or a black skimmer. There was no difference in nest density between groups. With other terns as neighbours, 50% (or more) of the clutch hatched in 29 of 40 nests; with skimmers as neighbours 24 of 28 nests had a clutch success of at least 50% ($\chi^2 = 1.71$, $P > 0.10$). There was, however, a difference in total egg success, with neighbouring common terns reducing hatchability (65 hatched of 99 total) more than skimmers (61 hatched of 76 total) ($\chi^2 = 4.59$, $P < 0.05$). Clutch success was independent of nearest neighbour species in black skimmer nests as well. With other skimmers as neighbours 21 of 30 nests had a clutch success of more than 75%; next to common terns, more than 75% of the clutch hatched in 17 of 30 nests ($\chi^2 = 1.41$, $P > 0.20$). Similarly, eggs were equally successful if neighbours were common terns (92 of 115 total) or other skimmers (98 of 116 total)

($\chi^2 = 0.80$, $P > 0.30$). The probability of a hatched chick surviving until fledged also seemed to be independent of the nearest-neighbour species in the nesting enclosures. Of 13 nests, 4 had all young fledge among common tern–common tern nesting pairs. With skimmers as neighbours, 3 common tern nests in 10 had all young fledge (Fisher Exact Probability value $D > 2$, $P > 0.05$). Among black skimmers, 6 of 10 nests produced no fledged young when common terns were neighbours; 3 of 10 nests were unsuccessful when other skimmers were adjacent ($D > 2$, $P > 0.05$). Larger samples might have shown that common terns adversely affected skimmer chick survival.

The nest-movement experiment similarly revealed no clear-cut effect of nearest-neighbour species on hatching success ($P = 0.14$; Table III). Additional tests showed that nest movement

Table III. Interspecific versus Intraspecific Effects on Clutch Success in Nest-Movement Experiments*

	Clutch success	
Neighbours	Hatched	Failed
(1) CT × CT	8	4
(2) CT × BS	11	1
(3) BS × BS	8	4
		$P = 0.14$ (for both comparisons 1 and 2 and 2 and 3)

*Fisher Exact Probability values are given. CT = common tern, BS = black skimmer.

had no effect on hatching success in either species (Fisher Exact Probability values, $P = 0.34$ for both species) and that the effect of reducing inter-nest distance was not significant (Fisher Exact Probability value, $P = 0.12$ for common terns; $P = 0.21$ for black skimmers). Again, an increased sample size might have revealed a more intense intraspecific effect on hatching for both species. In all cases of clutch failure, nests were deserted within three days after the manipulation.

I never witnessed any egg destruction or attacks on chicks by common terns, black skimmers or herring gulls. Food piracy also was never seen at any time.

Joint 'Predator' Responses by Terns and Skimmers

Both herring gulls (Hatch 1970; Nisbet & Drury 1972) and laughing gulls (Watson & Lashley 1915 as cited in Dinsmore 1972; Buckley & Buckley 1972) prey upon tern eggs and/or chicks. Fish crows are notorious egg predators of herons (M. Byrd, personal communication) and therefore might be expected to take seabird eggs on occasion. Royal terns, however, have never been seen eating eggs or chicks of any seabird species (Bent 1921; Buckley & Buckley 1972).

Flights of all of the above species over or near the colony elicited chasing by common terns and to a lesser degree, black skimmers (Table I). A disproportionate number of chases, however, were initiated by common terns ($\chi^2 = 13.6$, $P < 0.01$). In all cases, the invader was driven off and made no attempt to land. Occasionally several birds joined in a chase, but the data presented here are based only on the initiator.

Throughout the nesting season, I never witnessed any predation.

Common Tern Aggression Directed at Heterospecifics

As shown above, common terns chase and dive-attack black skimmers nesting among them. However, the three pairs of herring gulls nesting in the colony elicited both chases and dive-attacks significantly more often (relatively) than did skimmers ($\chi^2 = 20.0$, $P < 0.001$ (chases); $\chi^2 = 533$, $P < 0.001$ (dives)). Chase duration and intensity of dive-attacks by terns were also greater when gulls were targets but not significantly so (Table I: $Z = 0.05$, $P > 0.05$ (dive-attacks); $Z = 0.83$, $P > 0.05$ (chase duration)).

