FORAGING DECISIONS OF SANDWICH TERNS IN THE PRESENCE OF KLEPTOPARASITISING GULLS

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Abstract.—We studied prey selection of Sandwich Terns (*Sterna sandvicensis*) in the presence of kleptoparasitising Black-headed Gulls (*Larus ridibundus*) on Griend, Dutch Wadden Sea, from 1992 to 1998. Most often, gulls robbed larger sandeels rather than herring from terns. Provided that one parent attends the chick, energy intake would be too low for the chicks' survival if exclusively fed on sandeel. By provisioning an increasing proportion of herring, parent terns could theoretically overcome a potential food shortage when the chicks grow older. However, the proportion of herring did not increase with age of chicks in most years. Instead, parents increased their foraging effort with the growth of their offspring. In years with high proportions of food loss, parents left their chicks unattended at the nest more often. In that way, parents were largely able to counterbalance food shortage of offspring. In 1992 and 1996, when diet composition was unfavorable and food losses to gulls were high, parents left their chicks unattended at the nest for ~80% of the daylight period. It is argued that the present working level of parents might be higher than in the 1960s. *Received 3 January 2000, accepted 30 January 2002.*

Resumen.—Entre 1992 y 1998, estudiamos la selección de presas por parte del gaviotín *Sterna sandvicensis* en presencia de la gaviota cleptoparasítica *Larus ridibundus* en Griend, Mar Holandés Wadden. De los dos tipos principales de presas, las gaviotas robaron con mayor frecuencia el aguacioso (*Ammodytes* sp.) que el arenque, siendo el primero de mayor tamaño. En consecuencia, si los polluelos fueran alimentados exclusivamente con aguacioso, su adquisición de energía sería demasiado baja para sobrevivir, suponiendo que uno de los padres cuida de ellos. Teóricamente, si los gaviotines aumentaran la proporción de arenque que suministran a sus polluelos con el correr del tiempo, podrían sobreponerse a una deficiencia inminente de alimento cuando los polluelos se hacen más viejos. Sin embargo, en la mayoría de los años la proporción de arenque no aumentó con la edad de los polluelos. En cambio, los gaviotines disminuyeron su esfuerzo de forrajeo a medida que sus crías crecieron. En años con altas proporciones de pérdida de alimentos, los gaviotines dejaron a sus polluelos solos en el nido más frecuentemente, de modo que tuvieron la capacidad de compensar el déficit alimenticio de sus crías. En 1992 y 1996, cuando la composición de la dieta fue desfavorable y la pérdida de alimentos fue alta, los gaviotines dejaron a sus polluelos solos en el nido durante el ~80% de las horas de luz del día. Se argumenta que el nivel actual de actividad de los parentales podría ser mayor que el de los años 60.

A central theme in animal ecology is how animals organize their foraging activities to maximize rate of energy intake (e.g. Schoener 1971, Krebs 1973, Charnov 1976). Orians and Pearson (1979) developed a foraging model that incorporated the special problems of travel restrictions encountered by animals returning to a central place after each foraging trip (see

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also Lessels and Stephens 1983). More complex models have incorporated additional costs, like competition and predation risk (review in Stephens and Krebs 1986). In this article, we discuss some foraging decisions that Sandwich Terns (*Sterna sandvicensis*) must make to maximize food intake rate of their chicks in the presence of kleptoparasites. Sandwich Terns are almost strictly piscivorous birds and their food choice is highly specialized. Chicks are almost exclusively fed with high-energy prey species (e.g. Pearson 1968, Campredon 1978). On Griend, Dutch Wadden Sea, diets of chicks mainly consist of Clupeidae (herring [*Clupea*

harengus] and sprat [*Sprattus sprattus*]) and Ammodytidae (mainly sandeel [*Ammodytes tobianus*]; Veen 1977, Stienen et al. 2000). The specialized food choice of Sandwich Terns makes them extremely sensitive to changes in availability of one of their prey species. It therefore seems likely that the large between-year variation in diet composition on Griend (Veen 1977, this study) reflects strong fluctuations in food availability. This study examines effects of changes in food composition on growth and survival of chicks, and the parent's ability to buffer food shortages by increasing their foraging effort.

