FOOD PARASITISM AND COMPETITION IN TWO TERNS

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FOOD parasitism occurs when an individual of one species steals an item of food from an individual of another species after the victimized individual has already located and caught the food. During a trip to Maine in 1968 we noticed that Common Terns, *Sterna hirundo*, on Petit Manan Island regularly pursued and stole fish from Arctic Terns, *Sterna paradisaea*, nesting on the same island. In 1969 we returned to this island to extend our observations of food parasitism and to obtain some information about other types of foraging behavior by these species. These studies suggest the possibility that both parasitic and competitive interactions might operate concurrently between Arctic and Common Terns.

We visited Petit Manan Island (Washington County, Maine) twice: 26–29 June 1968 and 27–30 June 1969. The island (Figure 1), about 300 meters in diameter and 4 km southeast of the nearest land, had 1,200–1,500 pairs of nesting terns, about one-third of which were Common Terns while nearly all the rest were Arctic Terns (Hatch, 1970). These two species were not randomly interspersed, for each tended to aggregate roughly at one end or the other of the island. Arctic Terns were densest near the north end of the island, Common Terns in the south. In both years the terns had chicks of various ages or were incubating eggs. Large chicks seemed relatively fewer during our 1969 visit, which probably indicates that the nesting cycle was slightly later than in 1968. Terns returned to the colony in a continuous stream all day, most of them carrying a fish or some other food object in the bill. We built two blinds on the island to allow close observation of the terns near their nests.

FORAGING BEHAVIOR OF THE TWO SPECIES

Common Terns and Arctic Terns appeared to bring the same kinds of food back to the nesting colony. In 1968 we distinguished two kinds of fish, an unidentified brownish species, and more often herring, *Clupea harengus*, identified from several specimens dropped by the terns. Again in 1969 most of the fish we saw looked like herring, but terns also occasionally brought in small crustaceans. The terns flew away from the island in all directions and usually foraged out of sight. Occasionally we noted groups of 20–30 terns fishing in flocks a mile or more off shore. Also terns fished in the surf on the reef south of the island one day after a storm.

We could distinguish the two species reliably by the color of their bills and by the pattern of dark gray in their primaries. On the upper surface of their primaries Common Terns in breeding plumage have a dark gray,

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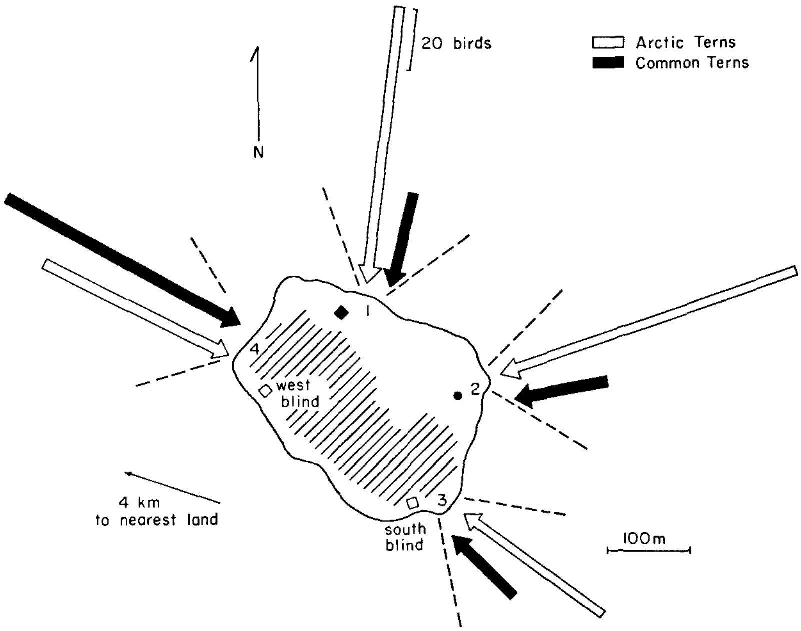

Figure 1. Petit Manan Island. Terns nested densely in the hatched area. Dashed lines indicate the four sectors in which we recorded terns returning to the island. The length of each arrow is proportional to the total number of terns arriving within each sector during two standard watches. Black arrows, Common Terns; open arrows, Arctic Terns.

subterminal wedge, which the Arctic Terns lack. Bannerman (1962: 165) also recognizes this mark, and it is well illustrated in Robbins et al. (1966).

