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Size-selective Predation by a Specialist Forager, the Roseate Tern

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Parent birds must be able to recognize and provide for the energetic demands of their chicks. In semiprecocial species, including many seabirds, the energy requirements of young birds reach a peak at some point before fledging, coinciding with the period of maximum growth (Dunn 1980, Ricklefs and White 1981). Thus, older chicks that are still growing require more food than they did at a younger age. During this time, the energy budgets of parent birds increase sharply, because they must maintain a positive energy balance as well as provide for the energy requirements of their chicks (Ricklefs 1983). Parents can adjust to this increased burden in three ways: (1) they can deliver a constant quantity of food to their young at an increasing rate, (2) they can maintain a constant feeding rate but deliver a larger quantity of food per trip, or (3) they can increase both food load and feeding rate. Terns appear to meet the increased demands of their chicks by delivering increasingly larger prey items rather than by increasing provisioning rate (Miller and Confer 1982, Wiggins and Morris 1987, Burger and Gochfeld 1991, Smith 1993, Shealer 1995) .

The increases in prey size observed in terns suggest that they are capable of size-selective predation. Evidence in support of size-selective predation by adult seabirds has been weak, however, primarily because of confounding factors. First, terns and other seabirds feed primarily on small fish, usually young-of-the-year, or the "0" age class (Harris and Wanless 1991, Monaghan et al. 1992, Bertram and Kaiser 1993). Juvenile fish also are growing at this time, such that as seabird chicks grow larger, the average size of individuals in the prey base increases as well (Miller and Confer 1982). Therefore, studies that document an increase in the size of prey fed to chicks over time cannot infer size-selective predation without using other methods. For example, Burger and Gochfeld (1990) found that some Black Skimmers (*Rhynchops niger*) fed their mates consistently larger fish than were fed to chicks at similar times throughout the breeding season, suggesting that adults recognized and provided for the different needs of their dependents.

Second, previous studies of piscivorous birds have demonstrated that size-selective predation differs with the structural complexity of the foraging habitat. In simple habitats without vegetative cover or shelter, predators showed a consistent preference for larger prey; however, when vegetation or cryptic substrates were added, this preference was less pronounced (Trexler et al. 1994, Kelly 1996). Moreover, prey-size selectivity has been shown to increase as a function of prey depth in a piscivorous bird (Labinger et al. 1991).

A third possible confounding factor is that, because adult seabirds forage for themselves as well as for their chicks during a feeding trip, adults may continue to sample the prey base until they catch a prey item of the appropriate size for their young. Supporting evidence for this strategy comes from studies showing that adult terns usually eat smaller prey than they feed to their mates or chicks (Taylor 1979, Hulsman and Smith 1988, Shealer 1995), suggesting that parents make post-capture "decisions" about which prey items they will deliver to their chicks. Thus, feeding studies conducted at breeding colonies in which an increase in prey size is documented over time, and in which size selection is inferred, cannot determine whether this selection occurs before or after the prey are captured by the adults.

I conducted an observational and experimental study of prey selection in breeding Roseate Terns (*Sterna dougallii*) in Puerto Rico to establish whether size-selective predation occurs in this species, and if so, whether the selection is pre- or post-capture. This determination was accomplished by comparing the size of prey fish adults delivered to their chicks with the size distribution of prey fish collected by net beneath foraging terns. Incongruity in the two data sets would suggest that Roseate Terns are capable of size-selective predation. I also conducted paired prey-choice trials on free-flying Roseate Terns to determine if they could discriminate between prey of different sizes prior to capturing them. I chose this species and location because I had found previously that Roseate Terns in Puerto Rico delivered increasingly larger prey to their chicks as the chicks grew older (Shealer 1995).

Roseate Terns are plunge divers, and in Puerto Rico they forage primarily in deep water over schools of predatory fishes that drive smaller fishes to the surface (Shealer and Burger 1993, Shealer 1996). Prey availability is mediated by the activities of these predatory fishes, and as a result, prey are accessible only for very brief periods. In such situations, Roseate Terns probably cannot discriminate among prey of different sizes, because the terns average about one dive every six seconds and have low capture success (ca. 28%; Shealer 1996). However, Roseate Terns also forage in shallow inshore areas in the absence of predatory fishes. Here, their capture success can approach 60%, but they dive much less

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frequently (Shealer 1996), suggesting that they have the opportunity to discriminate among prey of different sizes.