Sandwich Tern colonies are characterized by a high degree of synchronized breeding and very high nest densities (e.g. Veen 1977). After foraging, parents return to the colony with one prey item held in full view in the bill. Under those conditions, kleptoparasitism is likely to evolve (Brockmann and Barnard 1979). In fact, prey-carrying Sandwich Terns arriving in the colony are often heavily parasitized by neighboring gulls and terns (e.g. Fuchs 1977, Veen 1977, Gorke 1990, Ratcliffe et al. 1997). On Griend, the current rate of kleptoparasitism by Black-headed Gulls (*Larus ridibundus*) has serious consequences for growth and survival of tern chicks (Stienen and Brenninkmeijer 1999). In some subcolonies, parents can escape from high losses of food inflicted by gulls by guiding their chicks away. However, not all subcolonies provide suitable escape routes; some are surrounded by dense vegetation. In this study, we simulated that nonescape situation by keeping chicks in enclosures, making it possible to study how parent terns faced with kleptoparasitism organise their feeding activities to maximize energy intake of their chicks. Only a few studies have addressed prey selection in the presence of kleptoparasites. Because kleptoparasites often select specific prey items, it may be economical for hosts to avoid those prey items, as for example has been observed in American Oystercatcher (*Haematopus palliatus*), Eurasian Golden Plover (*Pluvialis apricaria*), and Lapwing (*Vanellus vanellus*) (Thompson and Barnard 1984, Tuckwell and Nol 1997). In this article, several behavioral strategies employed by Sandwich Terns to avoid or compensate for the losses inflicted by kleptoparasitising Black-headed Gulls are discussed.

STUDY AREA AND METHODS

Study area.—Sandwich Terns were studied on the Isle of Griend (~57 ha during high tide), The Netherlands (53°15′N, 5°15′E), from April to August 1992–1998. Apart from Sandwich Terns, three other species of gulls and terns nested on Griend in large numbers during the study period: Black-headed Gulls (16,000–28,500 pairs), Common (*Sterna hirundo*; 1,500–3,300 pairs) and Arctic (*S. pardiseae*; 800–1,250 pairs) terns. During the study period, the population of Sandwich Terns fluctuated between 5,000 (1997) and 8,300 (1994) pairs, consisting of 8–14 subcolonies.

Observations of chicks and parents.—Each year, a part of a subcolony containing 50–150 nests was fenced to prevent chicks from walking away from the nest site (see Stienen and Brenninkmeijer 1999). Within the enclosures, all chicks were banded as soon as possible after hatching so that their age could be determined accurately. In addition, each year ~20 chicks were color-marked to enhance individual recognition. In 1992–1998, observations on diet composition, prey length, and parental nest attendance were made from an elevated blind placed ~3 m from the fenced colony. In general, observations were made continuously from 0430 to 2230 h local time. Prey size was estimated in quarters of the adult's bill length. Estimating prey size was calibrated per observer by holding fishes of different species and length in front of a stuffed tern's bill at a distance comparable to the field situation. Calibration greatly increased accuracy of the estimates, and the largest error an experienced observer made was 0.25 bill lengths. Bill length of 697 adults trapped on their nests varied between 47.60 and 62.80 mm, corresponding with a deviation from the mean (54.31 ± 2.54 mm) of −0.12 to 0.16 bill lengths. Three prey types were distinguished: herring and sprat, further referred to as "herring"; sandeel and greater sandeel, further referred to as "sandeel"; and other prey. The category "other prey" can largely be ignored because it amounted to <1% of all prey items (Stienen et al. 2000). The fate of food was categorized as eaten by the chick, robbed by Black-headed Gulls, or lost (e.g. through intervention of other gulls and terns, fallen on the ground or lost out of the observer's sight).

In 1993–1996, parents of 6, 6, 1, and 1 nests, respectively, were individually followed to obtain information on round-trip travel time. Parents of each nest were distinguished from each other by characteristics of head molt, the presence of a ring or the yellowish color of feathers we had dyed with picric acid. Mean trip duration was computed when more than four measurements for a specific prey length were obtained. Foraging trips lasting >180 min were excluded from the analysis because there was reason to believe that those parents either spent considerable time roosting or had already returned to the col-

ony earlier but lost their fish out of the observer's sight and subsequently returned to forage before being observed by us.