We looked for differences in the kinds and sizes of food the two species carried and in the directions from the island they foraged. In 1968 during four observation periods (20–45 minutes each) from the west blind (Figure 1) we tried to select flying terns at random through binoculars and to determine for each tern the size of the fish it was carrying. In 1969 we made similar estimates of fish sizes during 11 watches of 5–10 minutes each from the west or south blind at various times throughout the day. In these watches from the blinds we might have recorded some terns more than once in a given sampling period. More satisfactory were counts in 1969 of terns returning to the island. We stood on the shore and recorded all terns returning from sea within a 50–60° sector from our vantage point (dotted lines in Figure 1 show the sectors we used). On each of 2 days we conducted four 10-minute watches, one from each of four points around the island within the span of an hour. Thus we could compare the terns arriving from different

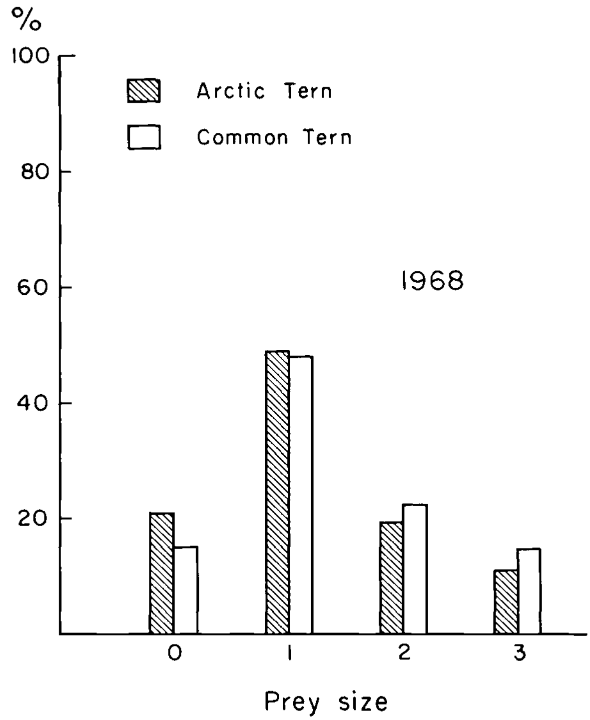

Figure 2. Sizes of fish carried by Common and Arctic Terns during standard watches from blinds in 1968. Hatched bars, fish carried by Arctic Terns (N = 98); open bars, fish carried by Common Terns (N = 27). Abscissa represents increasing sizes of fish. Ordinate represents percentages of each N.

directions within an hour's time. In each 10-minute watch we probably never recorded the same bird twice. A Chi-square test showed that fish sizes in observations from the shore differed significantly from those in observations from the blinds. Observations from the shore probably yielded less biased samples of terns.

We roughly estimated fish sizes by comparing the fish with the length of the tern's bill. Four size classes, 0–3, included fish respectively less than, roughly equal to, slightly greater than, and at least twice the length of the tern's bill. One herring that we had classified as size 3 before the tern dropped it in a chase measured 137 mm long and weighed 14 g. In Chi-square tests we lumped class 0 with class 1 and class 2 with class 3 whenever necessary to avoid numbers less than 10 in any box.

We found no striking differences in the food items that the two species of terns brought to the island (Figures 2 and 3). Both species brought many small fish and a few large ones. Observations from the blinds in both years revealed no significant differences between the sizes of fish

