

BLACK SKIMMER BREEDING ECOLOGY AND BEHAVIOR

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ABSTRACT.—Black Skimmers arrive in their breeding colonies at approximately the same time as most of the terns, usually in late April or early May. They are commonly found in dense colonies on open sandy beaches in association with other seabirds, most frequently Common Terns in Virginia.

The usual clutch size is large for a seabird ($\bar{X} = 3.6$), with 4-egg clutches being most common. Incubation begins with the first egg laid.

Hatching success was high (nearly 80%) in the colonies studied, but fledgling success was low in both 1973 (0.40 young per pair) and 1974 (0.37 young per pair).

Probably food acts to limit production as 10 of the 11 surviving fledglings were the first hatched in the brood. Survival of 2nd, 3rd, and 4th hatchlings drops off precipitously.

Adult skimmers are sexually dimorphic, the male being approximately $\frac{1}{4}$ larger than the female. Both parents incubate and share parental duties until fledging.

The growth characteristics of the Black Skimmer appear to follow the logistic model developed by Ricklefs. Only after the midpoint of the fledging period (about 11 days) do male chicks begin to grow more rapidly than females. Male chicks fledged at an average of 295.2 g while females fledged at 264.4 g.

Adults captured a fish approximately every 5 minutes. Most foraging was done at low tide in marsh habitats. No pulse of high-fishing activity at dawn and dusk was noted as has been reported in the literature. Birds foraged alone in most cases, except when the immatures begin fishing. Apparently learning occurs at this time.

Each young was fed on the average of 0.43 fish/hour during the day; the low rate may largely explain the low fledging success in 1973–1974. The extent of nocturnal feeding requires investigation. The diet consists of 100% fish, with silversides and killifishes predominating.—*Department of Zoology, University of Maryland, College Park, Maryland 20742. Present address: Massachusetts Cooperative Wildlife Research Unit, University of Massachusetts, Amherst, Massachusetts 01003.*
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ALTHOUGH the Black Skimmer, *Rynchops niger*, is a familiar bird along the Atlantic and Gulf coasts of the United States, comparatively little is known of its breeding ecology. Wolk (1959) and Pettingill (1937) studied the species' reproductive behavior but made little mention of its ecology. A brief synopsis of the literature on the Black Skimmer reveals the paucity of (and discrepancies in) information on a number of critical aspects of its biology.

Skimmers arrive in the mid-Atlantic states in late April or early May and courtship and pair formation begins immediately (Bent 1921). They breed in colonies, usually on bare or sparsely vegetated sand substrate on dredge spoil or natural barrier islands (Bent 1921, Soots and Parnell 1974, 1975). Skimmers commonly form mixed-species colonies, usually with Gull-billed Terns, *Gelochelidon nilotica*, and Common Terns, *Sterna hirundo*, in North Carolina (Soots and Parnell 1975). After the simple nest scrapes are made, egg-laying begins (reportedly later than in most seabirds) with as many as five eggs in a clutch being common (Bent 1921). The incubation period is unreported. No hatching/fledging success data or growth rates of young are available in the literature. Sexual dimorphism in Black Skimmers, unusual in the closely related gulls and terns, is generally recognized by ornithologists, yet no morphometric analyses have been published since Ridgway's (1919:452), which shows the males larger than the females with very little overlap in all measurements.

The skimmer's unusual feeding technique has received the most attention (Arthur 1921, Potter 1932, Davis 1951, Tomkins 1951, and Zusi 1959), but only in a few cases (Davis 1951, Zusi 1959) has anyone tried to quantify foraging success. The results, from different areas, are strikingly different. Disagreements concerning foraging periods are found; while time of day is considered critical by some authors (Arthur 1921, Zusi 1959), others (Tomkins 1951) emphasize the importance of the tidal stage. Only very general descriptions of the diet are given, with no quantitative analyses available. Finally, no mention is made of any social feeding tendencies. It is unestablished whether they feed solitarily or in flocks or how this relates to resource abundance or habitat.