Growth rate.—When weather conditions were favorable, chicks were weighed to the nearest gram every third day. For days in between, body mass was interpolated assuming linear growth. If a chick was measured at least four times until day 21 (day 0 = day of hatching), its average growth rate between age 3 and 21 (phase of linear mass growth) was computed. Individual growth rates varied between 0.0 and 10.6 g day^{-1} and averaged 6.25 ± 2.01 g day^{-1} (n = 181). Growth rate of surviving chicks was significantly higher than that of nonsurvivors (7.03 ± 1.19, n = 131; and 4.22 ± 2.28, n = 50, respectively; Student's t-test, t = 8.29, $P < 0.001$).

Energy intake.—An allometric equation relating fish length to mass was obtained for both herring and sandeel, using least-squares analysis on fish found in the colony and fish sampled in the Wadden Sea (Stienen et al. 2000). Water content measured for 10 herring and 12 sandeel ranging in length from 4.6 to 18.4 cm amounted to 74.51 ± 1.12% and 75.05 ± 2.43%, respectively. Energy density of the fish was measured by bomb calorimetry and amounted to 20.54 ± 1.50 kJ g^{-1} and 20.30 ± 1.81 kJ g^{-1} dry matter for herring and sandeel, respectively. From that the following equations relating fish length (L, in centimeters) to energy content (E, in kilojoules) can be computed $E = 0.0371 \times L^{2.996}$ for herring; and $E = 0.01499 \times L^{2.982}$ for sandeel.

In this article, length-specific round-trip travel time combined with energy content of the fish is used to predict energy provisioning to chicks for each prey length and species, assuming a daylight period of 18 h. Further incorporation of length-specific consumption rates yields a prediction of daily energy intake of chicks, assuming all prey provisioned to chicks are of the same species and length. These predictions were then used to compute predictive foraging effort of parents, which was compared with observed foraging effort.

Energy requirements of the chicks.—Klaassen et al. (1992) raised Sandwich Tern chicks in the laboratory under two feeding regimes. Four chicks, which were fed herring and sandeel *ad libitum*, achieved an average growth rate of 12.8 g day^{-1}, whereas restricted food intake in four other chicks resulted in an average growth rate of 5.0 g day^{-1}. Those growth rates are close to the limits measured in the field, where minimum and maximum growth rates of surviving chicks amounted to 3.3 and 9.8 g day^{-1}, respectively. We therefore used daily gross energy intake of the two groups of laboratory raised chicks as upper and lower boundaries for our calculations. Daily gross energy intake of the slow growing chicks must therefore be reached to survive and daily gross energy intake of the fast growing chicks can be regarded as the maximum amount of energy chicks can assimilate ef-
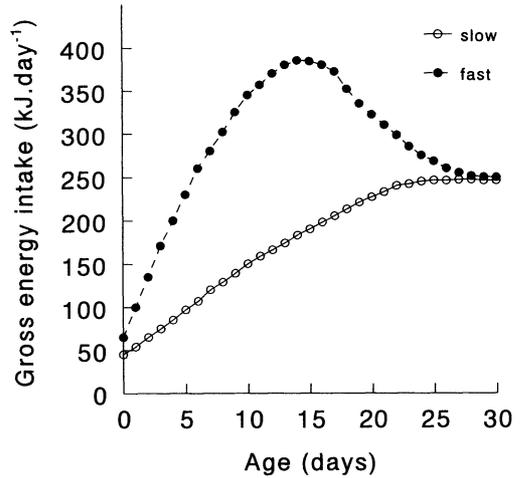

