ROBBING BEHAVIOR OF ROSEATE TERNS

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THE increasing number of reports in recent years show the habit of stealing food from other birds (cleptoparasitism) to be a fairly widespread phenomenon among the Laridae (Rand 1954, Nørrevang 1960, Hatch 1970, Hays 1970, Hopkins and Wiley 1972). Where Laridae or Stercorariidae are the antagonists, they often band together into chasing groups of varying size (Belopol'skii 1957, Meinertzhagen 1959, Grant 1971) and the interactions can be complex (Hatch 1970). On Coquet Island (55° 20′ N, 1° 32′ W) and the nearby Farne Islands off the northeast coast of England, Roseate Terns, *Sterna dougallii*, rob other terns of their fish (Watt 1951, Bannerman 1962, Langham 1968). These parasitic terns operate singly, rather like foraging raptors, and the robbing behavior is therefore particularly suitable for studying the relationships between the parasites and their hosts. This paper describes the behavior on Coquet Island and considers various responses by the Roseate Terns to changes in the abundance and nature of the food supply brought to the island by the host population of terns.

Coquet Island is flat and low, rising only about 10 m above sea level. It has an area of almost 70,000 square meters, most of which is covered by low-lying vegetation. Between May and August each year, some 50,000 square meters are occupied by breeding terns of various species. In 1969 when the major part of this work was undertaken, the island supported about 250 pairs of Roseate Terns, 1,300 pairs of Common Terns, *S. hirundo*, 700 pairs of Arctic Terns, *S. paradisaea*, 200 pairs of Sandwich Terns, *S. sandvicensis*, and, in addition, 105 pairs of Black-headed Gulls, *Larus ridibundus*.

METHODS

Between May and July 1968 the airspace above the island was monitored periodically to determine which tern species were being robbed and in what manner. In July 1969 a hide was situated facing area A (Figure 1), which was colonized mainly by Common Terns. Daily observations of robbing behavior were subdivided into 15-minute watches for a total of almost 61 hours (243 watches) on 10 days between 23 July and 7 August 1969. During each watch the total number of Roseate Terns actively parasitizing above area A was counted. Roseate Terns did not pursue other terns with fish but attacked them mainly by making brief, rapid swoops; all such flight maneuvers directed at terns carrying fish were scored as attacks, irrespective of whether or not the birds made physical contact. Successful attacks were those in which the parasite gained possession of another tern's fish.

All four tern species carry fish crosswise in the bill. Most birds (98 percent) carried only one fish but a few (2 percent) carried more than one and sometimes as many

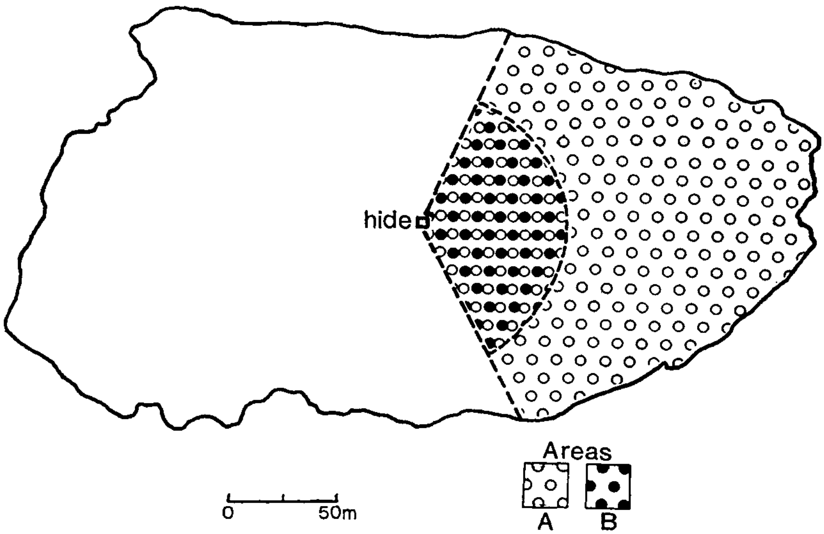

Figure 1. Coquet Island showing the study areas used in 1969. See text for details.