METHODS

The field work was conducted in Virginia at two locations. In 1973, three subcolonies of Black Skimmers were studied on Fisherman Island National Wildlife Refuge, Northampton County, Virginia. In 1974, in addition to the Fisherman Island site, the colony at Metomkin Island, Accomac County, Virginia was also included. Both sites are barrier islands, part of a chain lining the southeast coast of the Delmarva peninsula. Metomkin Island is approximately 65 km north of Fisherman Island.

During the 2-year study, 110 nests were marked with numbered stakes. The egg-laying date, incubation period, and hatching success were monitored every 2–3 days throughout May and June in both years. Because of the dispersal tendencies of the young, it was necessary to use enclosures around individual nests (Nisbet and Drury 1972). One-inch mesh poultry wire (30 cm high) circumscribed each of 29 nests, allowing approximately 1.5 m diameter. No desertion occurred as a result of the procedure. When hatching occurred, individual chicks were weighed every 2–3 days with Pesola spring scales.

Adult feeding was studied from posts at each island. Binoculars, Bauscope Zoom 60, and stopwatch were used to record feeding times, success rates, and prey sizes. The feeding of the young was watched from portable blinds erected in three places near the edge of the colony. Time of delivery of food, food size, and identity of prey were recorded throughout the nestling phase.

Museum specimens from the National Museum of Natural History were used to compare sexual differences in wing chord and mandible dimensions. In addition, Richard Zusi provided data on adult weights from several localities.

RESULTS

Arrival time.—The majority of birds arrive in the Virginia breeding colonies in very late April or early May and begin laying the third week in May. This observation contradicts Bent (1921) who states the Black Skimmers are one of the last seabirds to lay eggs, with Virginia birds postponing clutch initiation until mid-June or later.

Nest site selection.—In Virginia, Black Skimmers nest primarily in two types of habitats: either on small dredge spoil islands or on open, overwashed sand beaches on natural islands. The use of spoil islands appears to be widespread, occurring in North Carolina (Soots and Parnell 1974, 1975), New Jersey, and New York (Buckley and Buckley 1974). Undoubtedly, the high incidence of human disturbance on natural islands, such as the outer banks of North Carolina, has contributed to this shift away from natural island habitat (Soots and Parnell 1974, 1975).

Yearly variability occurs in colony site location (Beckett pers. comm., Byrd pers. comm.). On Fisherman Island, 5 discrete subcolonies were occupied in 1973 while, in the following year, only 2 of the original 5 sites were reestablished. The instability of the nesting habitat (open sand/spoil) precludes selection for strong site tenacity (McNicholl 1975). The Black Skimmer apparently has opted for a strategy of rapidly colonizing newly created (spoil banks) or ephemeral habitats rather than returning to traditional sites (an r- rather than a K- selector?).

TABLE 1a
FLEDGING SUCCESS AND SURVIVAL IN RELATION TO HATCHING ORDER

	Number of nests	Total eggs	Number hatched	Number fledged	Number young/egg	Number young/pair	Rank order of fledglings			
							1	2	3	4
1973	10	38	34	4	.10	.40	4	0	0	0
1974	19	73	65	7	.11	.37	6	1	0	0

The presence of other, earlier nesting colonial species (especially Common Terns in Virginia) may be an important proximal cue in nest site selection. In 12 Black Skimmer colonies visited over the 2-year period, Common Terns were found nesting in 11. In North Carolina Soots and Parnell (1975) found a positive association among Black Skimmers, Common Terns, and Gull-billed Terns. A complete survey of the Virginia coastal region in 1975 (M. Byrd pers. comm.) revealed a high frequency of mixed-species colonies of Common Terns and Black Skimmers. A contingency test showed that the two species are significantly associated; V (correlation coefficient) = .453, $\chi^2 = 9.21$, $P < 0.005$ (Pielou 1969). It is doubtful whether this association is due strictly to similar habitat requirements. Both species show considerable variation in their nesting microhabitat, ranging from open sand to dense sea rocket, *Cakile edentula*. At present, there appears to be an abundance of available, unoccupied nesting habitat. The selective basis for this species association requires investigation. Perhaps by nesting with an aggressive species (Common Tern), Black Skimmers avoid egg predation by neighboring Laughing (*Larus atricilla*) and Herring Gulls (*L. argentatus*) (analogous to the Sandwich Tern/Black-headed Gull (*Thalasseus sandvicensis*/*L. ridibundus*) association in Europe (Lind 1963)).