FIG. 1. Gross energy requirements of growing Sandwich Tern chicks. Redrawn from Klaassen et al. (1992), lines are fitted by eye. Slow (circles) = chicks growing at 5 g day^{-1}; fast (dots) = chicks growing at 12 g day^{-1}.
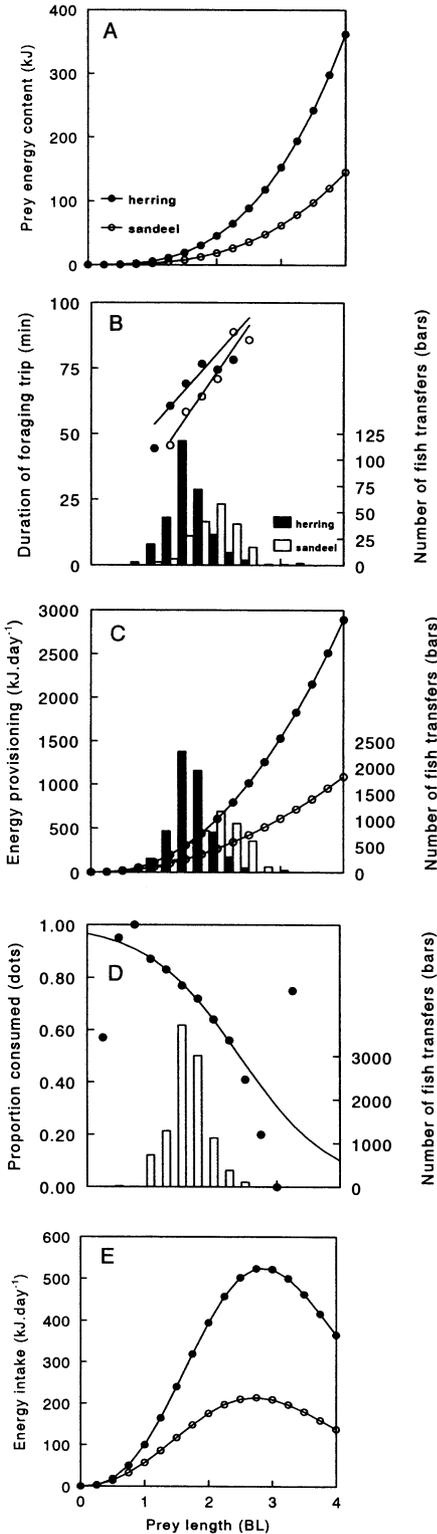
fectively. Energy intake of slow-growing chicks gradually increased from 45 kJ day^{-1} at hatching to 247 kJ day^{-1} near fledging (Fig. 1), whereas daily energy intake of the fast growing chicks was generally higher and reached a maximum of 385 kJ day^{-1} when the chicks were two weeks old.

Data analysis and statistics.—Data analyses were performed using SPSS/PC+ 4.0 statistical package (Norušis 1990). All statistical tests were performed using the Genstat statistical package (GENSTAT 5 Committee 1993). For logistic regression analyses, logit-transformed estimates of coefficients are presented in the tables. Linear terms were included in logistic regression analyses irrespective of the significance level if the quadratic term proved significant.

Although clutch size averaged 1.6 eggs per nest during the study period, Sandwich Terns hardly ever raise two chicks to fledging. Second-hatched chicks receive almost no food parents bring to the nest (Stienen et al. 2000). During this study, 34% of the second hatched chicks died within 10 days from hatching and only 0.7% of all pairs raised two chicks to fledging. The computations in this study referring to optimal prey size, diet selection, and biparental foraging time therefore assume that only one chick is present in the nest.

RESULTS

Foraging yield.—Round trip travel time was highly variable and ranged from 2 to 178 min. The duration of a foraging trip significantly in-

creased with prey length (analysis of covariance, $F = 21.56$, df = 1 and 487, $P < 0.001$; Fig. 2B). Foraging trips for herring generally lasted longer than for sandeel, and the added effect of prey species was almost significant ($F = 3.64$, df = 1 and 487, $P = 0.06$). For that reason, we used separate regression equations for herring and sandeel (Fig. 2B) to compute daily foraging yield for each prey length, using the allometric relationships given in equations 1 and 2, and assuming a daylight period of 18 h. Energy provisioning to the chicks can be greatly improved by feeding on large prey items (Fig. 2C). Maximum prey length observed in the field was 4 bill lengths, corresponding with a foraging yield of 1,089 and 2,892 kJ day^{-1} for sandeel and herring, respectively, which is far greater than the energy needed for maximal growth. However, such large prey were rarely brought to colony. Average prey length observed in the colony (2.0 and 1.6 bill lengths for sandeel and herring, respectively) corresponds with a foraging yield of 270 and 359 kJ day^{-1}, respectively, less than energy demands for maximal growth, but well above minimum energy requirements.

