THE ROLE OF REPRODUCTIVE SUCCESS IN COLONY-SITE SELECTION AND ABANDONMENT IN BLACK SKIMMERS (*RYNCHOPS NIGER*)

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ABSTRACT.—I examined colony-site tenacity and reproductive success in 19 colonies of Black Skimmers (*Rynchops niger*) for 5 yr in New Jersey. Frequent colony-site shifts occurred, and only two sites were occupied in all 5 yr. Although in one year fledging success was nearly zero due to flood tides, in most years tides destroyed less than 25% of the colonies, while predators destroyed up to 50% of the colonies. Skimmers usually abandoned unsuccessful sites and continued to nest in successful sites. Colony abandonment was greater in colonies subjected to predation pressures than in those subjected to flooding. I suggest that this difference related to the high predictability of future low reproductive success when a colony was destroyed by predators (high probability of future loss) as compared to floods (low predictability). *Received 26 January 1981, accepted 6 July 1981.*

MOST colonial seabirds exhibit colony- and nest-site tenacity, often for years or decades (see review in Bongiorno 1970, Southern 1977). Other species, however, shift locations frequently. Such species include Black-billed Gulls (*Larus bulleri*) nesting on sand bars in rivers (Beer 1966) and Franklin's (*L. pipixcan*) and Brown-hooded gulls (*L. maculipennis*) nesting in prairie marshes (Burger 1974a, b). Similarly, Laughing Gulls (*L. atricilla*) can shift habitats under flood conditions (Montevecchi 1978). These differences in the occurrence of tenacity led McNicholl (1975) to conclude that tenacity has evolved under conditions of habitat stability, while species nesting in unstable habitats show less fidelity to colony sites, shifting sites as the environments change. Since then, several authors have reported great variability in the types of colony sites selected and in the degree of colony tenacity exhibited (see Southern 1977, Burger and Shisler 1980, Erwin et al. 1981). Under stable environmental conditions, species such as Ring-billed Gulls (*L. delawarensis*) show remarkable colony-site fidelity, but fluctuating water levels can result in immediate desertion of colony sites.

In all of the above studies habitat stability is viewed as the primary selection pressure in colony-site tenacity, whereas habitat instability results in greater plasticity in use of colony sites (see McNicholl 1975). Gross habitat changes rendering a colony site unsuitable are obvious reasons for colony-site shifts (see Morris and Hunter 1976). It can be shown that gulls nesting in peripheral sites (in terms of habitat) produce fewer young (see Brown 1967). If birds suffer lowered reproductive success because of any factor, they might shift habitats or move to new colony sites. Thus, other factors, such as predation pressures, social factors (e.g. absence of other nesting species), and weather events (heavy rains, flood tides, hail), might contribute to lowered reproductive success and subsequent colony desertion the following year. The relationship of reproductive success to colony-site tenacity and abandonment has not been examined for any species except Black-legged Kittiwakes (*Rissa tridactyla*; Coulson 1966, 1972; Coulson and White 1960), although several authors have speculated on the causes of colony abandonment (but see Southern 1977, Erwin 1978, Patton and Southern 1978, Southern and Southern 1979).

In this paper I examine the relationship of reproductive success to future use of colony sites by Black Skimmers (*Rynchops niger*) nesting in *Spartina* salt marshes in Barnegat Bay, New Jersey (from 1976–1980). I predicted that colony sites that were unsuccessful one year would be abandoned as nesting colonies the following year, whereas successful colony sites would be occupied the next year (prediction one). I reasoned that predators on a salt marsh island might be expected to be present the following year, while the effects of flood tides

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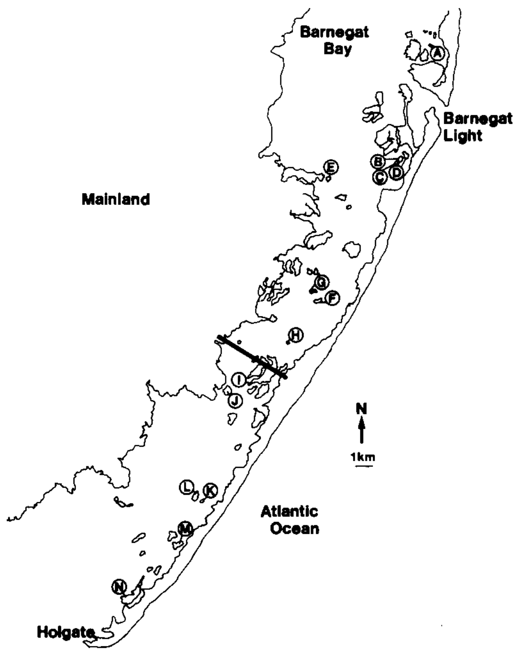