Methods.—Data used here were from a larger study conducted during the breeding seasons (May to July) of 1991 to 1994 in southwestern Puerto Rico, south of Parguera (17°56′N, 67°05′W). In each year, Roseate Terns nested on two cays with Sandwich Terns (*Sterna sandvicensis*), but the choice of colony sites differed among years. In this area, nesting islands for terns consisted of sparsely vegetated coral rubble cays along the outer reef zone, approximately 2 to 4 km offshore (see Shealer 1996). Terns arrived at the colonies in early to mid-May and began laying eggs shortly thereafter. By late July, most terns had dispersed from the area.

During the breeding season, Roseate Terns foraged almost daily at a small tidal lagoon at Cayo Turrumote (Shealer and Burger 1995, Shealer et al. 1997), and they reared chicks on this island in 1992 and 1994. Thus, I could confirm that they were feeding their chicks with prey caught in the lagoon. In 1991 and 1993, terns nested on adjacent islands 1 to 3 km away. However, terns continued to fish in the lagoon and were seen daily carrying fish from the lagoon toward the nesting colonies. For this reason, I assumed that in all years Roseate Terns relied, at least in part, on fish from Turrumote lagoon during the chick-rearing period.

Detailed methods for determining the size of prey delivered to chicks are given in Shealer (1995) and summarized briefly here. From 1991 to 1993, 10 study nests (each containing one chick) were observed from a hide during the first three weeks of the chick-rearing period, beginning approximately 12 June each year. To eliminate potential seasonal variation in prey deliveries, study nests were chosen such that all chicks hatched within five days of one another. During these daily watches (2 to 4 h each), the species and sizes of prey delivered to chicks were recorded, using the adult's bill as a template to estimate size. Prey were grouped into one of four size categories (tiny, small, medium, large) corresponding to one-half bill-length increments (e.g. tiny, <0.5 bill lengths; medium, 1 to 1.5 bill lengths). Prey deliveries from all nests were pooled into three one-week periods in each year. I compared differences in prey size among chicks that were 0 to 1 week, 1 to 2 weeks, and 2 to 3 weeks of age. To make the data more categorical, I allowed two days to elapse before collecting data for the next week.

In 1993 and 1994, I conducted prey-choice experiments on adult Roseate Terns that were foraging in Turrumote lagoon. Feeding trials were conducted on 19 and 20 July 1993, when adults were feeding large chicks or fledglings; trials in 1994 were conducted from 20 May to 1 June, prior to chick hatching but while adult terns were feeding their mates. Thus, these trials were conducted during periods when adult terns should have selected the larger fish, if they were able to do so. I used the false pilchard (*Harengula clupeola*) in all feeding trials because it is variable in size, can be caught with relative ease, and is an important prey species of Roseate Terns in this area (Shealer 1995). Prior to the feeding experiments, I conditioned adult terns to accept fish that I threw to them in the lagoon. By the time the feeding trials commenced each year, a flock of 5 to 20 terns regularly flew over and circled above me when I entered the water.

A feeding trial consisted of tossing two freshly killed pilchards of different sizes simultaneously into the water, after a hovering tern had positioned itself overhead. The fish were thrown to either side of the target bird and equidistant from it so that the bird had to veer to the left or right when diving. I randomized the order of presentation of fish so that the same-sized fish was not always thrown to the same side of the bird. The sizes of the fish offered during each trial were disparate enough to be in separate size classes described below. Most of the fish offered were between medium (35 to 52 mm) and large (52 to 65 mm) size; the remainder were between medium and small (18 to 35 mm) size. All fish were well within the size range of prey normally taken by Roseate Terns. The fish sank to the bottom immediately after hitting the water at the rate of approximately 10 cm/s. Thus, a tern had to make an instantaneous decision or both fish were lost. I believe that the length of this decision-making process was reasonably similar to what Roseate Terns face when foraging.

