PREY DYNAMICS AND THE BREEDING PHENOLOGY OF COMMON TERNS (*STERNA HIRUNDO*)

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ABSTRACT.—We examined fish dynamics within the temporal framework of the reproductive cycle of Common Terns from 1982–1985. The hypothesis that the breeding season of terns is timed to overlap with a seasonal increase in food abundance was supported by the data. Prey fish were more available during breeding than postfledging. However, the further hypothesis that the timing of tern breeding is adapted to exploit peak prey availability while feeding growing chicks was not generally supported over the course of the study. Food for terns peaked and began to decline before the period of peak demand of food by chicks. *Received 24 February 1988, accepted 20 June 1988.*

FOOD seems the most important ultimate factor influencing periodic reproduction in birds (Immelmann 1971), and it may be the most important proximal factor as well (Harris 1969). Food availability limits the timing of egg laying (e.g. Perrins 1965, 1970; Møller 1980; Becker et al. 1985), and supplemental feeding will experimentally advance the start of courtship and egg laying (review by Drent and Daan 1980, Ewald and Rohwer 1982, Powell 1983, Hepp 1986). Given the importance of food, the regularity of seasonal trends of food dynamics in many regions, and the adaptability of organisms, one would expect breeding and food availability to co-occur at the time of maximum need, when parents are feeding rapidly growing chicks. However, several studies have found that the time of peak food availability has passed by the time the young hatch (Perrins 1965, 1970; Drent and Daan 1980). Drent and Daan concluded that most birds delay breeding beyond the date giving the maximum probability of nestling survival, and that "achievement of the most productive laying date . . . must entail a substantial decline" in subsequent survival of breeders.

Drent and Daan view the breeding delay as a strategy. Others (e.g. Perrins 1970) have seen delayed timing not as a strategy, but as a predicament. When females must wait until food availability allows nutrient reserves to reach a breeding threshold, but when food then peaks and declines before the young can be raised, birds may not achieve a maximally productive laying date (Perrins 1970). Conceivable adjustments, e.g. shortening the incubation period, may be limited by physiological constraints on characteristics such as the time required for embryo development.

In several species, early hatching chicks have higher chances of survival than delayed cohorts (see Perrins 1970, Gochfeld 1980, Morris 1986). If this was due ultimately to seasonality of environmental conditions (rather than, for example, simply seasonal differences in the mean age and experience of nesters over the course of the season), then an optimal coincidence of breeding phenology and resource availability should occur. However, natural selection requires both selective pressure and genetically-based phenotypic variability. Limits on phenotypic variability, which often are not considered (Ramsay and Dunbrack 1986), probably play a significant role in evolution (Maynard Smith et al. 1985). Even if no biological factor is completely immutable, it is probable that some traits are relatively invariant because of constraints (limitations on phenotypic variability) not because they represent optimal solutions to every problem posed by ecological contexts (Gould and Lewontin 1979). In discussing the possible role of constraints, we define "optimization" as the evolutionary response which would be possible if the phenotype was highly responsive to selective pressure. Optimization is distinguished from "maximization," defined here as the best response possible within existing constraints. If evolutionary adaptation can be thought of as the processes by which changes in morphology and behavior allow increasingly efficient use of resources, then the degree of adaptation which

an organism achieves is inversely proportional to the difference between optimal and maximized response.

The prey fish of breeding Common Terns (*Sterna hirundo*) arrive in the area before their piscine predators and the arrival of predatory fish correlates with dramatic reductions in prey fish numbers and density, changes in vertical distribution of prey, and reduced prey availability to terns (Safina and Burger 1985, in press, MS). We examined the implications of fish dynamics to tern reproduction. We tested the hypothesis that the phenology of terns' breeding is timed to coincide with peak prey availability. We predicted that prey would be more available during the breeding season than during the postfledging period and that peak prey availability would occur during the terns' chick-rearing phase.