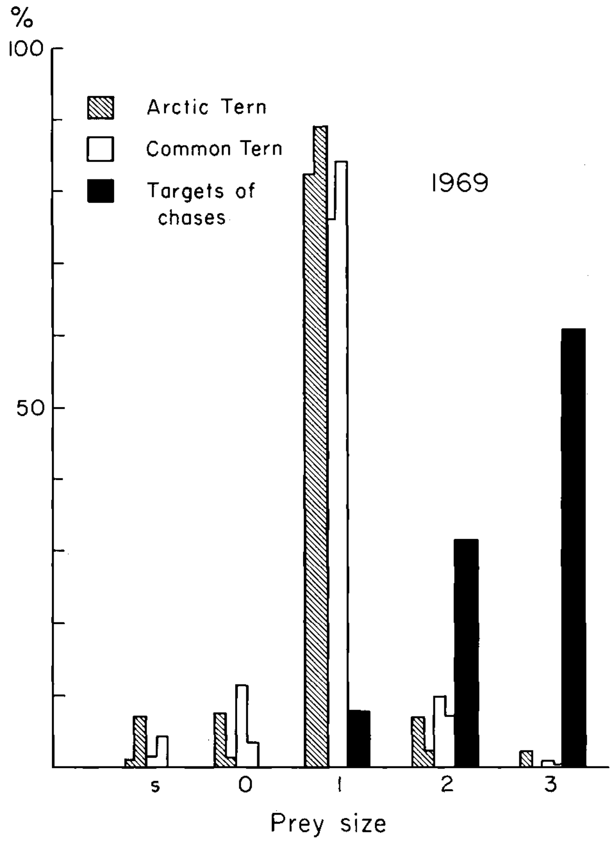

Figure 3. Prey carried by Common and Arctic Terns during standard watches and by targets in chases in 1969. Hatched bars: prey carried by Arctic Terns during standard watches from blinds (left half of bar; N = 322) and from shore (right half of bar; N = 472). White bars: prey carried by Common Terns during standard watches from blinds (left half of bar; N = 128) and from short (right half of bar; N = 206). Black bars: prey carried by target individuals in chases (N = 51). Abscissa represents size classes of prey (S, small crustaceans; 0–3, increasing fish sizes). Ordinate represents percentages of each N.

carried by the two species (1968: $\chi^2 = 0.660$, 3 df, $P > 0.8$, N = 125; 1969: $\chi^2 = 5.862$, 2 df, $0.05 < P < 0.1$, N = 445, size classes 2 and 3 lumped). Observations from shore suggested that the two species might in fact tend to select different kinds of prey ($\chi^2 = 12.50$, 2 df, $P < 0.005$, N = 679). Common Terns carried proportionately fewer crustaceans and more large fish. Boecker (1967) also found that Arctic Terns in the North Sea included a greater proportion of crustaceans in their diet than did Common Terns.

Both species brought in large fish more frequently in 1968 than in 1969 (Arctics: $\chi^2 = 25.48$, 1 df, $P < 0.005$, N = 417; Commons: $\chi^2 = 6.30$, 1 df, $P < 0.025$, N = 153) (Figures 2 and 3). The decrease in the frequency of large fish seen in 1969 might reflect either a change in the composition of fish schools in the vicinity of the island or the fewer large chicks during our visit that year.

The two species differed clearly in the directions from which they returned to the island. Figure 1 shows the total number of individuals of each species recorded during two 10-minute watches at each of four locations (for each series of four watches, $\chi^2 \geqslant 16.77$, 3 df, $P \leqslant 0.005$, N $\geqslant$ 220). Common Terns predominated from the northwest. From the east Arctic Terns predominated, perhaps even more than in the overall population on the island. The nearest mainland, Petit Manan Point, was 4 km northwest, the direction preferred by Common Terns. Thus Common Terns might forage especially near the mainland, where we saw them frequently during our trips to and from the island. By contrast Arctic Terns in the North Sea foraged more often in shallow water near land than the Common Terns did (Boecker, 1967).

These observations of fish sizes and the directions of returning birds indicate that the two species overlap considerably in these parameters of their feeding ecology. The clearest distinction we discovered between the two species was the Common Tern's tendency to feed in the direction of the nearest land.

Piratic chases.—Flying chases were seen regularly on the island. In some of these chases Laughing Gulls, *Larus atricilla,* pursued terns (Hatch, 1970). In others one tern chased another, and these we watched systematically. Many chases resulted from agonistic and epigmatic interactions instead of attempts at food piracy. We noticed only occasional "fish-flights" (Tinbergen, 1931; Palmer, 1941; Cullen, 1960), which function in pair formation and occur most frequently before incubation begins. In these aerial displays one tern leads the other with characteristic "V-flying." Also easily distinguished from attempts at food piracy were the frequent agonistic rising duels between two terns. We included among piratic chases only fast, energetic chases in which the pursued tern, or target, carried a fish. We eliminated all equivocal chases, such as swoops and brief passes, even if the target carried a fish. These criteria probably excluded all agonistic and epigmatic chases.