as five (based on 3,011 sightings). The terns brought back two main fish species to the colony. Almost all (98 percent) were either sand eels, *Ammodytes marinus*, or sprats, *Clupea sprattus*. The remaining food items were usually Gadidae or Crustacea and comprised a negligible proportion of the terns' diet. Fish lengths were estimated to the nearest inch (i.e. 2.5 cm) by comparison with the approximate length of the tern's bill: Sandwich Tern, 5 cm; Common and Roseate Terns, 4 cm; Arctic Tern, 3 cm. All observations were made by the author, so ensuring consistent estimation throughout. Previous practice in estimating fish lengths reduced the possibility of progressive change in assigning fish to particular length categories. For each interaction seen in area A, the species of host tern involved, the species and length of fish, and the success or failure of the robbing attempt were recorded. When necessary these details were verified with 10 × 50 binoculars.

Within area A (about 25,000 square meters), a smaller representative area (about 5,000 square meters) called B in Figure 1 was selected and its boundary marked out with conspicuously colored stakes. Area B was of such a size that all host terns entering the airspace above it could be seen easily. The species of all host birds and the length and species of their fish were recorded to provide an index of the relative numbers (density) and kinds of fish potentially available to Roseate Terns in area A. The number of fish considered to be available during each 15-minute watch was the average of three rapid spot counts made in area B at 5-minute intervals.

RESULTS

A Roseate Tern intent on robbing easily distinguishes itself from other Roseate Terns by flying high (about 10–20 m) above the colony where it can watch other terns returning with fish. The most common subsequent behavior pattern resembles the fishing method used by Roseate Terns at

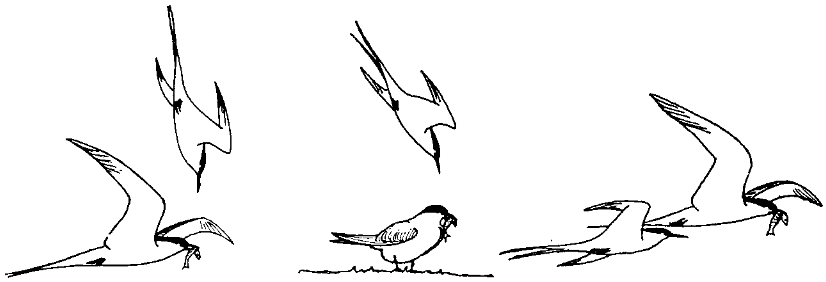

Figure 2. The three robbing strategies used by Roseate Terns. In each case the tern being attacked is the one with the fish.

sea; the parasitic tern suddenly dives—but without a preparatory hover—and tries to seize the fish from the other (host) tern's bill. Occasionally a brief tussle ensues over the fish when the host keeps a firm grip, but usually the attack is an instantaneous, all-or-nothing attempt.

Three distinct variations in the parasite's strategy were seen. In most encounters, the host tern was attacked from vertically above, usually in midair (Figure 2a) but sometimes on the ground (Figure 2b). Considerable skill was evidently required in the latter method to strike a fine balance between the rapid, unchecked stoop needed to surprise the host and the sudden arrest of downward movement necessary to prevent collision with the ground. Frequently instead of following through either kind of diving attack, the Roseate Tern would terminate its descent prematurely and regain height to search for another victim. In the third method (Figure 2c) the Roseate Tern approached the host from behind and dipped below the apparently unsuspecting tern to snatch the dangling fish from the underside of the bill. This variation was not seen till the summer of 1969 and then in only 15 out of 2,114 attacks.