Egg-laying.—The peak of egg-laying occurred during the third week of May in both years, with clutch initiation spanning several weeks in late May and early June. In general the egg-laying patterns shows a considerable degree of asynchrony, with an average clutch of 4 requiring 4 to 6 days. Rarely two eggs may be laid on the same day, a phenomenon also noted in Long Island colonies (Gochfeld pers. comm.). Incubation begins with the first egg and both sexes participate.

Clutch Size.—The mean clutch size in Virginia was 3.55 with 4-egg clutches being most common. Five-egg clutches were rare, contrary to the findings of Bent (1921). Gochfeld (pers. comm.) found that four-egg clutches are most common in New York. Clutches in excess of five may be the result of two females laying in one scrape.

Incubation Period.—The mean incubation period for 110 nests was 22.9 ± 2.2 days. Contrary to earlier anecdotal notes, skimmers incubate throughout the day.

Hatching Success.—Pooled results from 95 nests in 2 years gave a hatching success of 78.6% for a total of 336 eggs. No difference was found between years. In most cases the fate of lost eggs was undetermined. No predation was witnessed, although

TABLE 1b
SURVIVORSHIP IN NESTS (IN DAYS) IN RELATION TO HATCHING ORDER*

Hatching order	N	Mean survival time (days)
1	23	16.93 ± 1.16
2	22	9.30 ± 1.47
3	17	2.50 ± 0.61
4	6	0.50 ± 0.22

* Survival times listed are means \pm 1 standard deviation.

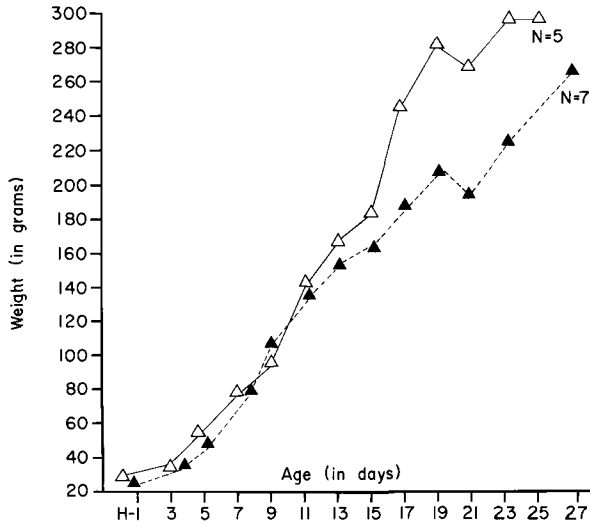


Fig. 1. Weight gain in young Black Skimmers. Averages of 5 males (solid line, open triangles) and 7 females (dashed line, closed triangles) are shown. Only 4 individuals (2 males, 2 females) of the original 12 fledged.

large breeding colonies of Laughing and Herring Gulls, known egg predators, were located on the same islands. No ground predators were present on either island studied. Gochfeld (pers. comm.) found a high rate of clutch abandonment in several Long Island colonies, resulting in lower hatching success.

Fledging Success.—The results from 29 individually enclosed nests are summarized in Table 1a. Fledging success was very low in both years, less than one young being produced per nesting pair. Ten of the 11 fledged young were the first hatched in the brood. Table 1b illustrates the difference in the mean survivorship (days) for each nestling in a brood during June and July. Chicks were followed until fledging or disappearance. First-hatched young have nearly twice the life expectancy of the second, and nearly seven times that of the third. Most fourth-hatched chicks failed to survive beyond the first day after hatching. Although I did not mark each chick in the brood, the larger chicks (first hatched) were noted to procure food from the parent more often than their smaller sibs. This suggests that the differential brood mortality is probably food-related (see below).