The seasonal change in dive attacks showed that, at hatching, common terns attack black skimmers more frequently and with more intensity than either during incubation or later during the chick phase (Table IV; $H = 7.18$, $P < 0.05$) (frequency); $H = 6.69$, $P < 0.05$ (intensity)). Dive-attacks on herring gulls showed no significant seasonal effect ($H = 5.16$, $P > 0.05$ (frequency); $H = 1.49$, $P > 0.05$ (intensity)) but there was an indication of a decline late in the season. The variation in dives per attack on gulls was considerable, ranging from 2 to 180. On all occasions, only terns nesting adjacent to gull nests initiated dive attacks.

The duration of common tern chases directed at each species (except fish crows), including conspecifics, was compared (Table I). Pairwise comparisons using Mann–Whitney U tests showed that common terns discriminate royal and common terns from gulls and black skimmers, but that no discrimination (i.e. statistically

Table IV. Seasonal Changes in Dive-Attack Frequency and Intensity by Common Terns Directed at Black Skimmers (BS) and Herring Gulls (HG)*

Attacked species		Period		
		Incubation	Hatching	Chick
BS	Mean no. dive-attacks/h	2.70 ± 1.1	3.14 ± 1.4	1.68 ± 0.9
	Median	3	4	1
	Mean intensity (dives/attack)	7.79 ± 9.0	9.30 ± 12.0	4.14 ± 2.6
	Median	4.5	5	3
	n	28	33	29
HG	Mean no. dive-attacks/h	1.81 ± 1.4	2.20 ± 2.0	0.93 ± 0.7
	Median	1.5	2.7	1.2
	Mean intensity (dives/attack)	16.00 ± 40.1	13.20 ± 18.8	6.95 ± 9.1
	Median	3	5	4
	n	19	23	20

*Observation periods same as in Table II.

significant) occurs between the two gull species and black skimmers. No significant difference between chase duration of herring gulls and royal terns resulted due to small samples and high variation. In effect, based only on chase duration, non-terns are treated similarly and are pursued with greater intensity than either common terns or royal terns. Although not statistically significant, the longer chases of laughing gulls may reflect their greater threat as predators. They have been seen eating royal tern eggs on numerous occasions on Fisherman Island (Buckley & Buckley 1972; Erwin 1975).

Colony Association

In New York, New Jersey, and Virginia in 1977, black skimmers were associated almost exclusively with common terns (Table V). Of a total 3352 pairs of skimmers in the three states, only 242 (7%) nested in 'pure' colonies, with just one colony (230 pairs at Avalon, New Jersey) accounting for most of the total. On the other hand, the majority of common tern colonies were monospecific. Such colonies were smaller, however, than the mixed colonies. Mixed common tern colonies averaged ($\pm$ SD) 788 $\pm$ 1100, 125 $\pm$ 219, and 187 $\pm$ 182 pairs in New York, New Jersey, and Virginia, respectively, while pure tern colonies averaged only 143 $\pm$ 381, 64 $\pm$ 69, and 47 $\pm$ 42 pairs, respectively.

Discussion

Black skimmers are positively associated with common terns on the breeding grounds in Virginia, New Jersey, New York (Gochfeld 1977; Erwin 1977a, this study), and North Carolina (Soots & Parnell 1975).

Several non-mutually exclusive hypotheses may be generated to explain why these species nest together in the same colonies: 1. Nest-site

Table V. Frequency of Colony Association of Common Terns and Black Skimmers during 1977

	No. of colonies		
State	'Pure' black skimmer	'Mixed' tern–skimmer	'Pure' common tern
New York	0	9	27
New Jersey	1	12	31
Virginia	2	17	5

