

EVIDENCE FOR PREY LIMITATION OF COMMON AND ROSEATE TERN REPRODUCTION¹

CARL SAFINA

National Audubon Society, 306 South Bay Ave., Islip, NY 11751

JOANNA BURGER

Department of Biology, Busch Campus, Rutgers University, New Brunswick, NJ 08903

MICHAEL GOCHFELD

Robert Wood Johnson Medical School, Environmental and Community Medicine, Piscataway NJ 08854

RICHARD H. WAGNER

Edward Grey Institute of Ornithology, Oxford OX1 3PS, United Kingdom

Abstract. We tested hypotheses that prey population fluctuations limit reproduction in Common (*Sterna hirundo*) and Roseate (*S. dougallii*) terns. In a 2-year study, both species laid earlier, delivered more fish/hour to nests, grew faster, and survived better in the year when prey populations were higher. Common, but not Roseate, terns had larger clutches and broods in the better food year.

Key words: *Common Tern*; *Sterna hirundo*; *Roseate Tern*; *Sterna dougallii*; *seabird*; *food limitation*; *fish population*.

INTRODUCTION

Recent changes in the reproductive success of several fish-eating birds have been linked to food shortages caused by overfishing and human-induced foraging habitat degradation (Crawford and Shelton 1981, Furness 1982, Poole 1985, Powell and Powell 1986). Powell and Powell (1986) found that current reproductive productivity in Great White Herons (*Ardea herodias*) is now significantly lower than in 1923, except in artificially supplemented nests. Nisbet (1973a) suggested that low breeding success in Common Terns since the 1950s has been related to food scarcity. If the reproductive success of a species is limited by food availability, then this species is placed at risk by environmental changes and fisheries which lower prey populations. Here we investigate whether Common and Roseate terns' reproduction may be sensitive to food resource changes.

For seabirds which forage over relatively deep water, measuring prey is particularly difficult and has seldom been accomplished, because prey are usually highly mobile, patchily distributed, and difficult to observe. When prey fish abundance has been measured and compared to seabird re-

production, variability in reproductive performance of ocean-ranging seabirds has appeared sensitive to prey fluctuations (Anderson et al. 1982, Anderson and Gress 1983, Schaffner 1986). Safina and Burger (1985, in press) developed a method for using sonar to obtain quantitative indices of the relative abundance and density of prey beneath foraging flocks of terns. We showed that prey declined over the course of the breeding season, and this decline coincided with the arrival of large numbers of predatory bluefish (*Pomatomus saltatrix*).

In this study we examine whether fish population fluctuations may limit reproductive output of Common and Roseate terns. Our purpose is to examine reproductive dynamics at several stages from egg laying through fledging, to elucidate when and how in the reproductive cycle the birds might be sensitive to prey population fluctuations.

We test two hypotheses: (1) Availability of food influences temporal patterns of breeding. We predicted that: (a) mean date of clutch initiation varies inversely with amount of food in waters where terns are foraging, and (b) variance around the mean laying date is inversely correlated with food availability. (2) Variations in prey density and abundance are reflected in productivity; egg size, clutch size, chick growth, and chick mortality. These are not exclusive of hypotheses that

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weather or other environmental variables are partial determinants of prey availability (LeCroy and Collins 1972, Becker et al. 1985, Dunn 1975).

METHODS

We obtained data on reproductive productivity of Common and Roseate terns nesting at Cedar Beach, on the south shore of Long Island, New York in 1984 and 1985. Cedar Beach is located on the barrier beach approximately 2 km west of Fire Island Inlet. The Common Tern population averaged approximately 5,500 pairs during these 2 years (4,800 in 1984 and 5,900 in 1985). The Roseate Tern population averaged approximately 100 breeding pairs.

We obtained data on prey fish densities and abundance under foraging flocks of terns by using sonar (Safina and Burger 1985, in press) during the terns' breeding season in 1984 and 1985. Flocks were composed primarily of Common Terns. Sonar transects were run in the ocean within an approximately 10-km radius of Fire Island Inlet, anywhere where birds were diving; their length was dictated by the area covered by bird flocks. We worked with foraging birds from dawn to noon approximately 3 days per week between mid-May and early August. Fieldwork was terminated when terns dispersed. We ran 64 transects during the season of 1984 and 69 in 1985.