I accepted a feeding trial as valid only if there was a single bird hovering above me, if no other bird interfered with the target bird's attempt at prey capture, and if the target bird successfully captured a fish and immediately flew off with it in the direction of the breeding colony (presumably to feed a mate or chick). Because I was interested in size-selective predation as it related to the diet of the chicks, I did not include birds that ate the fish themselves because adults often eat prey smaller than those they feed to their chicks (Taylor 1979, Hulsman and Smith 1988). In addition, three to five individual terns were regular participants in the feeding trials (identified by colored leg bands and unique bill coloration). Because of statistical problems resulting from multiple data collected from the same individuals (Machlis et al. 1985), I excluded these birds from the analysis. The core group of participants was useful, however, in attracting other terns in the vicinity. Because of these stringent criteria, and because most target birds ate the fish themselves, I accepted only a small fraction of my trials as valid (81 out of more than 1,000 attempts).

To determine whether the sizes of prey delivered to chicks were random with respect to the available prey base, in 1993 I sampled fish on 12 dates between

14 May and 16 July. One sample was collected using a monofilament cast net (2.5 m in diameter, 6-mm mesh) between 0900 and 0930, Atlantic Standard Time, at each of 12 stations in Turrumote lagoon. Turrumote lagoon is shallow, and the waters over which terns usually foraged were <1.2 m deep; therefore, prey caught in the net likely were representative of prey available to terns. Evidence of size-selective predation would exist if the size distribution of prey differed between net samples and deliveries to chicks. All fish caught in the net were stored in ethanol for later measurement and identification in the laboratory. I measured the standard length (SL) and body depth (BD) of all fish using calipers (±0.1 mm) and wet mass using an electronic balance (±0.01 g). Fish lengths were converted into four categories (tiny, 0 to 18 mm; small, 18.1 to 35 mm; medium, 35.1 to 52 mm; large, >52.1 mm) to correspond to one-half bill-length increments of adult Roseate Terns (Shealer 1995). This conversion allowed me to make prey-size comparisons between net samples and observations of prey delivered by adults to chicks in 1993.

Prey sizes were compared between net samples and deliveries to chicks using chi-square tests of association. Data from the prey-choice experiment were analyzed with *G*-tests using the criterion of 50% selection of the larger fish offered as the expected value for the null hypothesis of no selectivity. Data from 1993 and 1994 were first analyzed separately because of temporal differences in the experiment and because of the different situations (adults feeding chicks vs. mates). I used a one-tailed test of significance for all comparisons of prey choice because I expected that if a preference existed, it would be for the larger fish.

Results.—In all three years of the chick-provisioning study (1991 to 1993), the average size of individual prey items delivered to chicks differed significantly throughout the chick-rearing period ($X^2 > 35$, df = 6, $P < 0.001$ for all three years). In general, adults delivered increasingly larger prey to their chicks throughout the three-week period in each year (Fig. 1).

In 1993 when adults were feeding large chicks and fledglings (19 to 20 July), Roseate Terns selected the larger fish in 31 of 47 (66%) trials, a result that deviated significantly from 50% ($G = 4.17$, df = 1, $0.01 < P < 0.025$). In 1994 during the mate-feeding period (20 May to 1 June), Roseate Terns selected the larger fish in 22 of 34 (65%) trials. Despite the similar results to 1993, the difference in 1994 did not deviate significantly from 50% ($G = 2.38$, df = 1, $P > 0.05$), but the power (1 − ß) of the test was low (i.e. 0.45) due to a small sample size.

To examine possible differences in discriminatory abilities of Roseate Terns as a result of fish size, I pooled data from 1993 and 1994. The terns selected the larger fish in 34 of 54 (63%) presentations of a large- versus a medium-sized pilchard, and selected the medium fish in 19 of 27 (70%) presentations of a small- versus a medium-sized pilchard. Both of these results deviated from 50% (large vs. medium, $G = 3.12$, df = 1; medium vs. small $G = 3.70$, df = 1; $0.025 < P < 0.05$ for both tests).