Fig. 1. Map of Ocean County, New Jersey showing the locations of all Black Skimmer colonies occupied from 1976 to 1980. The Manahawkin bridge is shown as a bar from the barrier beach to the mainland near colonies M and L.

would be less predictable from year to year. Washouts from high tides do not necessarily occur throughout the bay but are influenced by wind direction, which usually piles up water at only one end of the bay (pers. obs.). Therefore, I predicted that in colonies where predators destroyed most nests, the sites would not be occupied the following year, while colonies where flood tides destroyed nests might be reoccupied more frequently (prediction two).

Black Skimmers generally nest on sand bars and sandy beaches (Stone 1937, Gochfeld 1978, Erwin 1979). The sand bars and low sand beaches selected for colony sites frequently wash away in winter storms, and storm tides during the breeding season often destroy breeding colonies, forcing them to shift colony sites (Stone 1937). Recently, in New York and New Jersey, skimmers have started to nest on wrack in *Spartina* salt marshes (Frohling 1965, Gochfeld pers. comm.) in association with Common Terns (*Sterna hirundo*; Stone 1937; Gochfeld 1978; Erwin 1977, 1979).

Study Area and Methods

I studied colony-site fidelity and breeding success in Black Skimmers nesting in Barnegat Bay, New Jersey. Barnegat Bay, extending from Holgate (39°29′N) to Normandy Beach (40°29′N), is a shallow bay bordered by the mainland and barrier beaches (see Fig. 1). Only two inlets enter the bay, resulting in a low tidal shift each day. There are 259 islands in the bay, and over half are less than 0.5 ha in area.

From 1976 to 1980 I censused the nesting colonies of birds in Barnegat Bay by helicopter in early May to determine nesting locations, population sizes, and colony composition by species. Thereafter, each colony was surveyed from the ground 6–25 times (most colonies were surveyed at least 10 times) during the nesting season. Most nesting colonies were censused at least four times during incubation and at least six times during the chick phase. I also censused all colonies after very high tides, so that I could assess flood damage. While censusing, I walked through the colony checking all skimmer nests, eggs and young. This usually could be accomplished in 10–20 min. From 1976–1978 I lived on Clam Island (near Barnegat Light) and was able to monitor tide conditions daily. In 1979 all colonies were censused every 4 days, and in 1980 high tides were monitored by another observer living on Barnegat Bay.

I defined a colony as a group of nesting terns and skimmers that contained more than 20 nesting pairs of either species. Such groups of nesting birds (= colony) were separated on discrete islands. I defined a site occupancy as an active colony in any year at any site. Therefore, if one island contained a colony for 5 yr I considered it to have five site occupancies.

During each census at each colony I estimated the number of terns and counted the number of all adult skimmers and the number of skimmer and tern nests. For skimmers, I recorded clutch size, number and age of chicks (banded), eggs or chicks that suffered predation or drowned, eggs washed out of nests, and flying young. Skimmer chicks run when disturbed, making it difficult to assign them to particular nests. Thus, I computed fledging success as the number of almost fledged chicks (over 20 days) and flying chicks divided by the number of nests. I defined a successful colony as one in which mean fledging success was at least 0.4 young/nest, based on fledging success figures provided by Gochfeld (pers. comm.) and Erwin (1979). Although 0.4 young/nest may be a relatively low success rate, it is at present the only published success figure. Low colony success ranged from 0.01 to 0.39 young/nest, and unsuccessful colonies produced no young. Chi-square Goodness of Fit Tests were used to test for significant differences (assuming equal distribution among the classes).

I computed annual turnover rates using the following formula (Erwin 1978):

TABLE 1. Numbers of pairs of Black Skimmers nesting on Barnegat Bay salt marsh islands 1976–1980. All nested on wrack in salt marsh except on Mordecai, where they nested on a patch of sand in the marsh. Letters refer to colony locations shown in Fig. 1.