For each sonar transect, fish densities were quantified by overlaying the echo sounder paper with a transparent 7-mm square grid and visually estimating the percent coverage of prey fishes in each grid square at each depth. Relative indices of fish density and abundance were then calculated. Density was defined as the mean percent coverage of echo marks per grid square for the entire transect. Density 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. Density could thus be equal in transects of varying length and with varying fish biomass. Abundance, defined as an index of biomass, was calculated as density multiplied by transect length. Prey variables are reported in relative indices which are comparable only within each variable; i.e., a prey density of 70 is not comparable with a prey abundance score of 70.

During the breeding seasons in 1984 and 1985 we monitored Common Tern nests (1984 $n = 360$, 1985 $n = 837$) in randomly-selected 20-m

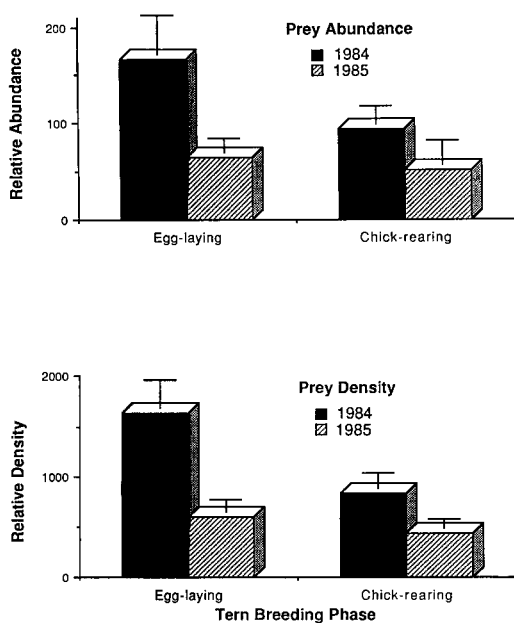


FIGURE 1. Prey fish density and abundance during the egg-laying (10 May to 10 June) and chick-rearing (11 June to 15 July) phases of the breeding cycle of terns at Cedar Beach in 1984 compared to 1985 ($\bar{x} \pm SE$). In 1984 $n = 22$ for egg laying and $n = 30$ for chick rearing. In 1985 $n = 27$ for egg laying and $n = 30$ for chick rearing. Interyear differences of prey abundance were statistically significant during both egg laying (Kruskal-Wallis $\chi^2 = 6.72$, $P < 0.01$) and chick rearing ($\chi^2 = 4.79$, $P < 0.03$). Interyear differences of prey density were statistically significant during egg laying ($\chi^2 = 14.28$, $P < 0.001$) but not chick rearing ($\chi^2 = 3.36$, $P < 0.07$).

square sample quadrats three to four times per week until hatching to obtain data on breeding phenology, clutch size, egg volume, and hatching success. To reduce any adverse effects of our presence on Roseate Terns prior to hatching, when they are somewhat more sensitive to disturbance, they were not monitored regularly until after hatching began, and we worked on relatively few of their nests. To monitor chick growth and fledging success, we surrounded Common Tern nests (1984 $n = 22$, 1985 $n = 43$) and Roseate Tern nests (1984 $n = 9$, 1985 $n = 22$) prior to hatching with 2.5-cm hexagonal mesh wire fences approximately 0.3 m high (Nisbet and Drury 1972). Each fence had a 10-cm band of fine mesh fiberglass screen along the bottom to prevent newly hatched chicks from leaving fenced areas. Each fence was large enough to facilitate easy landing and takeoff of adults and incorpo-

TABLE 1. Comparisons of egg-laying phenology for Common and Roseate terns at Cedar Beach in 1984 and 1985.

	Laying dates		Median	n**
	$\bar{x} \pm SD^*$	Mode		
Common Tern				
1984	May 23 \pm 10	May 17	May 19	360
1985	26 \pm 12	19	22	837
Roseate Tern				
1984	May 20 \pm 2	May 19	May 20	17
1985	24 \pm 7	23	23	34

* Descriptive statistics were calculated on a linear scale.

** n = number of nests from which laying date statistics were calculated.

rated enough vegetation to allow chicks to find shade and cover.