Seasonal variation.—All four tern species were attacked, but differences in their relative breeding times made seasonal changes in the species composition of birds attacked. On Coquet Island Sandwich Terns usually start laying in the second week of May, Common and Arctic Terns in the fourth week of May, and Roseate Terns in the first week of June. In May Roseate Terns concentrated most (> 90 percent) of their robbing effort on the Sandwich Tern, then the only species regularly returning to the colony with fish for presentation in courtship or to feed incubating mates. Compared with the other species, Sandwich Terns nested much more densely and in sparser vegetation, which resulted in conspicuous concentrations of birds alighting and displaying with fish. This offered

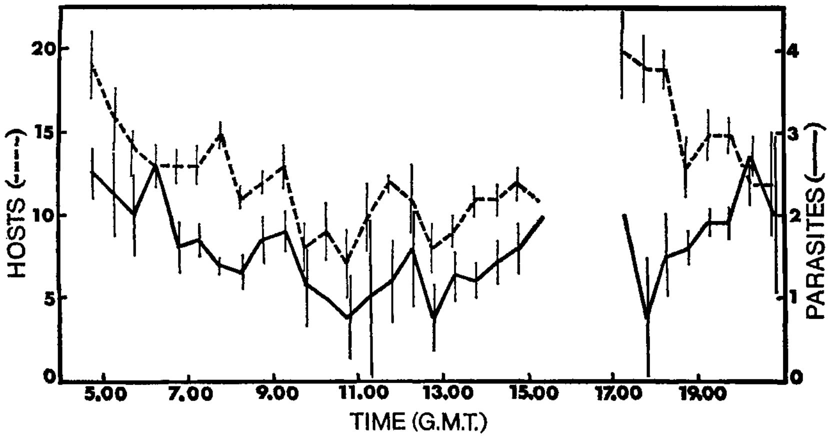

Figure 3. Diurnal patterns of host numbers (± 1 SE) and the number of parasitic terns active (± 1 SE). Points represent half-hourly means derived from 243 watches, each of 15 minutes, made on 10 days between 23 July and 7 August 1969.

ideal opportunities for ground attacks, which were more frequent in May than at any subsequent stage in the season, comprising 23 percent (N = 69) of attacks seen during 2 days in May 1968. By mid-July many Sandwich Tern chicks had fledged and dispersed from the colony, and fewer than 5 percent of robbing attacks were directed at Sandwich Terns. Robbing pressure shifted instead to the other tern species, which were still bringing fish to young chicks.

Robbing intensity.—Robbing occurred throughout the day but was most evident in the early morning and late evening. Figure 3 shows that more terns brought fish into the colony during these periods than at other times of day, a pattern which has previously been demonstrated for terns and other seabirds (Pearson 1964, Boecker 1967, Langham 1968). Between 05:00 (GMT) and 15:15, the number of Roseate Terns seen parasitizing over area A appeared to fluctuate in parallel with the availability of hosts (Figure 3). No observations were made between 15:15 and 17:15, but after 17:15 the numbers of terns robbing continued to increase despite a steady decline in the amount of fish entering the colony. This apparent reversal of the earlier trend may simply reflect a general buildup in colony attendance. The number of Roseate Terns parasitizing at any time was small (never more than five at once) and the addition of only one or two parasites in the evening could have produced the observed pattern. Data from the whole spread of diurnal activity showed the number of active parasites was positively correlated with the number of hosts carrying fish ($r = +0.37$, $P < 0.001$) (Figure 4).

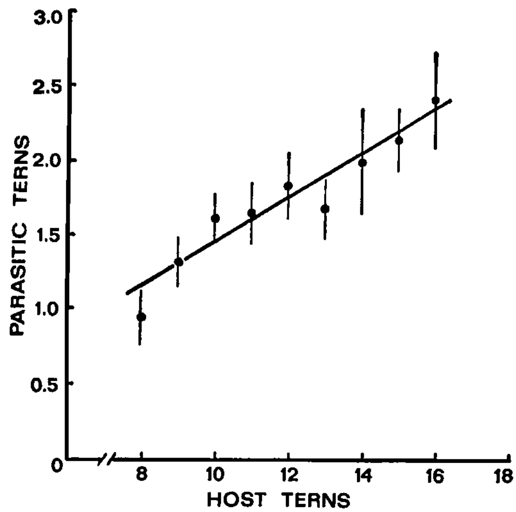

Figure 4. Relationship between the number of host terns and the number of parasitic terns (± 1 SE). The regression line (y = 0.15x − 0.03) is shown. The points are mean numbers active for given numbers of hosts, and are derived from 166 15-minute watches; host densities represented by fewer than 10 watches are not included.