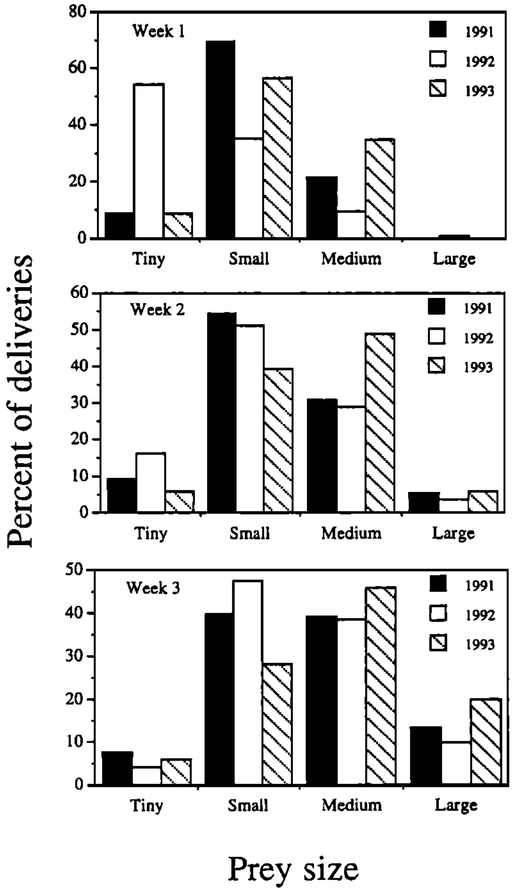

FIG. 1. Length-frequency distributions of prey items delivered by adult Roseate Terns to their chicks in each of the three-week chick periods from 1991 to 1993 (n = 1,187 in 1991, 376 in 1992, and 442 in 1993).

Four species of fish were caught by cast net at Turrumote lagoon in 1993, but their relative abundances varied throughout the season (Fig. 2). Dwarf herrings (*Jenkinsia lamprotaenia*) dominated net samples from 16 to 31 May. Other species began to appear in net samples on 31 May, with false pilchards becoming the most abundant species between 29 June and 7 July. By 20 July, dusky anchovies (*Anchoa lyolepis*) were the most abundant species in the lagoon.

Because dwarf herrings and false pilchards were the two species of fish caught consistently throughout the sampling period, and because they were principal prey items of Roseate Terns (Shealer 1995), I

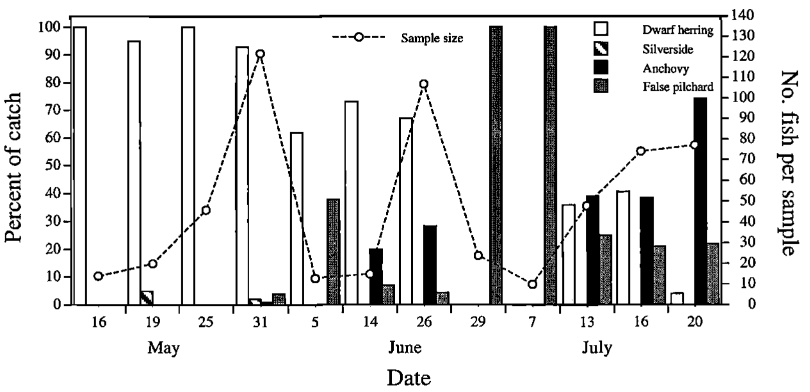

FIG. 2. Relative abundance (% of total catch) of four species of prey fish caught in cast-net samples at Turrumote lagoon on 12 dates from 16 May to 20 July 1993.

used them to gauge growth of prey throughout the season in 1993. The average sizes of these two fish species differed significantly from 16 May to 26 June (dwarf herring, $F = 15.4$, df = 8 and 317, $P < 0.001$, $R^2 = 0.280$; false pilchard, $F = 7.8$, df = 7 and 87, $P < 0.001$, $R^2 = 0.385$). However, during the three-week period in which Roseate Terns were feeding their chicks (14 June to 12 July), the average size of dwarf herrings and false pilchards fluctuated inconsistently among sampling periods (Fig. 3). When all fish species from net samples were combined and categorized according to size (tiny and small vs. medium and large), the length distributions varied among the three weeks of the chick-feeding period ($X^2 = 6.9$, df = 2, $P < 0.05$) but did not show a consistent increase in average length (Fig. 4). In general, fish length increased between weeks 1 and 2 and decreased between weeks 2 and 3.