In order to obtain quantitative data on the success rate and on the relative numbers of the two species among the pursuers and targets, we conducted 2 watches on different days in 1968 and 16 watches from the blinds during 4 days in 1969, a total of 12½ hours of observation. The watches were scattered throughout the daylight hours. Whenever possible

TABLE 1
PURSERER AND TARGET SPECIES IN PIRATIC CHASES

Pursuer		Target			
		Common	Arctic	Unidentified	Totals
Common	All chases, 1968	5	7	6	18
	Long chases, 1969	8(2)[1]	19(3)	1	28
	Short chases, 1969	10(1)	4	2	16
					62
Arctic	All chases, 1968	1	0	0	1
	Long chases, 1969	0	0	0	0
	Short chases, 1969	1	2	0	3
					4
Unidentified	All chases, 1968	0	0	1	1
	Long chases, 1969	0	1	2	3
	Short chases, 1969	1	1	0	2
					6
Totals	All chases, 1968	6	7	7	
	Long chases, 1969	8	20	3	
	Short chases, 1969	12	7	2	
Grand totals		26	34	12	72[2]

[1] Parentheses enclose the number of chases with two or three pursuers.
[2] Total number of chases, 1968: 20 (1.5 hours of observation). Total number of chases, 1969: 52 (11 hours of observation).

we recorded the species of the target and pursuer on each chase, the size of the fish involved, the approximate duration of the chase, and how the chase ended. Many other piratic chases were seen at times other than during these standard watches.

Common Terns predominated heavily among pursuers (94 percent of identified pursuers), in spite of the fact that they were less numerous in the colony than Arctics. Although both species were targets about equally often overall, the proportions of the two species differed in long and short chases. We divided the chases into two groups: short chases 50–100 m long, and long chases more than 100 m. The latter sometimes lasted a minute or more. In a long chase an Arctic Tern was usually the target, whereas Common Terns predominated slightly among targets in short chases (Table 1). Apparently when the target was a Common Tern, chases were often quickly discontinued.

In a successful chase either the pursuer managed to grab the fish or a part of it from the target's beak, or the target dropped the fish and the pursuer grabbed it just before or after it reached the ground. The success rate approached 10 percent of all chases recorded during standard

TABLE 2

RESULTS OF PIRATIC CHASES RECORDED DURING STANDARD WATCHES IN 1969

		Target Species					
		Common		Arctic		Unidentified	
Result	Pursuer(s)	Long chases	Short chases	Long chases	Short chases	Long chases	Short chases
Fish stolen	1 Common	1		3[1]		1	
(successful chase)	2 or 3 Commons			1[2]			
Fish dropped	1 Common	1		2[1]			
Fish	1 Common	3	1	3		1	
swallowed	2 Commons		1	3[2]			
Chase	Common	1	8	6	4		1
discontinued	Arctic		1		2		
	Unidentified		1		1		
Total chases of known outcome		6	12	16	7	2	1

[1] Double entry for one chase in which an Arctic Tern dropped its fish and a Common Tern caught it.

[2] Double entry for one chase in which a Common Tern stole a small piece of the fish before the Arctic Tern swallowed the remainder.

watches (6 of 52 chases in 1969, 1 of 20 chases in 1968). In a typical case seen on 29 June 1968 but not included in one of the standard watches, a Common Tern intercepted an Arctic returning to the island with a large fish. After a lengthy, tortuous chase along the shore, the Common Tern grasped the fish and, amidst frantic fluttering, wrenched it away. The successful attacker then flew to its nest and deposited the large fish beside two very small chicks; the fish was much larger than either of the two chicks. Sometimes the target individual dropped its fish into tall grass, so the fish was lost to both the target and the pursuer. Terns dropped their fish only during vigorous chases.

A hard-pressed target frequently tried to avoid losing its fish by swallowing it. Swallowing required temporary stalling in flight and for a few seconds an added risk of having the pursuer grab the fish. In other piratic chases the pursuer finally gave up. Table 2 presents the results of all chases of known outcome in 1969. These data, although insufficient for conclusions, suggest that in long chases pursuers might have somewhat greater success when Arctic Terns are targets than when Common Terns are. Multiple pursuers probably increased the risk for the target individual, as in four of six such chases the target dropped or swallowed its fish or had it stolen.