Robbing success.—Table 1 shows the percentage robbing success of attacks on Common Terns over 13 days in 1968 and 1969; the mean success was 7.5 ± 1.3 percent SE. The more terns that entered area B with fish, the higher was the subsequent robbing success (r = +0.98, $P < 0.01$) as shown in Figure 5. Of 911 attempts to take identified fish from Common

TABLE 1
DAILY ROBBING SUCCESS OF ATTACKS ON COMMON TERNS

Date	Length of observation (hours:min)	Number of attacks	Number successful	Robbing success (%)
16 July 1968	1:00	47	1	2.1
17 July 1968	7:15	148	7	4.7
18 July 1968	6:30	100	11	11.0
23 July 1969	9:00	92	12	13.0
24 July 1969	8:00	133	24	18.0
25 July 1969	3:00	185	17	9.2
27 July 1969	6:45	223	21	9.4
29 July 1969	8:30	471	18	3.8
31 July 1969	6:15	208	11	5.3
4 August 1969	3:15	161	8	5.0
5 August 1969	7:00	300	24	8.0
6 August 1969	6:00	182	12	6.6
7 August 1969	3:00	108	2	1.9
TOTALS	75:30	2358	168	7.5 ± 1.3 SE

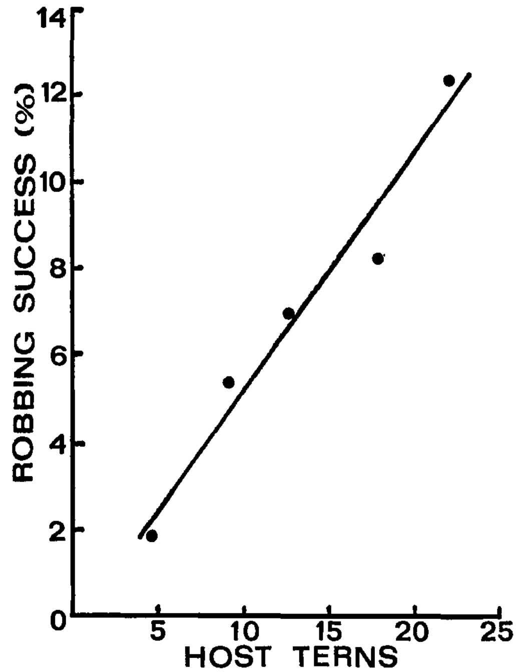

Figure 5. Relationship between the number of host terns and the robbing success of parasitic terns, based on 1,791 attacks. The regression line is $y = 0.55x - 0.32$. Observation watches were grouped according to host numbers in the ranges 0–5, 6–10, 11–15, 16–20, and 21–25, and each x-value represents the mean number of hosts within a range.

Terns in 1969, 896 (98 percent) were directed at either sprats or sand eels, and only 15 (2 percent) involved other fish species. From data collected during the 10 days in 1969, the mean robbing success was calculated for each length category of sprats and sand eels. Robbing success was found to be inversely proportional to fish length ($r = -0.94$, $P < 0.01$); attacks on hosts carrying the shortest fish (up to 2.5 cm) were about 15 percent more successful than attacks on hosts with the longest fish (10 cm) (Figure 6).

Mean weights of sprats and sand eels of given length were obtained from specimens collected in the colony and from additional data supplied by N. P. Langham. By combining values for robbing success (Figure 6) and weight, it is possible to estimate the weight of fish a Roseate Tern could expect to derive by attacking hosts that carry fish of known length (Table 2). It is clearly more profitable to challenge for large fish in spite of the greater success at robbing terns with small fish.