In 1993, comparisons between the size distributions of fish caught in the net and the sizes of fish delivered to tern chicks (Fig. 4) revealed significant differences in all three weeks of the chick-rearing period (week 1, $X^2 = 8.35$, $P < 0.05$; week 2, $X^2 = 48.8$, $P < 0.001$; week 3, $X^2 = 16.1$, $P < 0.001$; df = 3 for all tests). Thus, in general, the sizes of prey that Roseate Terns fed to their chicks were smaller than the sizes of prey caught by net in Turrumote lagoon.

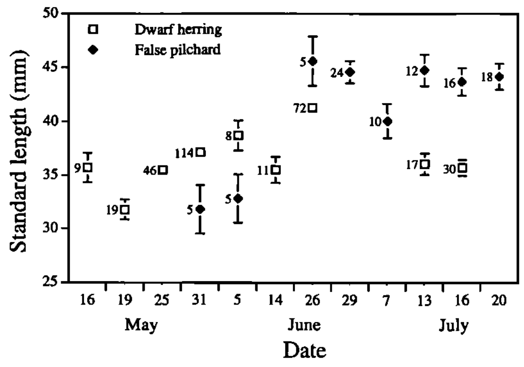

FIG. 3. Mean (±SE) standard lengths of dwarf herrings and false pilchards caught by cast net in Turrumote lagoon throughout the breeding season of Roseate Terns in 1993. Numbers denote sample sizes.

Discussion.—My results support the hypothesis that Roseate Terns in Puerto Rico are capable of some degree of size discrimination before they capture a prey item. The mean size of prey fed to chicks increased significantly throughout the breeding season from 1991 to 1993, but in 1993 the size distribution of fish fed to chicks differed from net samples in Turrumote lagoon throughout the chick-rearing period. In all three weeks, adults delivered smaller prey to their chicks relative to the available prey base. However, closer examination of Figure 3 suggests that adults adjusted to the food requirements of their chicks over the three-week period. No large fish were delivered or available during the first week; in the second week, large fish were delivered in proportion to their availability; and during the third week when adults were feeding older chicks, large prey were delivered in higher proportion relative to availability.

In prey-choice experiments, Roseate Terns selected the larger prey item 65% of the time in both 1993 and 1994, and did so consistently regardless of whether the choice was between large and medium, or medium and small fish. In both years, feeding trials were conducted when it was advantageous to deliver the largest fish possible, to either fledglings (1993) or mates (1994). This differential provisioning (small prey to chicks, large prey to mates and fledglings) relative to prey availability indicates that Roseate Terns are capable of size-selective predation. Moreover, results of the feeding trials suggest that this selection process can occur prior to capturing prey.