Chick growth.—Adult Black Skimmers are sexually dimorphic in at least three common morphological criteria: body weight, mandible length, and wing chord (see Table 2). As indicated, all three show statistically significant differences between males and females. The greater size of the male probably explains the other morphometric differences found.

Because of the significant sexual dimorphism in adults, it was essential to separate males from female chicks when plotting weights. As the sexes are indistinguishable at prefledging ages, the weight data were reexamined and sex was assigned on the basis of the final (fledging) weight, usually between days 23 and 25 in age. Birds exceeding 290 g were assumed to be male, those under 270 g were considered female.

In 1974 12 birds were included in the weight study, 5 males and 7 females. The results, though insufficient to be conclusive, are illustrated in Fig. 1. Only after 11–12 days is there divergence in size. The mean for the final weights was 295.2 g for males and 264.4 g for females.

TABLE 2
SEXUAL DIMORPHISM IN THREE MORPHOLOGICAL PARAMETERS

Criterion	N	Males	N	Females	Z value (Mann-Whitney U-test)
Adult weight (in grams)	13	343.5 ± 38.7	8	255.4 ± 18.1	Z = 7.1 P < 0.01
Lower mandible (length in mm)	15	95.1 ± 10.2	15	76.2 ± 8.1	Z = 3.59 P < 0.01
Wing chord (right)	15	37.4 ± 1.5	15	34.2 ± 1.2	Z = 2.12 P < 0.05

The inflection points on the graph fall close to the point at which 50% of the asymptote has been reached, indicating that the logistic growth equation is probably most appropriate to describe the growth of this species (Ricklefs 1967). To test this further, the raw data were transposed using the conversion factors described in Ricklefs. These factors, when plotted against time, provided a good linear fit except for the final two weights (over 18 days). Because of the good fit, it was concluded that the logistic form of the growth curve was the most appropriate. The rate constant, K_G , derived from the analysis was 0.228. This value is in line with the K_G values of several species of terns derived by Ricklefs (1968) from data from other workers, but is much higher than those from all the gull species analyzed.

Feeding.—Skimmers obtain food by immersing the mandible in water while cruising along shallow mudflats, tidal streams and marsh edges. Upon making contact with an object, the maxilla snaps down during rapid head flexion (Zusi 1959). As the feeding is based primarily upon tactile stimuli, inedible items (wrack shell) are occasionally taken and then dropped. A common behavior is repetitive "skimming" across a particular tidal pool. Skimming is usually performed into the wind.

I found that the tidal influence was more critical than time in influencing feeding, in accord with Tomkins (1951). At Metomkin Island, at low tide (± 1 h) over 30 individuals per hour were seen feeding, while at all other times fewer than 5 were seen per hour.

Foraging was usually solitary at Metomkin and Fisherman Islands, although pairs of birds were also commonly seen together (Fig. 2). The frequency of groups (more than one individual) occurrence increased after the young fledge, probably because imitative learning is taking place ($\chi^2 = 5.7$; $0.01 < P < 0.025$). The incidence with which fledglings forage alone increases as the season progresses (Table 3).

To see if recruitment into favorable feeding places occurred in skim-

TABLE 3
DECLINE IN IMMATURE SKIMMER DEPENDENCE UPON ADULTS AS A FUNCTION OF INCREASING AGE

Date	Observation hours	Number immatures seen foraging	Number associated with adults	Percent association
7/17	2.5	6	6	100
7/23	2.0	10	5	50
7/26	1.5	14	7	50
7/31	2.0	14	4	29
8/7	2.0	15	3	20
8/14	2.0	16	3	19