Island	1976	1977	1978	1979	1980
East Point (A)	0	0	0	1	0
East Vole (B)	0	0	1	2	0
West Vole (C)	0	15	19	19	14
Gulf Point (D)	0	0	1	1	0
West Sloop (E)	13	0	0	0	0
Flat Creek (F)	0	2	0	0	0
West Log Creek (G)	21	15	8	0	0
Log Creek (H)	14	0	0	0	0
West Carvel (I)	12	13	20	14	10
East Carvel (J)	16	14	7	14	45
Pettit (K)	0	0	0	1	20
Cedar Creek (L)	8	6	0	0	0
Southwest Cedar Bonnet (M)	6	4	0	13	10
Thorofare (N)	0	0	0	2	0
East Ham (O)	8	7	0	0	55
West Ham (P)	0	0	0	27	16
Marshelder (Q)	0	0	0	82	0
Little (R)	0	0	0	0	2
Mordecai (sand) (S)	0	0	6	71	1

$$T = \tfrac{1}{2}\left(\frac{S_1}{N_1} + \frac{S_2}{N_2}\right),$$

where S_1 = number of sites occupied *only* in the first year; N_1 = total number of sites in first year; S_2 = number of sites occupied *only* in second year; N_2 = total number of sites occupied in the second year. This rate cannot exceed 1.0 and can be computed as a percentage.

RESULTS

During the 5-yr period, Black Skimmers nested on 19 sites, and on all but Mordecai Island they nested on wrack in *Spartina* salt marshes. On Mordecai Island they nested on sand surrounded by marsh. In all colonies the skimmers nested with Common Terns.

The number of pairs of skimmers nesting each year is shown in Table 1 by colony location. From 7 to 12 colony sites were occupied by skimmers each year (Table 2). Only 2 of the 19 sites (11%) were used every year, and 6 (32%) were used during only one year. With two exceptions (Mordecai and Sloop islands), sites occupied only once contained only one or two pairs of skimmers nesting with Common Terns. The total number of skimmer nests varied each year from 63 to 247, although the mean number of skimmer nests per colony remained

TABLE 2. Summary of breeding characteristics of Black Skimmers in Barnegat Bay, New Jersey.

	1976	1977	1978	1979	1980
Number of colonies	8	8	7	12	9
Number of nests	98	76	63	247	173
Mean number nests/colony	12.3 ± 4.9	9.5 ± 5.32	8.86 ± 7.8	20.6 ± 27.5	29.2 ± 32.2
Median number nests/colony	12	7	7	13	14
Number of entire colonies lost to[a]:					
Predators	2 (25%)	3 (43%)	0 (0)	6 (50%)	0 (0)
Floods	1 (13%)	1 (13%)	7 (100%)	1 (8%)	0 (0)
Percentage of eggs lost to:					
Predation	30	34	19	20	6
Floods	10	3	81	36	0
Turnover rate[b] (%)	25 (1976–1977)	46 (1977–1978)	32 (1978–1979)	32 (1979–1980)	

[a] Over 95% of eggs or chicks destroyed.
[b] See methods for formula.

TABLE 3. Relative success of Black Skimmer colonies and cause of low success. S = successful, L = ≤0.39 young fledged/nest, U = no young produced; T = tidal destruction of most nests, t = tidal destruction of few nests, P = predation by Herring or Laughing gulls, Po = predation by Oystercatcher, Pm = predation by mink, —— = no skimmers nesting.

Island	1976	1977	1978	1979	1980
East Point (A)	——	——	——	U, P	——
East Vole (B)	——	——	U, T	U, P	——
West Vole (C)	——	S	L, T, p	S, t	S, t
Gulf Point (D)	——	——	U, T	U, Pu	——
West Sloop (E)	U, P	——	——	——	——
Flat Creek (F)	——	U, T	——	——	——
West Log Creek (G)	S	S	U, T	——	——
Log Creek (H)	L, P, t	——	——	——	——
West Carvel (I)	S	S, t	U, T	S	S
East Carvel (J)	S	S, t	U, T	S	S
Pettit (K)	——	——	——	U, Po	S
Cedar Creek (L)	S	U, Po	——	——	——
Southwest Cedar Bonnet (M)	S	U, P	——	S, t	S, t
Thorofare (N)	——	——	——	U, Pm	——
East Ham (O)	L, T	U, P	——	——	S
West Ham (P)	——	——	——	S	S
Marshelder (Q)	——	——	——	U, P	——
Little (R)	——	——	——	——	S
Mordecai (sand) (S)	——	——	U, T	L, T	S

relatively small (<30 pairs of skimmers/colony). Turnover rate varied from 25% to 46%.