competition. If two or more species require very similar habitats that are in limited supply and are not easily partitionable (Orians & Willson 1964), they may compete for these sites (Belopol'skii 1957). As a consequence, each species may sacrifice some reproductive success in mixed colonies compared to 'pure' ones. 2. Predator avoidance. Individuals may reduce the risk of nest predation in several ways: (a) by increasing the joint defence of the colony (Darling 1938; Kruuk 1964; Hooglund & Sherman 1976), regardless of species composition, individuals in larger colonies may deter predation; (b) by associating with an aggressive 'protector' species (Koskimies 1957; Lind 1963; Kruuk 1964); (c) by nesting in the centre of the colony (selfish herd phenomenon of Hamilton 1971); (d) adding to the visual and/or acoustical confusion effect (Breder 1959; Morse 1970). 3. Food 'information sharing'. Individuals may enhance their efficiency at finding and exploiting patchy, unpredictable food resources by observing the foraging movements and success of neighbours (Krebs et al. 1972; Krebs 1974; Emlen 1975). Such an advantage could also extend to non-conspecifics that feed in mixed-species assemblages (Ward & Zahavi 1973) as long as good patches are rich enough to preclude competition. Of course, more than one of these factors may operate simultaneously, reinforcing the selective advantage. Each of these hypotheses will be considered in the light of the findings described above and those of related studies.

The two-species association is unlikely to be based on strict nest-site competition (hypothesis 1) for several reasons: First, both species are eurytopic, nesting in a variety of microhabitats ranging from open sand to salt marsh (Burger & Lesser 1977; P. A. and F. G. Buckley, personal communication; Gochfeld 1977; Erwin 1975, 1977a). Second, large expanses of seemingly suitable nesting habitat are unoccupied in Virginia, even though these areas appear (at least qualitatively) to be identical to occupied sites. In addition, many of these unoccupied sites are often later used as nesting sites either in the same year, after storms have washed out earlier colonies, or in subsequent years (Erwin 1977a; Gochfeld 1977), even with no apparent vegetational succession. Third, Gochfeld's (1977) long-term studies show that when terns change sites, skimmers always accompany them, even though the original site remains apparently unchanged. All of these factors considered together provide strong inferential evidence that

specific nest-site limitation cannot account for the nearly universal association of skimmers with terns.

Whether black skimmers effectively aid common terns in deterring predators is doubtful (hypothesis 2a). Of the total number of predator chases, black skimmers were involved in only a small percentage and only on two occasions did they join the terns in a coalition (Belopol'skii 1957), chasing herring gulls. Instead of jointly mobbing ground 'predators' (including the observer), skimmers use distraction displays (injury-feigning) (Wolk 1959; Sears et al. 1976), a defensive rather than offensive strategy.

By nesting within already established terneries, skimmers may effectively use the aggressive common tern as 'cover' from aerial predators (hypothesis 2b). As shown above, most chases of potential avian predators were initiated by terns and were successful in driving off intruders. 'Refuging' by skimmers within colonies of aggressive terns might conserve energy that would otherwise be required to repel predators. However, no obvious 'centre-seeking' (Lind 1963; Hamilton 1971) within tern colonies was found in 11 mixed-species colonies examined over a two-year period (hypothesis 2c). In general, skimmer nests are clustered in the more open sand patches within the colony, while common terns tend to nest in or close to vegetation. These slight microhabitat preference differences appear to account for most of the within-colony nest distribution. The same pattern was found in New York (Gochfeld 1977).

The importance of a confusion effect (hypothesis 2d) cannot be adequately assessed in the present study. A detailed investigation of predator responses to individuals in colonies of several different sizes would address this issue. However, whether skimmers could amplify predator confusion in a common tern colony is doubtful. First, skimmers do not mob and dive-attack in concert with terns. Second, they may fly away from the colony area, rather than aggressively defend it (Pemberton 1922; Gochfeld 1977; unpublished observation) during visits by humans. Lastly, their alarm vocalization consists of a low-frequency, soft 'bark' (Wolk 1959; Sears et al. 1976) in contrast to the common tern's shrill, piercing 'ke-arr' (Palmer 1941) and loud, staccato 'kek-k-k' during mobbing and dive attacks. The defensive noise level in tern colonies, then, is probably amplified only slightly by the presence of black skimmers.

An interesting note here is that, except for two insignificant marsh colonies in Virginia, the only 'pure' skimmer colony was the large (230-pair) Avalon colony. It is tempting to consider that a certain numerical threshold may exist, beyond which it is 'safe' to nest in monospecific colonies. The fact that skimmers are usually found in the larger tern colonies is also consistent with a 'safety' threshold hypothesis although, alternatively, this could be explained by a coincidental attractiveness to areas favourable to both species (Gochfeld 1977). Separating these two explanations would be most difficult.