The ability to choose among available prey types

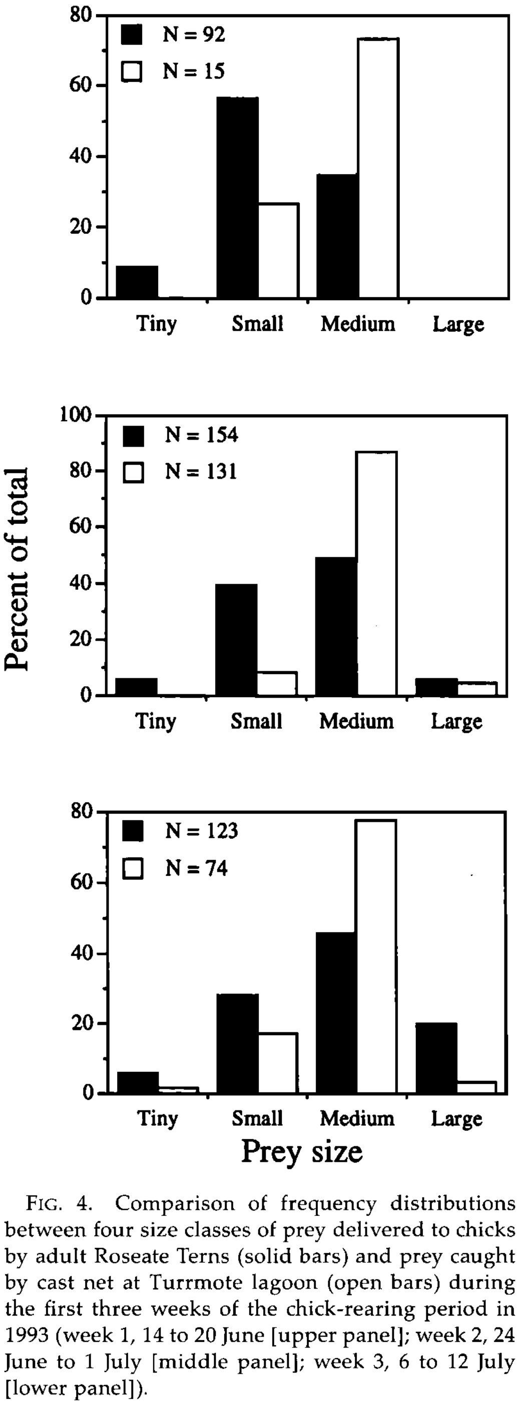

FIG. 4. Comparison of frequency distributions between four size classes of prey delivered to chicks by adult Roseate Terns (solid bars) and prey caught by cast net at Turrmote lagoon (open bars) during the first three weeks of the chick-rearing period in 1993 (week 1, 14 to 20 June [upper panel]; week 2, 24 June to 1 July [middle panel]; week 3, 6 to 12 July [lower panel]).

is advantageous if differences in prey size, quality, or transport costs exist. This ability is typical of a generalist forager that is able to sample a variety of available prey types. Roseate Terns, however, appear to be dietary specialists throughout most of their range (Randall and Randall 1978, Richards and Schew 1989, Safina et al. 1990) because they rely on only a few species of fish during the breeding season. Reasons for this specialization are not well understood but may relate to foraging competition with other flocking tern species (Duffy 1986, Shealer and Burger 1993) or to an attraction to specific physical or biological features of the ocean (Safina 1990a, Shealer 1996).

In Puerto Rico, Roseate Terns frequently feed in association with open-water schools of predatory fish that drive prey fish to the surface (Shealer and Burger 1993, Shealer 1996). In these situations, prey are available for only a few seconds at a time when they surface or leap from the water to avoid capture. This defensive behavior by the prey results in frequent dives by terns ($\bar{x}$ = 9.6 per min) but a relatively poor capture success ($\bar{x}$ = 28%; Shealer 1996), suggesting that terns cannot afford to be selective. In shallow waters, however, terns have a much lower dive rate ($\bar{x}$ = 1.5 per min). Shallow waters serve as prey refuges from predatory fishes, and prey schools are relatively stationary, allowing time for aerial predators to make foraging "decisions."

Although other studies of prey-size selection in birds have demonstrated preference for larger prey (Labinger et al. 1991, Trexler et al. 1994, Kelly 1996), these studies were designed such that prey were either contained or immobilized; therefore, predators had the opportunity to evaluate the prey resource for a period of time before making a decision. My study restricted the predator's evaluation time to only a few seconds, requiring it to make an immediate decision or risk losing a meal. The evidence from this study, although not overwhelming, suggests that Roseate Terns can discriminate between and make rapid decisions regarding prey of different sizes, an ability that would be advantageous for terns that forage over schools of predatory fish.

One possible limitation of my study is that I restricted my net sampling to only one habitat (shallow water) in which Roseate Terns forage. The prey base in Turrumote lagoon may not have been representative of the total prey base available to terns. Although I was unable to net fish in the open-water schools pursued by predatory fish, I was able to determine which fish Roseate Terns were catching in this situation by trapping terns that had just returned from feeding and then collecting regurgitations (Shealer 1996). Open-water feeding flocks frequently were visible from the nesting colony; thus, individual birds could be followed and then trapped after they relieved their mates at the nest. Analysis of boluses from these adult terns indicated that the prey fish in these schools were pelagic juvenile clupeids and engraulids (<35 mm SL; Table 1) that were smaller than the same species of fish (mostly adults) caught in Turrumote lagoon (>35 mm SL; Fig. 3; see

TABLE 1. Composition of individual boluses regurgitated by 13 Roseate Terns in southwestern Puerto, 1993. SL is standard length in mm.