However, not all food brought to the colony was actually eaten by chicks. Prey were sometimes lost to kleptoparasitising Black-headed

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FIG. 2.　Relations between prey length (BL = adult bill length) and species, and energy content of the prey (A), round trip travel time (B), daily foraging yield (C), consumption probability (D), and daily energy intake (E) of Sandwich Tern chicks on Griend in 1993–1996. (A) Drawn lines are allometric relationships given in text. (B) Drawn lines are results of linear regressions examining effect of prey size (BL) on the duration of the foraging trip (DF) (herring: DF = 26.37 + 17.16 × BL, $n = 301$, $r^2 = 0.04$, $P = 0.006$; sandeel: DF = 3.27 + 35.22 × BL, $n = 189$, $r^2 = 0.07$, $P = 0.004$). (C) Predictive daily energy provisioning (dots) to Sandwich Tern chicks on Griend if all food brought to the colony is eaten by chicks. The calculations are based on round-trip duration and energy content for each prey species and prey length. Frequency distribution of prey delivered to the colony (bars) is shown on the right axis. (D) Drawn line shows the regression equation from Table 1. Bars indicate observed number of fish transfers. (E) Energy intake was calculated by deducting length-specific consumption rates (Fig. 2D) from predictive daily energy provisioning to the chicks (Fig. 2C).

TABLE 1. Logistic regression analysis examining effects of prey length and species ($n = 10,976$) on the fate of prey brought to Sandwich Tern chicks on Griend in 1993–1996. Food losses other than robbed by Black-headed Gulls consisted of food robbed by other species, fallen to the ground, eaten by the tern parent, or lost by the adult when out of the observer's view.

Parameter	Estimate ± SE	Deviance change	df	P
Proportion robbed by Black-headed Gulls				
Constant	−4.311 ± 0.126			
Prey length	1.597 ± 0.071	587.8	1	<0.001
Prey species	−0.158 ± 0.055 if sandeel	7.6	1	<0.01
Proportion lost otherwise				
Constant	−3.156 ± 0.123			
Prey length	0.408 ± 0.071	42.5	1	<0.001
Prey species	0.233 ± 0.058 if sandeel	9.5	1	<0.01
Proportion eaten by the tern chicks				
Constant	3.180 ± 0.118			
Prey length	−1.279 ± 0.068	560.9	1	<0.001
Prey species	0.004 ± 0.052 if sandeel	0.01	1	NS

Gulls, robbed by other species, fell to the ground, eaten by the parent, or lost by the adult when out of the observer's view. In 1992–1998, 64–81% of all food items were ultimately ingested by chicks (Stienen et al. 2000). Food loss to gulls and other losses significantly increased with prey length (Table 1). Adding the effect of prey species to that of prey size significantly improved the models, but had opposite effects on the probability of losing a prey to gulls and to other causes. Taking prey length into account, sandeels were robbed less often than herring, while they were more often lost to other causes. Therefore, adding prey species after inclusion of prey size had no significant effect on probability of prey consumption. Because of high losses of long prey items (Fig. 2D), the prediction for the most profitable prey drastically changes (Fig. 2E). Now, herring of 2.9 bill lengths and sandeel of 2.7 bill lengths become the most profitable prey items, corresponding with maximum intake rates of 525 and 214 kJ day^{-1}, respectively.

Diet selection.—A maximum intake rate of 525 kJ day^{-1} can be achieved by exclusively feeding chicks on herring of 2.9 bill lengths. Provided that those large herring are available in sufficient quantities, adverse effects on chick growth are not to be expected because the maximum energy requirements of fast growing chicks amount to 385 kJ day^{-1} (see above). But when exclusively feeding on sandeel, chick growth will fall below the maximum rate within five days from hatching (Fig. 3). At day 5,

fast-growing chicks need 230 kJ day^{-1}, whereas energy intake is only 214 kJ day^{-1} when foraging on optimal sized sandeel of 2.7 bill lengths. When feeding entirely on sandeel, within 18 days from hatching energy intake would be insufficient even for minimum growth requirements (Fig. 3).

If we now compare average prey length as observed in the colony (dots in Fig. 3) with prey length needed for maximum and minimum growth, it shows that in the first six days after hatching parents increased the length of the supplied herring sufficiently to meet maximum growth requirements of their offspring. However, parents failed to increase prey length sufficiently for maximal development of their chicks between age 7 and 17, although minimum growth requirements were reached. For sandeel, the prospects would be even worse, because maximum growth requirements are not met from day 2 onwards. From day 14 onwards, the sandeel transported to the colony were on average even too small for minimum growth of the chicks.