Reproductive success varied markedly; in 1978 no colonies were successful, whereas in 1980 all colonies were successful (Table 3). Floods and predators were the main cause of low reproductive success. From 0 to 50% of colonies were destroyed by predators (Table 2), although the colonies lost to predators were generally small (except Marshelder Island, Table 1). I also computed the percentage of eggs (all colonies lumped) lost to predators, and it varied from 6 to 34% per year. Herring Gulls (*Larus argentatus*) were the primary predators on skimmer eggs, as they were responsible for the destruction of almost half of the colonies (n = 6) destroyed by predators; Laughing Gulls contributed to the demise of only one colony; oystercatchers (*Haematopus palliatus*) destroyed two colonies; a mink destroyed one colony, and the cause of predation in two colonies (Marshelder, Gulf Point) was unknown. I suspect that Marshelder and Gulf Point were destroyed by a large mammal (fox, raccoon), as the eggs and chicks completely disappeared, and both islands are close enough to land for a large predator to swim easily to the islands (see Fig. 1).

Floods caused by high storm tides destroyed from 0 to 100% of the colonies, and from 0 to 81% of the eggs (Table 2). In 1978 predators destroyed 19% of the eggs before the tides wiped out all the colonies. Only two chicks fledged in 1978 (from West Vole Island). High tides occured in most years (except 1980), but they wiped out all colonies only in 1978. Table 3 also shows (as S) the years when colonies produced at least 0.4 young/nest, despite some loss from flooding. Sometimes the pairs abandoned and did not re-lay (Log Creek in 1976, West Carvel in 1977), whereas in other cases (Cedar Bonnet in 1979) the pairs laid up to three clutches in the same nest cups.

Over the 4-yr period (1976–1979) there were 35 colony-site occupancies that could have been used the following year (in 1977–1980), and 23 (66%) were used the next year. From 1976 to 1980, 21 colonies (48% of the total colonies) had little or no success. Unsuccessful colonies were generally not occupied the following year (χ^2 Goodness of Fit = 5.36, df = 1, $P < 0.05$). From 1976 to 1980, 23 (52%) colonies were successful. All successful colonies were reoccupied the following year (χ^2 = 7.78, df = 1, $P < 0.01$). These results confirm prediction one.

I then examined the 12 colony sites that were not occupied the following year. Nine (75%) were primarily destroyed by predators, whereas only 3 (25%) were destroyed by flood tides. Thus, of the 12 colony sites that were not used for nesting the following year, none had been successful the previous year, and more of the unsuccessful colonies had failed due to predation than to tidal flooding ($\chi^2 = 10.45$, df = 2, $P < 0.01$).

Almost half of the 44 colony occupancies had little or no fledging success during the 5-yr study period (1976–1980). Of those colonies destroyed by predators from 1976–1979, significantly fewer than expected (based on the 66% overall rate for reuse the following year) were active the following year ($\chi^2 = 34.11$, df = 1, $P < 0.001$). For colonies destroyed by floods, there were no significant differences in the probability of occupancy the following year ($\chi^2 = 1.23$, df = 1, NS). These results confirm prediction two.

In summary, this study has shown that (1) turnover rates vary from 25% to almost 50% from year to year; (2) unsuccessful colony sites are abandoned the next year, whereas successful ones are occupied; and (3) colonies where nests are destroyed by predators are abandoned at a much higher rate than colonies where flooding is a major source of mortality.

Discussion

Historically, Black Skimmers have nested on sand bars and sand beaches in coastal areas. Such habitats are subject to frequent storm tides, which partially or completely wash away nests, eggs, and chicks. High tides during the pre-egg-laying period may result in early shifts to new locations, while later flooding frequently results in adults relaying in the same colony site (Stone 1937). Several authors (Stone 1937, Gochfeld 1978, Erwin 1979) have noted frequent colony abandonment from year to year.

The habitat shift of Black Skimmers from nesting on sand beaches to nesting in salt marshes appears to be a response to a decrease in available habitat due to human disturbance, rather than an escape from the effects of tides. Burger and Lesser (1978) showed that the colony sites of Common Terns (and associated skimmers) are limited in Barnegat Bay and that terns and skimmers have few available sites above storm tides that are currently unused. Although several authors have noted the shifting of colony sites and the dangers of storm tides, no study has shown the relationship between these two factors. Further, the role of predation in frequent colony shifts has not been examined in detail.

Indeed, Herring Gulls and Ring-billed Gulls exposed to continuous and prolonged predation by large mammals have often failed to shift colony sites (see Patton and Southern 1978, Southern and Southern 1979). In these gulls, desertion is viewed as an unusual event. The increase of nesting skimmers I found in 1979 may have been the result of high rat predation on a large colony of sand-nesting skimmers at the tip of Holgate Island. Forced to abandon Holgate, skimmers may have nested on Marshelder Island or Mordecai Island (both were occupied later in the season than the other nesting islands).