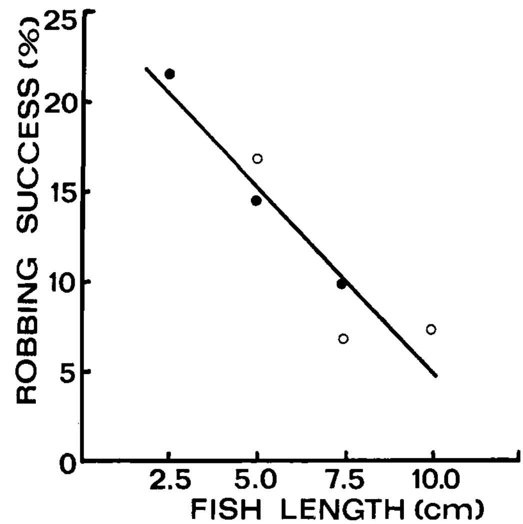

Figure 6. Robbing success of parasitic terns for different lengths of sprats (●) and sand eels (○) carried by host terns. The regression line is $y = -2.08x + 25.85$.

Selection of hosts.—Assuming that the fish brought into area B were representative of those available in area A, it is possible to compare the observed frequencies of attacks on each length class with the frequencies expected if parasites had encountered and attacked classes at random, i.e. simply according to availability. The distribution of attacks on available fish was examined only for Common Terns as the other host species provided too few data for separate analysis.

It is unlikely that a parasitic tern responds only to the length of fish it sees. Compared with a sand eel of the same length, a sprat is deeper-

TABLE 2

YIELD OF FISH TO PARASITIC TERNS WHEN THEY ATTACK HOSTS CARRYING SPRATS AND SAND EELS OF KNOWN LENGTH[1]

	Length of fish (cm)			
	2.5	5.0	7.5	10.0
Sprats				
Weight (g)	0.20	0.55	2.50	—
Success (%)	21.6	14.5	9.9	—
Yield (g)	0.04	0.08	0.25	—
Sand eels				
Weight (g)	—	0.25	1.30	3.00
Success (%)	—	16.9	6.8	7.4
Yield (g)	—	0.04	0.09	0.22

[1] Yield = weight of fish × robbing success appropriate to the fish's length.

TABLE 3

CHI-SQUARE VALUES FOR DIFFERENCES BETWEEN OBSERVED AND EXPECTED FREQUENCIES OF ATTACKS ON AVAILABLE FISH CARRIED BY COMMON TERNS

	Size class of fish[1]						
Date	2.5-cm sand eel 2.5-cm sprat	5-cm sand eel	5-cm sprat	7.5-cm sand eel	7.5-cm sprat 10.0-cm sand eel	$\Sigma\chi^2$	*P*
23 July	0.46↓[2]	0.00↓	11.76↑	5.16↓	2.20↓	19.58	0.001
24 July	2.00↑	6.21↓	1.78↑	0.50↓	0.19↓	10.68	0.05
27 July	4.99↓	0.31↓	9.42↑	2.40↓	3.49↓	20.61	0.001
29 July	7.11↓	1.77↓	0.06↑	17.01↑	0.31↓	26.26	0.001
31 July	2.49↓	4.70↓	7.38↑	5.31↑	0.29↓	20.17	0.001
4 August	5.48↓	2.62↓	19.84↑	0.30↓	1.92↓	30.16	0.001
5 August	8.29↓	8.83↓	55.56↑	6.22↓	5.43↓	84.33	0.001
6 August	6.20↓	4.05↓	16.50↑	3.04↓	0.80↑	30.59	0.001

[1] Ranked from left to right in order of increasing weight.
[2] ↑ = observed frequency > expected frequency. ↓ = observed frequency < expected frequency.