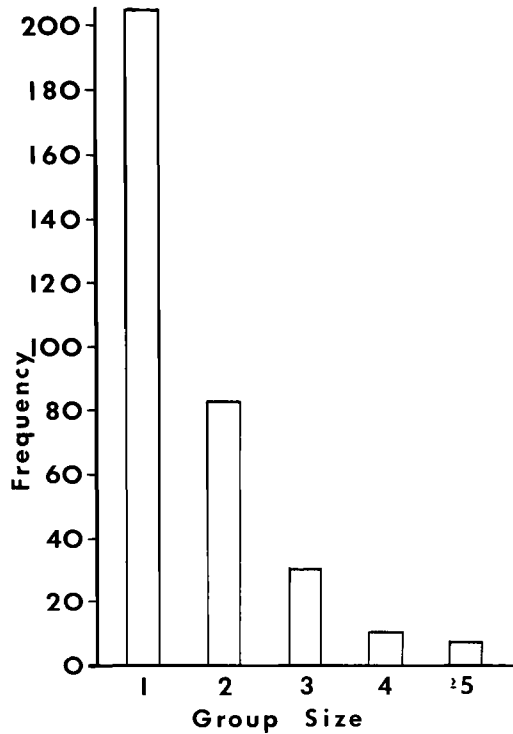


Fig. 2. Foraging group size in adult Black Skimmers.

mers (as in terns and gulls), the temporal pattern of adult feeding was examined. At Metomkin Island, at low tide period, observation periods were divided into 10-minute time blocks. Observations lasted from 2–3 hours on any particular day. The numbers of individuals feeding in each time block was recorded on nine different days in June 1974. Variance/mean ratios for each day were calculated and indicated little “clumping” (high V/M ratio) in time in shallow tidal flats at low tide (V/M average = 1.31).

Adult feeding success was determined by timing individuals feeding in shallow tide pools (Fisherman Island) and marsh channels (Metomkin Island). The total time that the mandible was immersed was considered foraging time. The results from 26 different foraging days in 1974 indicated that Black Skimmers capture prey every 5 minutes of foraging time ($\bar{X} = 0.21 \pm .09$ fish/minute). This result compares with Davis' (1951) of 1 fish per 6.5 minutes, but is less than the one per 1.6 minutes

TABLE 4
THE FEEDING RATE AND FOOD SIZE OF YOUNG BLACK SKIMMERS AS A FUNCTION OF AGE*

	Age of young			\bar{x}
	< 6 days	6–12 days	> 12 days	
Feeding rate (no. prey/chick/hr.)	0.53 ± .55	0.27 ± .13	0.12 ± .02	0.43
Biomass (prey item in grams)	3.5 ± 4.4	6.2 ± 5.8	10.5 ± 13.4	4.3

* Figures are means ± 1 standard deviation for 22 observation days (86 hours).

TABLE 5
PREY SIZE COMPOSITION (CM) OF ADULT BLACK SKIMMERS

Prey length (cm)	Percent composition (N = 224)
1-5	79
5-10	20
> 10	1

reported by Zusi (1959) from Texas. The catching rate probably varies considerably with season, tide, and locality.

Feeding of the young.—I watched 22 individual nests from a blind throughout the nesting phase on Fisherman Island. The results from 22 observation days (86 hours) are shown in Table 4. The age of the young is known to influence feeding, so three age classes are presented separately. The mean delivery rate of 0.43 fish/chick/hour is low considering the small prey fed to the young.

The size composition (overall) of the prey was obtained in two ways: (1) direct observation of parental feeding from the blind (size relative to culmen) and (2) specimens collected from the nest vicinity. Table 5 shows that the majority of prey fed to young were very small (5 cm) fish.

The diet consisted almost entirely of fish of which over 90% were silversides (*Menidia* spp.) and killifishes (*Fundulus* spp.). Also included in order of decreasing frequency were: bay anchovy (*Anchoa mitchilli*), mullet (*Mugil* spp.), spot (*Leiostomus xanthurus*), and bluefish (*Pomotomus saltatrix*).