Chicks were banded within 1 day of hatching, and we recorded wing length (to the nearest 2 mm) and mass to the nearest gram (using a Pesola spring scale). Chicks in fences were checked daily after hatching. In 1984 and 1985, respectively, growth and fate of 44 and 102 Common Tern chicks, and 18 and 44 Roseate Tern chicks, were monitored daily until disappearance, death, or fledging. Chicks were considered fledged when they had flown from the fences or when they were missing after surviving 22 days.

In 1984 and 1985, respectively, we watched prey deliveries almost daily throughout the pre-fledging period at five and six Common Tern and four and eight Roseate Tern nests from 06:00 to

09:00 for yearly totals of 71 and 75 hr of observation.

Data were analyzed using SAS, SPSS, and Statgraphics statistical software. To compare only peak-nesting birds, clutches initiated after 28 May were excluded from analyses of clutch size, egg volume, and hatching success. Chicks whose growth we measured were from main-peak nests, and only chicks which survived to fledging were included in growth analyses. All data were checked for normality of distribution using the SAS Univariate Procedure. Growth data were normalized by log-transformation prior to analysis.

RESULTS

PREY AVAILABILITY

Prey fish (primarily sand eels *Ammodytes* and anchovies *Anchoa* sp.) were more abundant under flocks of foraging terns in 1984 than 1985 (Kruskal-Wallis $\chi^2 = 8.05$, $P < 0.01$) and denser (Kruskal-Wallis $\chi^2 = 6.88$, $P < 0.01$; Fig. 1). Mean (\pm SE) prey deliveries at Common Tern nests were 1.44 ± 0.09 per nest per hour in 1984 and 1.13 ± 0.09 in 1985 (Kruskal-Wallis test, $\chi^2 = 11.16$, $P < 0.001$). Prey deliveries at Roseate Tern nests averaged 1.38 ± 0.08 per nest per hour in 1984 and 0.79 ± 0.05 in 1985 (Kruskal-Wallis test, $\chi^2 = 43.62$, $P < 0.0001$). These results suggest that our measures of fish abundance

TABLE 2. Interyear comparisons of clutch and egg sizes, clutch survival, and hatching success ($\bar{x} \pm SD$ or percentages) for Common and Roseate terns in 1984 and 1985.

	1984	n	1985	n	Statistic*	P <
Common Terns						
No. eggs/nest	2.52 \pm 0.58	294	2.12 \pm 0.59	531	F = 87.35	0.0001
% clutches abandoned	2%	294	2%	531	G = 0.53	0.5
No. eggs surviving incubation/nest	2.31 \pm 0.85	294	2.06 \pm 0.66	531	F = 20.87	0.0001
% eggs surviving incub.	92%	712	97%	1,125	G = 25.37	0.0001
No. eggs hatched/nest	2.25 \pm 0.87	294	1.98 \pm 0.71	531	F = 23.64	0.0001
% hatched of all eggs laid	90%	712	93%	1,125	G = 7.25	0.01
% hatched of all eggs surviving incubation	98%	655	96%	1,094	G = 3.59	0.1
Egg volume, clutches of 2	39.37 \pm 6.77	100	38.22 \pm 3.36	125	F = 2.62	0.1
Egg volume, clutches of 3**	37.64 \pm 3.46	189	37.80 \pm 3.11	57	F = 0.10	0.8
Roseate Terns						
No. eggs/nest	2.00 \pm 0.00	9	2.05 \pm 0.38	22	$\chi^2 = 0.15$	0.7
No. eggs hatched/nest	2.00 \pm 0.00	9	1.91 \pm 0.43	22	$\chi^2 = 0.45$	0.5
% hatched of all eggs laid	100%	18	93%	45	G = 1.7	0.3

* Test statistics: F = single classification ANOVA, G = R \times C test for independence (Sokal and Rohlf 1981:731), χ^2 = Kruskal-Wallis test.

** Egg volume index = (width² \times length)/1,000 (Becker et al. 1985). n = no. eggs measured.

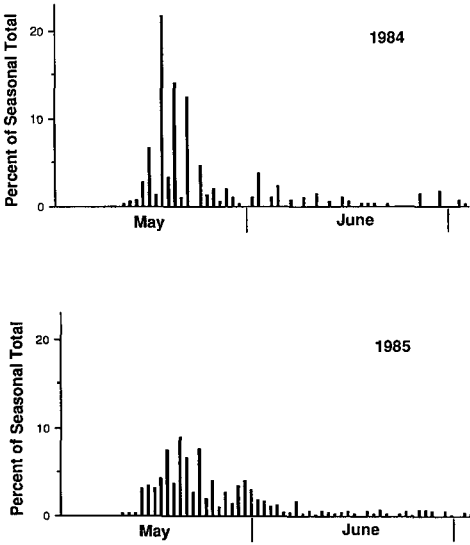


FIGURE 2. Temporal patterns of clutch initiation (percent of each season's total number of nests in monitored areas) among Common Terns at Cedar Beach (1984 $n = 360$, 1985 $n = 837$).

and density were reflected in the availability of food to chicks.