In the first two weeks after hatching, sandeel would suffice for minimum growth. However, sandeel should be largely avoided when the chicks grow older or if parents strive for maximal growth of their chicks during the early chick stage. One might, therefore, expect that as chicks grow, the diet would comprise more herring, with peak inputs of herring between ages 15 and 30, depending on the growth rate of chicks. Although in all years diet composition
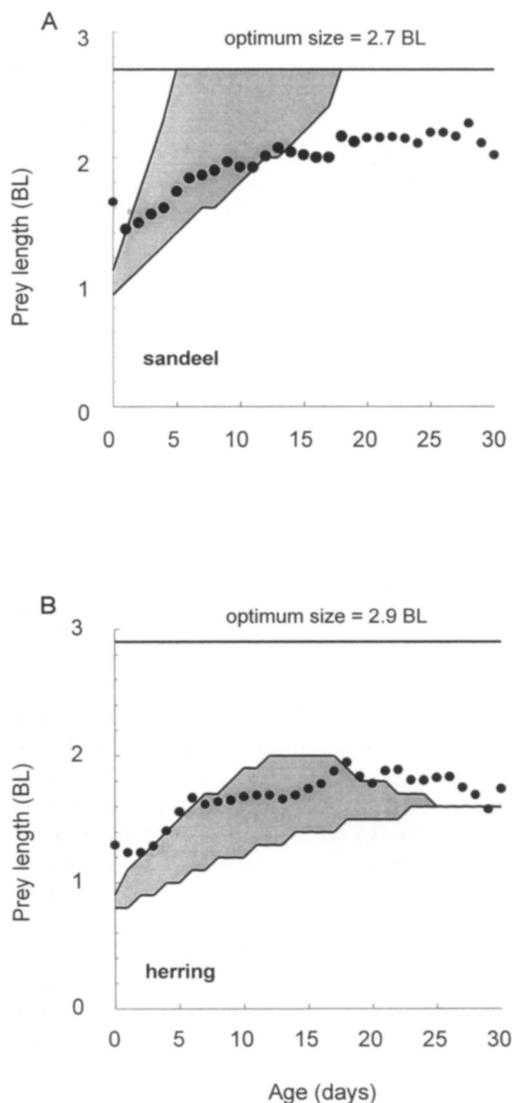
FIG. 3. Age-specific prey size (means, BL = adult bill length) of Sandwich Tern chicks as observed in the colony (dots). Shaded areas enclose theoretical prey size needed for minimum and maximum growth. Optimum size = prey length required for maximum energy intake rates. When Sandwich Terns exclusively feed on optimal sized sandeel (A), growth will fall behind maximum growth at day 5. At that point provisioning of even larger sandeel would not lead to increased energy intake by chicks as a result of the high incidence of loss of large prey. At day 18, energy intake would become too low for minimum growth, even if the terns would exclusively catch optimum-sized sandeel. When feeding exclusively on herring (B) maximal growth can be achieved.

varied significantly with the age of the chicks (Table 2), no general pattern was found. Only in 1996 and 1998, was the highest proportion of herring found between age 15 and age 30.

Effects of diet composition on energy intake, growth, and survival.—The yearly average proportion of herring in the diet of Sandwich Tern chicks on Griend ranged from 33% in 1996 to 85% in 1994. From the above paragraphs, one would expect that those large differences in diet composition would have effects on the rate of food loss and energy intake of chicks, and thus on chick growth and survival. Indeed, the average yearly rate of food loss significantly increased with higher proportions of sandeel (Pearson regression, $n = 7$, $r^2 = 0.57$, $P = 0.05$). Although energy intake was relatively low in years when sandeel dominated chicks' diets (Fig. 4), the relationship was not significant ($r^2 = 0.25$, $P = 0.25$). However, energy intake was positively correlated with the yearly proportion of fish eaten by the chicks ($r^2 = 0.63$, $P = 0.03$; Fig. 4). The average yearly growth rate of surviving chicks varied between 6.0 and 7.5 g day^{-1} and showed no relationship with the proportion of herring or food consumption probability ($r^2 = 0.18$, $P = 0.34$; and $r^2 = 0.39$, $P = 0.13$; Fig. 4). Also, fledging success showed no relationship with either diet composition or food consumption probability ($r^2 = 0.01$, $P = 0.88$; and $r^2 = 0.12$, $P = 0.45$, respectively; Fig. 4). Fledging success within the enclosures was lowest in 1992, when 46% of all first hatchlings survived until fledging, and highest in 1995, when 75% survived.