bodied and, as shown in Table 2, weighs about twice as much. I therefore decided to rank classes of the two fish species by weight. The smallest and largest sand eels (2.5 cm and 10.0 cm) were not available on all days and so were grouped with the weight classes adjacent to them. On 2 days (25 July and 7 August) too many of the expected frequencies were less than 5 to permit Chi-square analysis. Table 3 shows the Chi-square values for attack distributions on the remaining 8 days. On all days there was a significant difference between observed and expected frequencies of attacks. Inspection of Table 3 shows that the disparity between distributions was due to a strong tendency to select 5-cm sprats at the expense of fish that were smaller or larger than this. On 29 July 7.5-cm sand eels were exceptionally plentiful and were attacked more often than expected, but Roseate Terns did not simply select what was most common on any particular day; 5-cm sand eels, for example, were more abundant than 5-cm sprats on 5 days out of 8 and yet were less preferred than 5-cm sprats on all of these days.

The apparent preference for attacking Common Terns with 5-cm sprats is reflected in the composition of the 128 fish successfully robbed for which both species and length were determined. The mean length of these fish was 5.1 cm and they comprised 62 percent sprats and 38 percent sand eels. The mean length does not differ from the expected figure, which was derived by taking into account the length classes available and the robbing success appropriate to each class. The expected species composition of the robbed prey is 55 percent sprats and 45 percent sand eels. This difference from the observed composition accrues mainly from the tendency by parasites not to attack the smallest sand eels.

Discussion

The parasitic behavior of Roseate Terns is obviously a highly ordered activity that responds to a variety of subtle changes in the numbers and types of potential prey carried by hosts. Thus the number of Roseate Terns that engaged in robbing, though small, showed a direct numerical response (in the sense of Holling 1959) to changes in the numbers of host terns. The results indicate further that higher host densities were associated with better robbing success. A large number of terns entering the colony with fish caused intense and seemingly congested aerial activity to which birds both with and without fish contributed. At such times the hunting strategy of the parasitic terns may have been relatively inconspicuous, especially to flying birds preoccupied with avoiding other terns in front of them. This suggests that, in dense air traffic, hosts were less able to detect and anticipate the overhead threat of parasites, which thereby gained greater surprise and success in their attacks. It follows that robbing of this kind may be generally more successful in large tern colonies with a dense concentration of breeding birds.

The varying vigilance of the host terns may also explain why robbing success was better for small fish than for large ones. Since almost all (99.8 percent) unsuccessful attacks were characterized by curtailment of the attack just short of actual physical contact with the host, the relationship between fish size and robbing success can be restated as follows: the larger the host's fish, the greater was the probability of the parasite disengaging from its attacking maneuver. An aborted attack was sometimes preceded by anticipatory avoiding action by the host in the form of a slight downward or sideways deviation from the horizontal flightline. Lower robbing success when fish are large may therefore be related to more frequent or more effective (e.g. earlier) avoiding action by the host bird. Behavior of this kind by hosts could be reinforced by interactions with other species on the island. Firstly terns carrying large fish were also likely to be pursued by Black-headed Gulls, while terns with small fish usually passed by gulls with impunity. Furthermore Common Terns with large fish seemed more likely to be accosted by small bands of their own species that resort to chase-robbing on Coquet Island during times of food shortage. Thus a tern that carries a large fish through the colony has ample stimulus to take special caution. This implies that the host learns that danger is inherent in carrying a conspicuously large fish and is better prepared to forestall attack from Roseate Terns in these circumstances.