METHODS

We conducted field studies from late June–August 1982, and from May–August during 1983–1985 near Fire Island Inlet, New York (40°N, 73°W). Fire Island Inlet is ≈2 km east of a large tern colony at Cedar Beach. The Common Tern population at this colony was approximately 6,000 pairs in 1985.

We used a 5.5 m boat equipped with loran C and a Raytheon DC 200 paper-recording echo sounder. Transects were run through foraging flocks of terns and as far past the flock as the flock was wide. Transects were run anywhere in the ocean where birds fed within an approximately 10 km radius of the inlet.

For each transect, date and number of terns foraging in the area were recorded. Data on tern feeding success was obtained immediately after each sonar transect by observing adult Common Terns through binoculars for 5–10 min and recording successful and unsuccessful fish-capture attempts. If a target bird left the flock, another bird was followed. Thus, during our counts of fish-capture attempts, we constantly watched terns that foraged actively.

Fieldwork was generally begun when terns first arrived on the breeding grounds and terminated in August after most birds had left. Termination dates varied, depending on phenology of departure. Observations were usually begun at dawn and terminated at mid-day. Nearly 300 sonar transects were run over the 4 years.

For the printed output from each sonar transect, fish densities were quantified with a transparent 7-mm square grid overlay to estimate the percent coverage of both prey and predatory fishes in each grid square. Predatory and prey fishes were differentiated by their echo marks. Echoes of predatory fish tend to form discrete spikes while prey fish schools appeared as dark, irregularly shaped masses (see Safina and Burger 1985). From this method we calculated a variety of indices of fish density, abundance, school size, and fish depth. Density, the mean percent coverage by echo marks, was calculated as the sum of percent coverages in all grid squares with echo marks divided by the total number of grid squares with and without echo marks. Thus, density could be equal in very short and very long transects. Abundance, an index of biomass, was calculated as density multiplied by vertical area of the transect. Fish depth was defined as the mean depth of fish in the echo profile. Sonar records were partitioned vertically into discrete 1.5 m vertical depth segments. To calculate fish depth, fish density was multiplied by depth for each depth segment, these values were summed, and divided by the sum of percent echo-mark coverage for all grid squares (i.e. the total coverage for the transect). This yielded a depth-weighted mean. Due to their schooling nature, fish were usually either absent or present in substantial numbers, resulting in a bimodal distribution of data that was resistant to normalizing transformations. For this reason we used nonparametric analyses. Data were analyzed using SAS software.

We divided the terns' reproductive cycle into 4 temporal periods that corresponded to terns' reproductive stages: (1) pre-laying, prior to 10 May; (2) incubation, 10 May to 10 June; (3) chick rearing, 11 June to 15 July; (4) postfledging or postbreeding, after 16 July. Though breeding is not entirely synchronous, the seasonal divisions describe the predominant breeding activity at Cedar Beach during each period bounded by the calendar dates.

RESULTS

Prey fish, bluefish, and the breeding season of terns.—The most important prey fish in our study area were sand eels (*Ammodytes* sp.), anchovies (*Anchoa* sp.), and butterfish (*Peprilus triacanthus*). Bluefish (*Pomatomus saltatrix*) were the overwhelmingly dominant predatory fish. Prey and bluefish density, abundance, and depth all changed significantly among breeding stages (Figs. 1 and 2, Tables 1 and 2). Very small sample sizes for pre-laying ($n = 4$) precluded meaningful quantitative analysis of that period. Of the 3 later breeding phases ($n = 66$, 134, and 73, respectively), prey density and abundance were highest during incubation and lowest postfledging, and predator density and abundance were highest postfledging and lowest during incubation (Table 2). Prey declined and bluefish increased as the season progressed (Table 3).