Nesting in close proximity to the aggressive tern does not appear to be very harmful to skimmers, since reproductive success was no different between individuals nesting next to terns and those nesting adjacent to conspecifics. There was a tendency (non-significant), however, for skimmer chick survival to be lower when nesting adjacent to terns. Of course, I considered only hatching success and chick survival (to fledging) as measures of reproductive success. Other measures (e.g. growth rates of young) might reveal important differences.

An explanation of 'information sharing' about food location (hypothesis 3) is also unlikely to explain the nesting association. Even though they feed on similar prey sizes and species (Erwin 1975), they feed separately both in space (Erwin 1975, 1977b) and, to some extent, in time since crepuscular and nocturnal feeding is common in skimmers (Arthur 1921; Pettingill 1937). Most black skimmers forage alone or in pairs (Erwin 1977a) in shallow marsh flats and channels, while common terns actively join in large, mixed-species feeding assemblages over open-water fish shoals (Erwin 1975, 1977b).

Because skimmers are docile (Bent 1921; Wolk 1959; Gochfeld 1977) and pose no threat to tern eggs or chicks, the sustained attacks by terns do not appear to be adaptive. The incitement to chase and dive-attack skimmers might be expected to cause 'aggressive neglect' (Ripley 1961) or disruption (Darling 1938; Palmer 1941) of common terns, but this did not reduce either hatching or fledging success. Nonetheless, season-long attacks are certainly energetically costly.

There was some tendency for conspecific neighbours to be more detrimental, especially before hatching. Even though skimmers do elicit agonistic behaviour, tern attacks were relatively less frequent and/or intense toward skimmers than toward either herring gulls or laughing gulls.

Probably gulls are recognized as being dangerous (Markgren 1960; Lind 1963; Kruuk 1964; Hatch 1970).

Lastly, it would be very useful to monitor the reproductive success of a number of 'pure' skimmer and tern colonies to compare with that of mixed-species colonies over a series of years, to assess the long-term costs and benefits of the association. Given the nearly universal association of skimmers with common terns throughout their range of sympatry, the costs of the association appear to be minimal, at least to black skimmers.

Acknowledgments

REFERENCES

Arthur, S. 1921. The feeding habits of the black skimmer. *Auk*, **38**, 566–574.

Belopol'skii, L. 1957. *Ecology of Sea-Colony Birds of the Barents Sea*. Tel Aviv: Israel program for Scientific Translations Ltd.

Bent, A. C. 1921. Life histories of North American Gulls and Terns. *U.S. Nat. Hist. Mus. Bull.*, **113**, 1–337.

Breder, C. M., Jr. 1959. Studies on social groupings of fishes. *Bull. Am. Mus. Nat. Hist.*, **117**, 397–481.

Buckley, F. G. & Buckley, P. A. 1972. The breeding ecology of royal terns *Sterna* (*Thalasseus*) *maxima maxima*. *Ibis*, **114**, 334–359.

Burger, J. & Lesser, F. 1977. Determinants of colony site selection in common terns (*Sterna hirundo*). In: *Proceedings 1977 Conference of the Colonial Waterbird Group* (Ed. by W. E. Southern), pp. 118–127. DeKalb, Ill.: Northern Illinois University Press.

Cody, M. 1974. *Competition and the Structure of Bird Communities*. Princeton: Princeton University Press.

Darling, F. F. 1938. *Bird Flocks and the Breeding Cycle*. Cambridge: Cambridge University Press.

Dinsmore, J. 1972. Sooty tern behavior. *Bull. Florida State Mus. Biol. Sci.*, **16**, 129–179.

Emlen, S. T. 1975. Adaptive significance of sychronized breeding in a colonial bird: a new hypothesis. *Science, N.Y.*, **188**, 1029–1031.

Erwin, R. M. 1975. Comparative foraging and breeding strategies among three seabirds: the royal tern, *Sterna maxima*, the common tern, *S. hirundo*, and the black skimmer, *Rynchops niger*. Ph.D. thesis, University of Maryland, College Park. Dissert. Abstr. 4893-B.

Erwin, R. M. 1977a. Black skimmer breeding ecology and behavior. *Auk*, **94**, 709–717.