CLUTCH AND HATCHING

Common Terns laid earlier (Kruskal-Wallis test, $\chi^2 = 23.01, P < 0.0001$) and more synchronously in 1984 than in 1985 (Table 1, Fig. 2). Common Terns had larger clutches and broods in 1984 than 1985, but we found no difference in egg volume (Table 2).

Roseate Terns also laid earlier in 1984 than in 1985 (Kruskal-Wallis test, $\chi^2 = 4.72, P < 0.03$; Table 1). Among Roseate Tern nests, there were no significant interyear differences in clutch or brood size, although our small sample size makes these results tentative (Table 2). We did not reg-

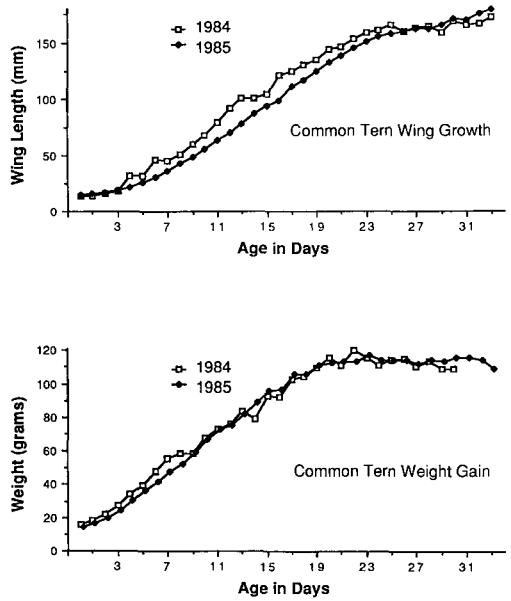


FIGURE 3. Mean wing length and mass of pre-fledging Common Terns at Cedar Beach in 1984 and 1985.

ularly monitor Roseate Tern nests until hatching had begun, and although laying dates could be estimated from hatching dates, we could not accurately estimate abandonment rates or egg survival rates for Roseate Terns. Our estimates of percent of eggs hatched for Roseate Terns is subject to greater possible error than for Common Terns because the greater time between Roseate Tern nest checks allowed more time for eggs to be taken by predators prior to being counted by us. However, we found little evidence of predation on the Roseate Terns' well-hidden nests.

CHICK GROWTH

For most of the pre-fledging period, chicks maintained greater mean wing length in 1984 than in

TABLE 3. Interyear comparisons of survival rates and fledging ages of Common and Roseate tern chicks for the years 1984 and 1985 (SAS General Linear Models Procedure). (In 1984 and 1985 respectively, for Common Terns $n = 13$ and $n = 52$, for Roseate Terns $n = 17$ and $n = 32$.)

	Fledglings/nest			Age at fledging			<i>n</i>
	$\bar{x} \pm SD$	<i>F</i>	<i>P</i> <	$\bar{x} \pm SD$	<i>F</i>	<i>P</i> <	
Common Terns							
1984	1.38 ± 0.52			25.8 ± 3.0			13
1985	1.07 ± 0.41	3.31	0.07	27.4 ± 3.1	6.5	0.01	52
Roseate Terns							
1984	1.89 ± 0.33			23.12 ± 1.6			17
1985	1.45 ± 0.51	5.51	0.02	25.38 ± 2.5	9.8	0.003	32