No. of items	Bolus mass (g)	SL ($\bar{x}$ ± SE)	Contents
		3 June	
Many fragments	4.23	unknown	Mostly *Jenkinsia*
12	1.61	28.5 ± 1.0	4 *Harengula*, 8 *Jenkinsia*
6 + fragments	1.49	31.1 ± 0.6	Mostly *Jenkinsia*
12 + fragments	1.69	28.6 ± 0.8	All *Jekinsia*
15	1.73	28.0 ± 2.2	13 *Jenkinsia*, 1 *Hemiramphus*, 1 *Harengula*
9 ± fragments	3.34	34.0 ± 0.6	Mostly *Anchoa*, *Jenkinsia*
Many fragments	1.49	Unknown	Unidentified
		6 June	
14	3.68	31.5 ± 1.5	8 *Anchoa*, 6 *Jenkinsia*
28 + fragments	6.05	30.4 ± 1.1	All *Anchoa*
		7 June	
15	2.80	29.7 ± 0.9	11 *Jenkinsia*, 4 *Anchoa*
		15 June	
5	1.82	33.8 ± 2.7	All *Anchoa*
5	3.49	41.6 ± 4.4	3 *Harengula*, 2 *Anchoa*
9	7.92	45.8 ± 1.3	5 *Jenkinsia*, 4 *Anchoa*

also Shealer 1995, 1996). Because these fish in the open water are juveniles, it is likely that they are growing rapidly during this time relative to adult fish in the lagoon. Powles (1977) reported that 50% maturation for dwarf herrings occurred between 30 and 34 mm SL. However, the increase in medium- and large-sized fish delivered to chicks over the season cannot be accounted for by growth of juvenile dwarf herring in open-water schools, because adult status of 34 mm SL in this species is still below the length criterion of 35 mm for a medium-sized fish in this study. Therefore, prey delivered to chicks appeared to have been captured primarily in shallow inshore waters. Conversely, adults appeared to use prey schools that were more pelagic to feed themselves (Table 1; Shealer 1995, 1996).

I did not evaluate potential gear-bias of the prey sampling method I used. The mesh size of the net (6 mm) may have under represented "tiny" and "small" fish (both size classes contained individuals <6 mm body depth) and thus biased the samples toward "medium" and "large" fish. However, any such bias should not have produced the results presented in Figure 3. "Tiny" fish appeared in week 3, and the proportion of small fish decreased from week 1 to week 2 and then increased from week 2 to week 3. Any systematic bias in net gear should have produced consistent trends.

Although Roseate Terns delivered increasingly larger prey items to their chicks in three consecutive years in my study, they did not do so during Safina et al's. (1990) two-year study of this species at Cedar Beach, New York. At Cedar Beach, Roseate Terns fed smaller sandlance (*Ammodytes* sp.) to their chicks than did Common Terns (*Sterna hirundo*) nesting in the same colony. Cedar Beach supported one of the largest colonies of Common Terns in the world, where Roseate Terns were outnumbered by a factor of 25 (Gochfeld 1976). Roseate and Common terns fed in mixed flocks near the colony, but Common Terns were numerically dominant and outcompeted Roseate Terns for positions in the center of these flocks (Duffy 1986, Safina 1990b). The fact that Common Terns, but not Roseate Terns, delivered increasingly larger prey to their chicks (Safina et al. 1990) may have resulted from this competitive difference in foraging flocks. In southwestern Puerto Rico, Roseate Terns nest with Sandwich Terns, but the two species partition foraging habitat (Shealer 1996) and do not appear to compete for prey (unpubl. data). Thus, Roseate Terns in Puerto Rico contend only with intraspecific effects in foraging flocks, which appear to be negligible (Shealer and Burger 1993).

In summary, Roseate Terns in Puerto Rico appeared to select smaller fish than random from the available prey pool when provisioning smaller chicks. When adults were feeding large chicks, fledglings, and their mates, they showed a preference for larger fish during paired prey-choice trials. These results indicate that, despite the constraints imposed upon them by the marine environment, Roseate Terns are capable of discriminating among prey of different sizes prior to capturing them.

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