Erwin, R. M. 1977b. Foraging and breeding adaptations to differerent food regimes in three seabirds: the common tern. *Sterna hirundo*, royal tern, *S. maxima*, and black skimmer, *Rynchops niger*. *Ecology*, **58**, 389–397.

Erwin, R. M. & Korschgen, C. E. In press. Coastal waterbird colonies: Maine to Virginia 1977. Office of Biol. Serv., U.S. Fish & Wildlife Service.

Evans, R. 1970. Oldsquaws nesting in association with arctic terns at Churchill, Manitoba. *Wilson Bull.*, **82**, 383–390.

Gochfeld, M. 1977. Colony and nest site selection by black skimmers on Long Island, New York. In: *Proceedings 1977 Conference of the Colonial Waterbird Group* (Ed. by W. E. Southern), pp. 78–90. DeKalb, Ill.: Northern Illinois University Press.

Hailman, J. 1975. Analysis of aggression in white-throated sparrow types of different proportions. *Bird-Banding*, **46**, 236–240.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31**, 295–311.

Hatch, J. J. 1970. Predators and piracy by gulls at a ternery in Maine. *Auk*, **87**, 244–254.

Hooglund, J. L. & Sherman, P. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.*, **46**, 33–58.

Kadlec, J., Drury, W. & Onion, D. 1969. Growth and mortality of herring gull chicks. *Bird-Banding*, **40**, 222–232.

Koskimies, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. *Ornis Fenn.*, **34**, 1–6.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodius*). *Behaviour*, **51**, 99–134.

Krebs, J. R., MacRoberts, M. & Cullen, J. 1972. Feeding and flocking in the great tit, *Parus major:* an experimental study. *Ibis*, **114**, 507–530.

Kruuk, H. 1964. Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus* L.). *Behaviour Suppl.*, **11**, 1–129.

Lind, H. 1963. Nögle sociale reaktioner hös terner (English summary: 'Notes on social behaviour of terns'). *Dansk. Ornithol. Foren. Tidsskr.*, **57**, 155–175.

MacArthur, R. 1972. *Geographical Ecology*. New York: Harper & Row.

Markgren, M. 1960. Fugitive reactions in avian behavior. *Acta vert.*, **2**, 1–160.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.*, **40**, 119–168.

Morse, D. H. 1974. Niche breadth as a function of social dominance. *Am. Nat.*, **108**, 818–830.

Murray, B. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology*, **52**, 414–423.

Nisbet, I. C. T. & Drury, W. 1972. Measuring breeding success in common and roseate terns. *Bird-Banding*, **43**, 97–106.

Orians, G. & Willson, M. 1964. Interspecific territories of birds. *Ecology*, **45**, 736–745.

Palmer, R. 1941. A behavior study of the common tern (*Sterna hirundo hirundo* L.). *Proc. Boston Soc. Nat. Hist.*, **42**, 1–119.

Pemberton, J. 1922. A large tern colony in Texas. *Condor*, **24**, 37–48.

Pettingill, O. 1937. Behavior of black skimmers at Cardwell Island, Virginia. *Auk*, **54**, 237–244.

Ripley, S. D. 1961. Aggressive neglect as a factor in interspecific competition in birds. *Auk*, **78**, 366–371.

Risch, S. & Boucher, D. 1976. Eco-forum: what ecologists look for. *Bull. Ecol. Soc. Amer.*, **57**, 8–9.

Sears, H., Moseley, L. & Mueller, H. 1976. Behavioral evidence on skimmer's evolutionary relationships. *Auk*, **93**, 170–174.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Soots, R. & Parnell, J. 1975. Ecological succession of breeding birds in relation to plant succession on dredge islands in North Carolina estuaries. *North Carolina Sea Grant Publication*, **UNC-SG-75-27**, 1–91.

Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information-centres' for food-finding. *Ibis*, **115**, 517–534.

Watson, J. & Lashley, K. 1915. An historical and experimental study of homing. Washington: Carnegie Inst. Papers from Department of Marine Biology, **7**, 7–60.

Wolk, R. 1959. The reproductive behavior of the black skimmer. Ph.D. thesis, Cornell University, Dissert. Abstr., **20**, 3449.