Targets of piratic chases tended to carry large fish (Figure 3). Every successful chase involved a size-3 fish. Furthermore the frequencies of

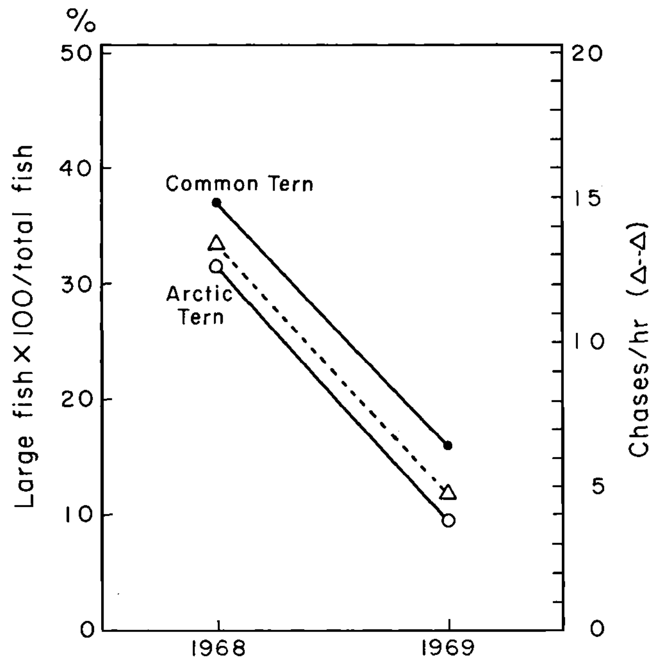

Figure 4. Comparison if data for 1968 and 1969: the percentage of large fish (sizes 2 and 3) recorded during standard watches (solid lines) and the frequency of chases in chases per hour during standard watches (dotted line).

chases in the 2 years of our observations correlated with the frequencies of large fish in the 2 years (Figure 4). Probably because they brought large fish back to the island slightly more often than did Arctics (Shown above), Common Terns are somewhat more common among the targets of piratic chases (Table 1: Grand Totals) than in the population as a whole. All our observations are thus consistent with the following hypothesis: a pursuer, usually a Common Tern, selects a target that carries a large fish, and then persists in a long chase especially if the target is an Arctic Tern.

DISCUSSION

Coexistence of the two species.—Several studies have compared the ecology of coexisting species of terns (Gause, 1934; Ashmole and Ashmole, 1967; Ashmole, 1968; Boecker, 1967). All have reported significant differences between species in their foraging behavior and diet. Yet in most cases the overlap between related species is more striking than their differences. In the diets of Common and Arctic Terns, Boecker (1967) found that the differences between years for each species exceeded the differences between species in any one year.

When two species exploit the same environmental resources and these resources limit their population sizes, the species are in ecological competition. Sympatric related species could reduce interspecific competition by occupying different habitats or, if food limits the species' population densities, by specializing on different food resources in any one habitat (Lack, 1944). In ether case morphological or behavioral differences would correlate with the ecological differences. For two species to coexist in equilibrium their ecological differences must normally exceed some minimum (Hutchinson, 1959; MacArthur and Levins, 1967), otherwise interspecific competition should result in local extinction of the less efficient competitor.

Several alternatives reviewed by Hutchinson (1965) might explain how two species could coexist and still show wide overlap in their feeding ecology, as Common and Arctic Terns apparently do. One possible explanation is that the food supply does not limit the populations of these two species in the breeding season, so that the ecological differences relevant to their coexistence would not involve food resources. We have no information on whether or not food ever becomes a limiting resource for terns on Petit Manan Island. Alternatively, as little is known about what determines the minimum ecological differences sufficient for equilibrial coexistence, the differences in the foraging behavior of Common and Arctic Terns, although small, might in fact reduce interspecific competition enough for sustained coexistence. Terns seem unlikely to qualify as "fugitive species" (Hutchinson, 1951), species exposed to such wide fluctuations in their environment that they essentially never attain equilibrium with their food or their competitors. Instead, coexistence of related terms might depend on their long adult life expectancies (Austin and Austin, 1956; Cullen, 1957), if slight competitive advantages shifted from one species to the other from year to year (Hutchinson, 1953). In general when two species have long life expectancies in relation to the period of some qualitative fluctuation in the environment, they might successfully specialize on different alternately recurring environmental states. Facultative parasitism might also facilitate the coexistence of two species. If the poorer competitor is a facultative parasite on the better competitor, then its population size might never fall to zero. Facultative parasitism by one species would thus allow it to coexist with its victim, even though the victim could prevail in purely competitive interactions.

Could facultative parasitism help explain the coexistence of Common and Arctic Terns? As we observed 7 successful chases during 12½ hours of standardized observations, perhaps only 8 to 10 successful chases occur each day on the island. As the frequency of chases correlated with the availability of large fish, and as large fish are brought more frequently to larger chicks (Boecker, 1967), the frequency of chases might well increase later in the nesting cycle than the periods of our observations (see Hatch, 1970, for such an effect in food parasitism by Laughing Gulls). Nevertheless food parasitism by the Common Tern probably only slightly influences its ecological relationships with the Arctic Tern.