Seasonal changes in terns' foraging activities.—Opportunities to capture fish were highly vari-
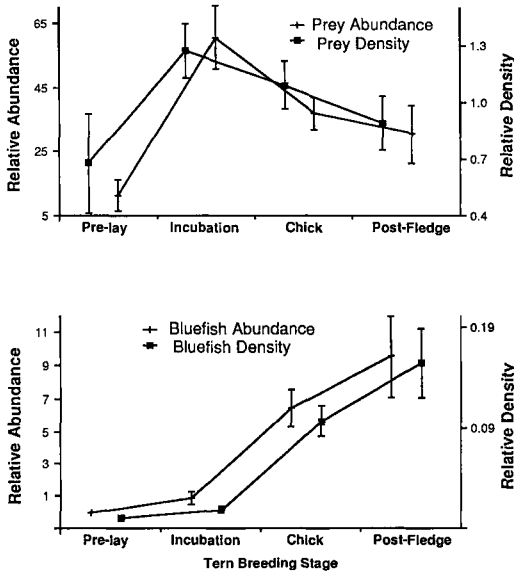
Fig. 1. Changes in prey (top) and predatory (bottom) fish abundance and density (± SE) during the breeding season of Common Terns.

Fig. 2. Changes in mean fish depth (± SE) during the breeding season of Common Terns.

able early in the season and declined as the season progressed (Fig. 3). The rate at which terns dove for fish was correlated inversely with the date ($tau = -.15, n = 274, P < .0004$). The percentage of successful dives tended weakly to increase ($tau = .09, n = 194, P < .07$). This increase notwithstanding, the rate at which terns captured fish declined as the season progressed ($tau = -.10, n = 275, P < .02$).

The decline in fishing success was related to the declines in prey density and abundance. Terns' diving rate was related significantly to prey density ($tau = .12, n = 243, P < .007$) and abundance ($tau = .14, n = 243, P < .002$), which declined (Table 3). Prey fish density and abundance were correlated with prey depth ($tau = .12, n = 234, P < .006; tau = .12, n = 234, P < .007$ respectively). Thus, although prey became shallower over the course of the season, this prey availability did not increase as measured by the number of prey captures per unit time.

The percentage of dives resulting in prey capture was higher in the presence of bluefish than in their absence (Kruskal-Wallis Test, $\chi^2 = 2.47$, df $= 1, P < .06$). The weak increase over the season in the percentage of successful dives probably resulted from the effect of predators chasing prey to the surface and fragmenting their schools. However, this slight increase in
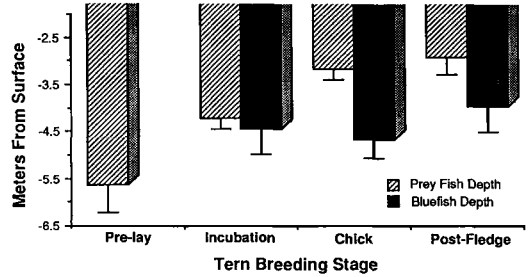
the percentage of successful dives was not enough to offset the reduction in the diving rate, and the number of successful dives/minute declined. The rate of successful dives was significantly correlated to prey density divided by mean prey depth ($tau = .11, n = 255, P < .02$), prey abundance multiplied by prey density ($tau = .10, n = 255, P < .04$), and to prey density ($tau = .09, n = 255, P < .04$). Common Terns often track schools of prey which are too deep to capture (e.g. 5–6 m). Opportunities to dive occur when individuals or portions of the school come close to the surface. These fish movements, and consequent prey availability to terns, change from minute to minute. Vertical movements of prey on a very short temporal scale are important and prey availability to terns at a given moment is related to the density of prey throughout the water column.

After young fledge in mid-July, birds visit the colony less and less frequently and begin to disperse. Subsequent to mid-July, flock size decreased (Kruskal-Wallis test, $\chi^2 = 7.99$, df $= 1$, $P < .005$), and fewer birds foraged on the study area ($\chi^2 = 7.22$, df $= 1, P = .007$).

DISCUSSION

Prey fish numbers were low at the time of terns' first arrival. Prey increased as tern numbers increased and egg laying began early in the season. A decrease in prey numbers and prey depth coincided with the arrival of predatory bluefish. We believe the inverse relationship between predatory and prey fish is a causal one. Bluefish seem to have a rapid and significant effect on prey numbers and prey behavior.