DISCUSSION

Limitation of bird populations has been a subject of considerable interest since Howard's (1920) treatise on territoriality appeared. The importance of density-independent factors (climate, disease in some cases) versus density-dependent regulation (via competition for food or shelter, predation) has been debated for the past 20 years (Andrewartha and Birch 1954; Lack 1954, 1966; Murdock 1966, Hairston et al. 1967). Lack contended that clutch size and ultimately breeding densities are controlled by density-related food conditions. In North Temperate seabirds he felt that winter feeding conditions may influence survival, not the breeding season, but Ashmole (1963) argued that tropical terns probably deplete the resources adjacent to breeding sites to a degree that competition may become intense. He felt these pressures explain the discrete foraging zone differences (and size differences) among sympatric breeders.

I believe that Black Skimmers are frequently food-limited during the breeding season in Virginia. The fact that 10 of the 11 fledged young were the first hatched in the brood strongly suggests that food limitation curtailed production. A number of workers (Lack 1954, Dunnet 1955, Langham 1968) have suggested that asynchronous hatching is an adaptation to a variable food supply. In good years all members can survive, while in poor years only the more aggressive (= largest = earlier hatched) live beyond a few days. If other factors were more important (climate, predators), one would expect more equitably distributed mortality within broods. At four nests I saw strong expressions of sibling dominance, with first-hatched young chasing and pecking younger sibs when parents arrived with a fish. Dorward (1962) suggested that sibling aggression is found in the Sulidae and is related to severe food

limitation. It would be enlightening to compare interactions among brood members in regions of high versus low food abundance.

The low fledging rates of 0.37 and 0.40 young/pair in 1973 and 1974, respectively, in Virginia are comparable to those found recently in New York skimmer colonies (Gochfeld pers. comm.) and in South Carolina (Beckett, pers. comm.), but in other years, skimmers have much higher success. In South Carolina, often 1.4–1.6 young per nest are raised with as many as 3 young being raised in the same brood (Beckett pers. comm.). Gochfeld (pers. comm.) also indicated that the Long Island colonies were much more productive in 1975 than they had been in the two previous seasons.

Climatic impacts, such as storm washouts, can certainly be deleterious to successful reproduction, but skimmers can mitigate these damages by reneesting and moving to different sites. Replacement clutches can be laid as late as mid-August in Virginia. No evidence of predation was seen in any of the skimmer colonies in Virginia in either year.

Whether food is limiting in a density-dependent or independent manner is difficult to assess. No data are available on large colony versus small colony success in similar habitats. The local fluctuation of inshore fish abundance from year to year (Erwin 1975) suggests that food conditions for skimmers might be related largely to environmental factors that impose variability upon fish populations. Despite the apparently poor food years in the Virginia colonies in 1973 and 1974, I saw no evidence of competition among adults, such as attempted food piracy or aggressive interactions at foraging sites.

Foraging behavior.—The fact that skimmers usually forage either singly or in pairs and use their foraging area uniformly (in a temporal sense) suggests that interference or low resource abundance might reduce the advantages to flocking, which is prevalent among other seabirds. The tendency for skimmers to forage along edges restricts them spatially. Recher (1966) found that aggressive encounters within shorebird flocks were highest where foraging space was restricted (e.g. at the edge of the receding tide).

Although no comparative data are available for Virginia, it is doubtful that the total biomass of inshore silverside shoals approaches that in the open-water herring and menhaden schools. Thus, skimmers probably are exploiting a lower yield resource but one more predictable in space (Erwin 1975).

The low rate at which skimmer pairs feed their young (0.43 fish/chick/hour) is inconsistent with the success rate of 1 fish/5 minutes skimming time. The discrepancy is due to the fact that feeding of the young is discontinuous throughout the day. Bouts of heavy feeding occur in which 3–5 fish are delivered in a brief (20–30 min) period followed by a quiescent period of several (3–4) hours. It is questionable whether this behavior is totally tide-dependent because this behavior was noted in feeding habitats that were not under strong, direct tidal action. Perhaps the heavy energetic demand in skimming as a foraging technique accounts for this behavior. Nocturnal feeding is well documented, so the absolute period of time available for feeding is substantially longer for skimmers than for terns or gulls.

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