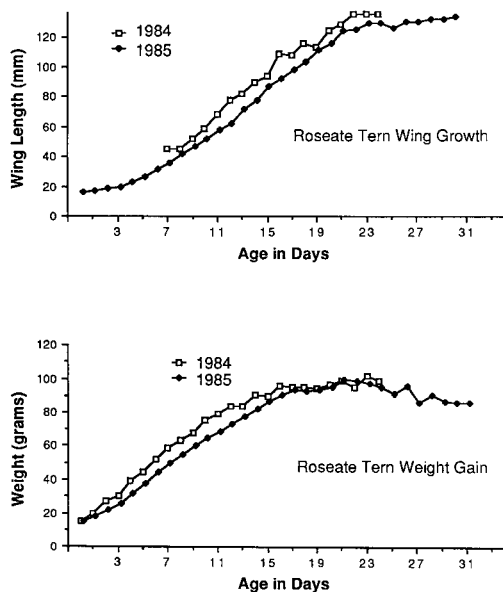


FIGURE 4. Mean wing length and mass of pre fledging Roseate Terns at Cedar Beach in 1984 and 1985.

1985 among both Common (SAS General Linear Models procedure, $F = 18.2$, $P < 0.0001$) and Roseate terns ($F = 58.2$, $P < 0.0001$; Figs. 3, 4). Chicks also maintained greater mass in 1984 than in 1985 for both Common ($F = 5.8$, $P < 0.02$) and Roseate terns ($F = 42.9$, $P < 0.0001$). However, Common Tern chicks gained mass more slowly in 1985 for only the first third of their pre fledging period, after which their mean weights were similar to those of 1984 Common Tern chicks. For most of the pre fledging period, 1984 Roseate Tern chicks maintained greater mass at each day of age than 1985 chicks.

CHICK SURVIVAL

For both tern species, more chicks survived and survivors fledged at earlier mean ages in 1984 than 1985 (Table 3). Fewer Common Tern chicks per nest died prior to fledging in 1984 (0.75 ± 0.46) than in 1985 (1.12 ± 0.68 ; 2×2 contingency table, $\chi^2 = 7.05$, $P < 0.01$). Of Common Tern chicks that hatched, 67% survived to fledging in 1984, compared to 52% in 1985 (Kruskal-Wallis test; $\chi^2 = 3.92$, $P < 0.05$). Likewise for Roseate Terns, fewer chicks per nest died prior to fledging in 1984 (0.11 ± 0.33) than in 1985 (0.45 ± 0.46 ; 2×2 contingency table, $\chi^2 = 3.88$, $P < 0.05$). Of Roseate Tern chicks that hatched, 94% survived to fledging in 1984, compared to

76% in 1985 (Kruskal-Wallis test; $\chi^2 = 3.04$, $P < 0.08$).

DISCUSSION

Few other seabird studies have measured ambient food levels among foraging birds, but many studies which have examined food provisioning to chicks and reproductive performance in seabirds have found results similar to ours. Laying dates, clutch sizes, growth, and fledging success of seabirds have been linked to food availability by a number of workers (e.g., Hunt 1972; Nisbet 1977, 1978b, 1981; Viksne and Janaus 1980; Gaston and Nettleship 1982; Anderson and Gress 1983; Braun and Hunt 1983; Graves et al. 1984; Murphy et al. 1984; Becker et al. 1985; Winkler 1985; Hunt et al. 1986; Verbeek 1986; Nelson 1987).

Prey fish were more abundant under flocks of foraging terns in 1984 than 1985, and the reproductive productivity of terns was greater in 1984 for most parameters measured. Although we studied productivity for only two seasons, these results suggest that prey population fluctuations may limit reproductive success in the terns we studied.

PREY POPULATIONS AND TEMPORAL PATTERNS OF BREEDING

Clutch initiation was earlier in the year of greater food abundance. Authors disagree on the importance of food in affecting the timing of clutch initiation (see Powell 1983, Murphy et al. 1984), but several believe that the level of food availability prior to egg laying may be the most important factor in the timing of avian reproduction (Harris 1969, Perrins 1970, Ashmole 1971, Immelman 1971) presumably due to the female's need to build nutritional reserves prior to clutch initiation. Nisbet (1973b, 1977, 1978b) believed this was true for Common and Roseate terns. Comparing two Common Tern colonies, he found mean laying date to be earlier at the colony which he inferred from rate of courtship feeding to have better food resources available (Nisbet 1977).