Tern prey fish abundance and density were already declining by the time chicks hatched. Terns took longer to locate prey and caught

TABLE 1. Variations in fish parameters among tern breeding stages. Kruskal-Wallis Test, df = 3.

	χ^2	P	Highest, lowest
Prey fish			
Density	12.07	<.007	Incubation, postfledged
Abundance	13.54	<.004	Incubation, postfledged
Depth	44.12	<.0001	Pre-lay, postfledged
Predatory fish			
Density	31.15	<.0001	Postfledged, pre-lay
Abundance	28.73	<.0001	Postfledged, pre-lay
Depth	5.77	<.06	Incubation/chick, postfledged

fewer prey/unit foraging time as the season progressed (Fig. 3). Thus, the hypothesis that terns' breeding times coincided with the maximum prey availability (number of fish caught/unit of foraging time) at the time of maximum need (raising chicks) was not supported. Safina and Burger (1985) showed that, in 1982, prey was higher when terns were feeding young chicks than later, but did not sample prior to the chick phase (i.e. pre-laying or incubation) that year.

Increased mean prey fish size could conceivably offset the decline in terns' prey capture rate. It did not appear that mean prey fish size increased seasonally, as judged by the fish caught or from the contents of bluefish stomachs, but we did not measure prey size. Seasonal increases in the size of prey brought to chicks may have more to do with selectivity by parents than with mean prey size. For example, Wiggins and Morris (1987) found that size of prey delivered by male Common Terns increased with chick age, whereas prey delivered by females did not.

Terns' foraging behavior suggests that foraging is more difficult during the postbreeding period. Diving and prey capture declined later in the season. Additionally, the decrease in the number of birds present may indicate fewer opportunities to forage. Thus, foragers may not be able to compensate for reduced capture rates by foraging longer during the day. Dispersal begins soon after fledging, and numbers of foraging birds decline quickly, despite the fact that the local population increased by more than 50% in most years due to the fledging of young.

Seasonal declines in prey may result from factors other than bluefish predation. Possible reasons include water temperature effects on prey migration, plankton bloom patterns, and bird predation. However, bluefish presence correlates so strongly with prey behavior and numbers that they are almost certainly a significant factor, if not the driving force, in intraseasonal prey declines. Seabird communities appear capable of taking significant portions of local prey populations (review in Furness 1982), but in our studies prey fish and birds increased at the same time, yet prey declined abruptly when bluefish arrived. Where fish and birds compete for the

TABLE 2. Paired comparisons of fish parameters among tern breeding stages. Kruskal-Wallis Tests, df = 1.

	Breeding stage ranks	χ^2	P
Prey density	Incubation = chick	1.86	<.2
	Incubation > postfledged	12.39	<.0004
	Chick > postfledged	5.48	<.02
Prey abundance	Incubation > chick	3.84	<.05
	Incubation > postfledged	14.13	<.002
	Chick > postfledged	4.54	<.03
Predator density	Postfledged > chick	6.04	<.01
	Postfledged > incubation	30.10	<.0001
	Chick > incubation	12.01	<.0005
Predator abundance	Postfledged > chick	5.10	<.02
	Postfledged > incubation	27.52	<.0001
	Chick > incubation	11.44	<.0007

TABLE 3. Correlations between date and fish variables (Kendall's *tau*).

	tau	P	n
Date versus:			
Prey fish density	−0.14	<.0007	278
Prey fish abundance	−0.16	<.0001	278
Prey fish mean depth	−0.31	<.0001	250
Predatory fish density	0.28	<.0001	277
Predatory fish abundance	0.27	<.0001	277
Predatory fish surface activity	0.33	<.0001	296
Predatory fish feeding intensity	0.31	<.0001	294

Fig. 3. Changes in fishing success (± SE) during the breeding season of Common Terns.

same resource, fish have an advantage and can limit birds (Zaret and Paine 1973; Eriksson 1979, 1983; Eadie and Keast 1982; Pehrsson 1984; Hunter et al. 1986).