In the present study, over half of the unsuccessful colonies were destroyed by predators. Most of the destruction, however, was by avian predators (Herring and Laughing gulls, Oystercatchers) nesting on the same islands as the skimmers and terns. Although such avian predators pose less of a threat to adults than to young (see Kruuk 1964), they can effectively eliminate reproduction in any year. Because the avian predators are themselves nest-site tenacious, intense predation pressures in one year might predict intense predation pressures in subsequent years. This is particularly true of Herring Gulls, whose numbers are increasing yearly in the New Jersey salt marshes (Burger 1979). Because Herring Gulls select the highest islands for nesting, they are usurping the nesting habitat that is safest from high tides. Thus, Herring Gulls pose a double threat: habitat competition and predation. It should be noted that Herring Gulls were not predators on all islands where they nested. Herring Gulls tended to be predators on skimmers on islands located close to boat channels, suggesting that human interference contributes to the high predation rates. Islands were not abandoned by the skimmers simply because they contained nesting Herring Gulls (i.e. West Carvel, West Sloop), but only where Herring Gulls were predators on skimmer and tern eggs. In all cases, the Herring Gulls nested adjacent to the skimmers and terns, not among them.

Other studies of Black Skimmers (see Erwin 1977) have generally reported little or no evidence of predation. Modha and Coe (1969), however, observed both avian and mammalian predation on African Skimmers (*R. flavirostris*). Overall, predation on African Skimmers accounted for 29% of the egg loss, while storm floods destroyed 16% of the eggs. In the Black Skimmers I observed, floods destroyed 0–81%

(weighted mean = 19%) of the eggs and chicks, while predators destroyed 6–34% (weighted mean = 23%).

In the present study, changes in colony location were not random but were shown to be related to low reproductive success the previous year. Skimmers did not always shift colony sites, however, they shifted when predators caused low fledging success, but not when tidal floods caused low success. I believe this relates to the predictability of the event and the continued presence of the predators the following year. High predation rates were frequently caused by gulls nesting on the same islands. Because Herring Gulls are highly site tenacious (Tinbergen 1961, Ludwig 1963), they will be present the following year and can again pose a threat. Indeed, once Herring Gulls nested on any island in Barnegat Bay, they continued to do so in subsequent years unless they suffered high rates of predation. I know of two Herring Gull colonies that had low reproductive success because of fox and mink predation, and both sites were abandoned the following year. Further, Herring Gulls begin nesting in mid-April, almost a month before skimmers begin to nest. Thus, skimmers can observe the presence of the predators when they arrive in the spring. Nesting predators are not the sole cue used, however, because other unsuccessful colony sites were abandoned even though the predators (mammals) were not visible. Additionally, the occurrence of a mammalian predator on a nesting colony suggests that the conditions making it possible for a predator to be there in the present year may prevail the following year. Such conditions include closeness to the mainland, high areas where predators can avoid excessively high tides, and sufficient food reserves to allow predator survival when the birds are not breeding.

Flood tides are less predictable in several respects (see Storey 1978): (1) storm winds frequently force the bay waters over salt marshes in only one area of the bay, (2) the height of the wrack above the mean high tide level varies depending on the height of the winter tides, and (3) an overall high tide (not merely one induced by winds) might well inundate all colony sites in the bay (as in 1978). In all 5 yr of observation, high tides destroyed some nests each year, although washouts did not occur on the same islands every year (see Table 3, Fig. 1). Because Barnegat Bay has only two inlets, tide waters move slowly, and high winds can offset tidal effects. High winds can make the tide low in one end of the bay while making it high at the other end. Because wind direction varies, the location of the flood tides is unpredictable. Further, the location of wrack on the marsh is determined by the highest winter tides. Because winter tides also are influenced by wind direction, wrack is not equally high on all marshes. Without high tides in the period immediately before nesting, it might be difficult for the skimmers to assess a wrack's relative height above mean high water. A colony site (such as Carvel Island) that has been productive in past years is not abandoned solely on the basis of a flood one year. A new colony that is flooded out (where they have never been successful), however, or a colony that has been completely destroyed by predators is generally abandoned. In searching for new sites, skimmers usually move to other islands containing skimmers and terns (see Gochfeld 1978). The presence of an established colony is some indication of past reproductive success. New colonies often prove unsuccessful when they have not been used in the past by either terns or skimmers.

Despite numerous studies indicating colony shifts by a variety of species (see McNicholl 1975, Morris and Hunter 1976, Southern 1977), this study shows that colony shifts in skimmers are directly related to reproductive success. Further, predation pressures in skimmers exert an immediate effect on colony location, while flooding does not immediately result in abandonment. These results indicate that predation pressures and reproductive success can be important variables in colony-site selection in addition to habitat variables.

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