In northeastern North America, mean date of clutch initiation of Common and Roseate terns became progressively earlier in the 1970s (Nisbet 1981; H. Hays, pers. comm.; M. Gochfeld, unpubl.). This coincided with an increase in the abundance of sand eels (*Ammodytes* spp.; Sherman et al. 1981), a major prey fish (Safina and Burger 1985). Sand eel numbers seemed to re-

main high into the early 1980s. Mean Common Tern laying dates have generally become later in the 1980s. Since the present study, the mean clutch initiation date of Common Terns at Cedar Beach was 27 May in 1986 and 5 June in 1987 (Safina, unpubl.), suggesting that food may have become less abundant or that there has been a long-term temporal change in patterns of prey availability.

We also found greater synchrony of Common Tern clutch initiation in the year of greater food supply. If all birds were affected equally by food fluctuations, then we would expect interyear variability in mean laying dates but not synchrony. We postulate that the mechanism by which synchrony could be affected by food variability is differential ability of terns to build the nutrient reserves necessary for breeding. Younger seabirds nest later than older birds (e.g., Coulson and White 1960, Pugsek and Diem 1983). Age-related differences in foraging ability among seabirds are well-known (e.g., LeCroy 1971; Dunn 1972; Buckley and Buckley 1974; Burger and Gochfeld 1979, 1981; Porter and Sealy 1982; Greig et al. 1983; Maclean 1986; Burger 1987). These differences increase as difficulty in obtaining food increases (Burger and Gochfeld 1983). It thus seems reasonable to postulate that when food is scarce, individual variations in fishing ability may differentially limit the ability of females to build adequate reserves and of males to courtship-feed (Nisbet 1973b, 1978b) successfully. If nutrient reserves must reach a threshold before females can produce eggs, as concluded by Alisauskas and Ankney (1985), then birds that are less proficient foragers, either because of age or because of individual variations in the "skill pool" (Giraldeau 1984), should take longer to commence breeding when food is scarce, and variance about the mean clutch initiation date should increase.

PREY LEVELS AND REPRODUCTIVE OUTPUT

Clutch size. Consistent with our second hypothesis that food limits reproductive productivity, we found a significant increase in clutch size and brood size in the higher food year for Common Terns. Lack (1968) believed that clutch size may be limited by food at the time of egg formation. We did not find interyear differences in clutch or brood size for Roseate Terns. Nisbet and Cohen (1975) suggested that Common Terns were more limited by fluctuating food supplies than Roseate

Terns. In viewing our results it must be remembered that we did not concentrate our sampling of fish where Roseate Terns concentrated their foraging. Langham (1983) thought it unlikely that food limited egg production in several *Sterna* spp. terns, and recent food supplementation studies in other species are contradictory regarding influence of food on clutch size. In several studies, supplemented birds laid larger clutches (Hogstedt 1981, Dijkstra et al. 1982, Powell 1983), but in others they did not (von Bromssen and Jansson 1980, Ewald and Rohwer 1982, Poole 1985). A constant food supply led to less variable clutches in Eurasian Coots (*Fulica atra*) (Horsfall 1984). Clutch size in Glaucous-winged Gulls (*Larus glaucescens*) appears to be related to food type (Murphy et al. 1984). Female Common Terns laid larger clutches with larger eggs at a colony where they received two to three times more fish during courtship feeding than at another colony (Nisbet 1977).

Egg volume. Contrary to Nisbet (1973b, 1977, 1978b, 1981), we did not find a difference in egg size among years. Morris (1986) also failed to detect a food-related difference in egg size in three-egg clutches of Common Terns, and Poole (1985) did not detect food influence on egg size in Ospreys (*Pandion haliaetus*). Egg size has been reported to be responsive to food fluctuations in other seabirds (e.g., Gaston and Nettleship 1982, Pierotti and Bellrose 1986, Verbeek 1986).

Chick survival. Although Langham (1972) found that starvation was the major cause of chick mortality, he believed that parental conflict between brooding young chicks and foraging was responsible for chick starvation in Common Terns and that "Food supply in the foraging area does not seem to be a directly limiting factor." Even if conflict between motivation for brooding or foraging was responsible, hunger may intensify such conflict. During studies of chick provisioning in 1984 and 1985 (unpubl. data), we saw female parents beg for food that their mates brought to chicks several times at several nests in 1985, but not in 1984. This suggests possible greater food stress and motivational conflict in 1985, the year of lower food abundance.

This study provides further evidence that prey populations can limit seabird populations. We were able to measure fish directly, but circumstantial evidence is accumulating that many other seabird populations are food limited. Thus it is vital that future management of fisheries rec-

ognizes the need to allocate fish for seabird populations.

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