The Common Tern as a food pirate.—Feeding strategies should evolve to maximize the yield of usable energy in relation to the energy invested in locating, capturing, and digesting food items. Two coexisting species should both tend to evolve optimal feeding strategies, regardless of whether or not they compete for food, as individuals of each species should benefit from efficient feeding strategies.

Common Terns on Petit Manan Island have two distinct feeding techniques: (1) fishing at a distance from the island and then carrying some of the available fish back to their chicks (fishing at sea); and (2) chasing terns carrying large fish near the island (food parasitism). Two distinct feeding strategies should persist only when each is more efficient in particular circumstances. For instance, parasitism might pay only when a large fish is at stake. Because Common Terns stole fish on the average only once in every 10 chases, this low success rate would considerably decrease the yield/cost ratio for parasitism. Perhaps only when the target carried a large fish would the efficiency ratio, amount of food/parental cost, for parasitism exceed the comparable yield/cost ratio for fishing at sea. Parasitic chases were infrequent, probably because few terns carried large fish to the island. Thus when a higher proportion of terns carried large fish, the incidence of parasitism was higher (Figure 4). One might also speculate that the yield/cost ratio for parasitism would depend on the weather. As terns rarely brought food to their young during stormy weather on Petit Manan Island, when chick mortality was high, chicks that got large fish before a storm broke might survive better. In this case parasitic chasing for large fish might increase the efficiency ratio, chick survival/parental cost, in spite of a lower amount of food/parental cost. Chick survival is the more appropriate parameter for reproductive yield.

The regular success of Common Terns in piratic chases might depend on greater speed or maneuverability in flight. Piratic Common Terns were noticeably more successful in following the dodges of Arctic Terns than those of other Common Terns. When a Common Tern dodged to the side, its pursuer often seriously overshot the turn before once again closing with its target. Perhaps target individuals hampered by large fish in their beaks could not fly so fast nor dodge so quickly as less encumbered targets. Nevertheless, even when carrying large fish, Common

Terns evaded pursuers more effectively than Arctic Terns did. Clearly, though, the two species differ only slightly in flying abilities, one of the reasons that attempts at food parasitism so seldom succeed.

Another problem that might limit the Common Tern's success in food parasitism is their apparent failure to distinguish the two species in flight. If Arctic Terns do represent easier targets, then piratic Common Terns would do best to select Arctics for pursuit. The proportions of the two species among targets (Table 1) suggest that Common Terns initiating chases do not discriminate between the two species. Instead they apparently choose targets on the basis of the size of the fish and then continue chasing only those targets with somewhat less ability in dodging, usually Arctics. The Common Terns on Petit Manan Island manifest only the most rudimentary adaptations for food parasitism.

Possible effects of parasitism on food choice by the Arctic Tern.— Especially for an Arctic Tern, a large fish increased the risks of parasitism, which would offset the advantages of additional food for the chick. Piracy in the air, though, might not represent the greatest risk. When a tern with a fish landed near its chick, one or more neighboring chicks often tried to steal it. Frequently the adult took flight again, still holding the fish, to avoid these hungry chicks. Another disadvantage of a large fish is that a chick takes longer to swallow it. A strange adult occasionally can snatch a large fish from the mouth of a chick (Hays, 1970; pers. comm.). In one such instance that we recorded, the thief suddenly swooped in and grabbed the fish from a chick standing beside its parent. Thus a small fish is an easy burden to carry, attracts piratic pursuits less often, and can usually be delivered quickly to the chick, which can swallow it quickly. Yet a tern feeding its chicks small fish has to make more trips to provide the same amount of food. Intermediate fish sizes would probably maximize the efficiency ratio, amount of food/parental cost.

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Summary

We investigated possibilities for both competitive and parasitic interactions between Common and Arctic Terns on Petit Manan Island, Maine. Both species fed their chicks almost exclusively herring. In two parameters of their foraging behavior, the sizes of fish brought to their chicks and the directions from which they returned to the island, the two species

differed significantly in spite of extensive overlap. Common Terns were facultative parasites on their congener and they regularly, although infrequently, stole large fish from Arctic Terns after energetic chases. We discuss the implications of these observations for the coexistence of these two sibling species and for the evolution of their feeding strategies.

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