Despite the lower success at attacking terns with large fish, these yielded the best weight return per robbing attempt and it is not clear why parasitic terns chose instead to concentrate their attacks on birds carrying fish of intermediate size (5-cm sprats). In this respect the distribution of attacks differed from that shown for parasitic interactions between Common and Arctic Terns on Petit Manan Island, Maine, where the most frequent targets of piratic chases were those terns carrying the largest fish (Hopkins and Wiley 1972). In the present study the availability of prey exceeding 5 cm was relatively low and active selection of these items might have involved wasteful searching. In addition Roseate Terns and their chicks probably experience increasing handling difficulties with prey longer than about 7.5 cm. Observations of Roseate Terns plunge-diving at sea in July 1969 showed that they tended to take smaller fish (4.5 ± 0.2 cm SE) than did the bigger Sandwich Terns feeding in the same place, and other records (Langham 1968) suggest that 5–7.5 cm is the optimum range of prey size for Roseate Terns. The bias against attacking host terns with very small fish is indicative that such prey fail to provide the Roseate Terns with sufficient energy yield to warrant the effort involved in their pursuit and capture (cf. Root 1967). This is an especially important consideration in the breeding season, which imposes heavy flight demands on parent birds. There is little doubt that parasitism by Roseate Terns was a means of providing food for growing chicks rather than for self-maintenance. In 146 successful attacks on Common Terns, the parasitic tern swallowed only 16 fish (11 percent) on the spot. The other fish were carried towards parts of the island occupied by breeding Roseate Terns and whenever a parasite was seen to land at its nest site with a stolen fish, the chick rather than the mate was fed.

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SUMMARY

Describes the robbing strategies of Roseate Terns on Coquet Island, England. The terns robbed both intraspecifically and interspecifically (Common Terns, Arctic Terns, and Sandwich Terns). Sandwich Terns were the most frequently robbed species in May but later in the season the other tern species were the main hosts. The intensity of robbing showed a marked diurnal pattern that corresponded closely with variations in the number of terns carrying fish into the colony. The number of terns

actively parasitic was correlated directly with the numbers of available hosts. Mean robbing success was 7.5 percent. As robbing success was also correlated directly with host density, it is suggested that parasitic terns benefited from the apparent confusion that attended dense "air traffic." Robbing success was inversely correlated with the length of fish attacked; terns carrying large fish may be more vigilant and so better prepared to forestall attack. Although terns with fish of all sizes up to about 10 cm were attacked, parasites tended to select for attack those hosts carrying fish of an intermediate size, namely 5-cm sprats. Possible reasons for this preference are discussed.

Literature Cited

Bannerman, D. A. 1962. The birds of the British Isles, vol. 11. Edinburgh, Oliver and Boyd.

Belopol'skii, L. O. 1957. Ecology of sea colony birds of the Barents Sea. (Jerusalem, Israel Program for Scientific Translations, 1961).

Boecker, M. 1967. Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Fluss-seeschwalbe (*Sterna hirundo* L.) und der Küstenseeschwalbe (*Sterna paradisaea* Pont.). Bonn. Zool. Beitr. 18: 15–126.

Grant, P. R. 1971. Interactive behaviour of Puffins (*Fratercula arctica* L.) and Skuas (*Stercorarius parasiticus* L.). Behaviour 40: 263–281.

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

Hays, H. 1970. Common Terns pirating fish on Great Gull Island. Wilson Bull. 82: 99–100.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. Canadian Entomol. 91: 293–320.

Hopkins, C. D., and R. H. Wiley. 1972. Food parasitism and competition in two terns. Auk 89: 583–594.

Langham, N. P. E. 1968. The comparative biology of terns. Unpublished Ph.D. dissertation, Durham, England, Univ. Durham.

Meinertzhagen, R. 1959. Pirates and predators. Edinburgh, Oliver and Boyd.

Nørrevang, A. 1960. Søfuglenes udvaelgelse af ynglebiotop på Mykines, Faerøerne. Dansk Ornithol. Foren. Tids. 54: 9–35.

Pearson, T. H. 1964. Aspects of the feeding biology of certain sea-birds. Unpublished Ph.D. dissertation, Durham, England, Univ. Durham.

Rand, A. L. 1954. Social feeding behavior of birds. Fieldiana, Zool. 36: 1–71.

Root, R. B. 1967. The niche exploitation pattern of the Blue-grey Gnatcatcher. Ecol. Monogr. 37: 317–350.

Watt, G. 1951. The Farne Islands. London, Country Life.

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