Many aspects of this system are dynamic. Changes in the timing of predatory fish arrival, prey fish numbers, and prey species composition occur from year to year. Intermediate-term changes can be dramatic, and affect the apparent response of terns to prey dynamics. Earlier in the past century, there were apparently periods when bluefish were virtually absent in Long Island waters (Matthiessen 1986). The reasons for such perturbations are unknown, but they were probably not humanly induced because fishing and pollution pressures were incomparably less than at present. Other changes, such as the increase in sand eels (*Ammodytes* sp.) in the 1970s, may be related to overfishing of their competitors (Sherman et al. 1981).

Seasonal declines of food over the course of birds' breeding seasons have been found in several studies; for example, a sharp decline followed a spring increase in food for Great Tits (Gibb 1950). Lack (1966) thought seasonal declines in food availability were a major influence on the evolution of clutch size. Perrins (1965, 1970) found that food for Great Tits was lowest prior to breeding and that, after a peak early in the breeding season, food supply steadily worsened. Schluter (1984) reported seasonal declines in food for Galápagos finches. Unlike most studies, Anderson and Gress (1983) reported that food for pelicans in southern California did not decline in a consistent seasonal manner.

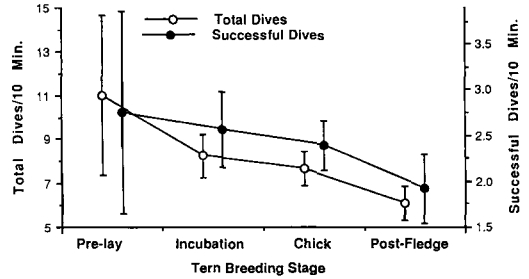Food demands on parents are greatest when producing eggs and feeding young, not during incubation. A critical period for parents and juveniles occurs immediately postfledging, when the number of individuals is highest and young are without the foraging skill afforded by experience (Immelman 1971, Nisbet 1977). Yet we found food most available during incubation and least available postfledging. Indeed, lack of food immediately postfledging seemed to induce dispersal. Tern breeding was not timed so that most chicks appeared at the time of maximum food availability.

Only seldom has breeding been found to be so well timed to food dynamics that chicks hatch into an environment of maximal food availability. Cassin's Auklet hatch coincides with plankton peaks (Vermeer 1981), Mallard ducklings hatched within the time of peak insect emergence (Pehrsson 1984), and the preferred food of California Gulls first became available during the chick phase (Winkler 1985). More often, as in our study, breeding is post-optimal in terms of food available for chicks (e.g. Perrins 1965, 1970; review by Drent and Daan 1980; Dijkstra et al. 1982).

Laying date may be determined by the earliest date at which food becomes abundant enough for females to form eggs, perhaps leaving some buffer of bodily reserve to reduce risk to the female's own survival in the process (Perrins 1965, 1970; Harris 1969). Møller (1980) reported that food availability was low for Gull-billed Terns upon arrival on the breeding grounds, and he thought that food scarcity delayed breeding. Supplemental feeding can indeed advance egg laying (e.g. Ewald and Rohwer 1982, Powell 1983). Reduced food availability may restrict breeding so that only a minority can achieve optimal timing (Perrins 1965, Lack 1968). In our study, terns were limited by time in arriving, laying, and incubating.

It seems unlikely that breeding activities could have occurred early enough to allow hatching to coincide with maximum food availability. In 2 years terns layed earlier, more synchronously, and had larger clutches in the year when food was more plentiful during the egg-laying period (unpubl. data).

We suggest that tern breeding phenology may be constrained physiologically. Absolute constraints on achieving optimal timing of breeding may be dictated by annual cycles and incubation capacity (Dijkstra et al. 1982). Terns and many other birds may be breeding as fast as they can, but may be unable to shorten incubation in response to environmental pressures. The breeding activities of the terns we investigated did not occur fast enough to exploit optimally the patterns of prey dynamics during the years of study (Safina and Burger 1985).

ACKNOWLEDGMENTS

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