Parental foraging effort.—One of the assumptions used so far is that one parent stays with the chick when the partner goes out foraging. In fact, that assumption is not supported by observations in the field. Not only did parents spend some time together at the nest, but even more importantly they sometimes left their offspring unattended at the nest. The time that both parents were present at the nest can be neglected because on Griend it was on average <1% of the daylight period. The time that both parents were absent averaged 16.5% of the daylight period and showed considerable variation with chick age and between years (Fig. 5). Because small hatchlings must be brooded (Klaassen et al. 1994) and because they have low energy needs, those chicks were almost never left alone at the nest. When chicks grew older, they

TABLE 2.	Logistic regression examining relationship between diet composition (proportion herring) and the age of Sandwich Tern chicks on Griend in 1992–1998. Degrees of freedom (df) refer to the number of chick days.

Year	Parameter	Estimate ± SE	df	Deviance	P-value
1992	Constant	−1.181 ± 0.415	177		
	Age	0.2315 ± 0.0898		8.0	<0.01
	Age^2	−0.00912 ± 0.00433		7.4	<0.01
1993	Constant	0.060 ± 0.166	420		
	Age	0.0339 ± 0.0252		0.8	NS
	Age^2	−0.001296 ± 0.00084		4.3	<0.05
1994	Constant	0.544 ± 0.199	393		
	Age	0.2569 ± 0.0337		1.7	NS
	Age^2	−0.00899 ± 0.00112		103.1	<0.001
1995	Constant	−1.38 ± 5.86	146		
	Age	0.271 ± 0.567		4.7	<0.05
	Age^2	−0.0078 ± 0.0136		0.7	NS
1996	Constant	−0.437 ± 0.176	335		
	Age	−0.1560 ± 0.0303		80.2	<0.001
	Age^2	0.006296 ± 0.00098		77.3	<0.001
1997	Constant	1.606 ± 0.165	328		
	Age	0.0193 ± 0.0331		28.6	<0.001
	Age^2	−0.00192 ± 0.00125		4.1	<0.05
1998	Constant	1.136 ± 0.112	303		
	Age	−0.1742 ± 0.0243		0.1	NS
	Age^2	0.006647 ± 0.00090		55.7	<0.001

were left alone more often, and especially in 1992, 1996, and 1998, when the proportion of herring in the chicks' diet was <50% (Fig. 4), chicks were left unattended relatively often (Fig. 5). To describe the relationship between chick age and proportion of time chicks were left unattended at the nest, a logistic curve was fitted for each year (Fig. 5). Asymptotic values of the logistic equations were used as a measurement of parental effort. Only for 1995, when observations were restricted to relatively old chicks, the mean value of biparental foraging time in that year was used. Average yearly parental effort significantly decreased with higher proportions of herring in the diet (r^2 = 0.57, P = 0.05; Fig. 6) and strongly correlated with the average yearly proportion of food eaten by chicks (r^2 = 0.91, P < 0.001).

Increasing parental effort seems to be an important mechanism for buffering against fluctuations in food availability or kleptoparasitism, particularly where parental effort in Sandwich Terns is predicted from diet composition and growth rate of the chicks (Fig. 7). If the diet consists totally of herring, minimum growth requirements of chicks can be met without biparental foraging, whereas if the food were only sandeel, parents have to leave their chicks unattended for 40% of the daylight period (drawn lines in Fig. 7). If parents strive for

maximum growth, they have to leave the chick unattended for 43% of the daylight period if the diet consisted totally of herring. If the diet consisted entirely of sandeel, maximum growth requirements can not be met, even if the parents left their chicks unattended for the entire daylight period. Except for 1995, observed parental effort (dots in Fig. 7) was higher than predicted from average yearly diet composition and growth rate of the chicks (circles in Fig. 7). In 1992, 1996, and 1998, predictions of parental effort were much lower than observed parental effort.

DISCUSSION

Buffering against fluctuating environmental conditions.—Prey-stealing by Black-headed Gulls plays a crucial role in foraging decisions that Sandwich Terns on Griend have to make. Energy intake of Sandwich Tern chicks may be limited to a critical level as a result of high robbing pressure on large prey. Due to the higher energy content of herring, smaller fish can be taken to obtain the same amount of energy. Those smaller fish are less likely to be stolen by gulls, making herring a much more profitable prey species for terns. If parent terns would exclusively forage on sandeel, energy intake would be too low for chicks to survive. By also
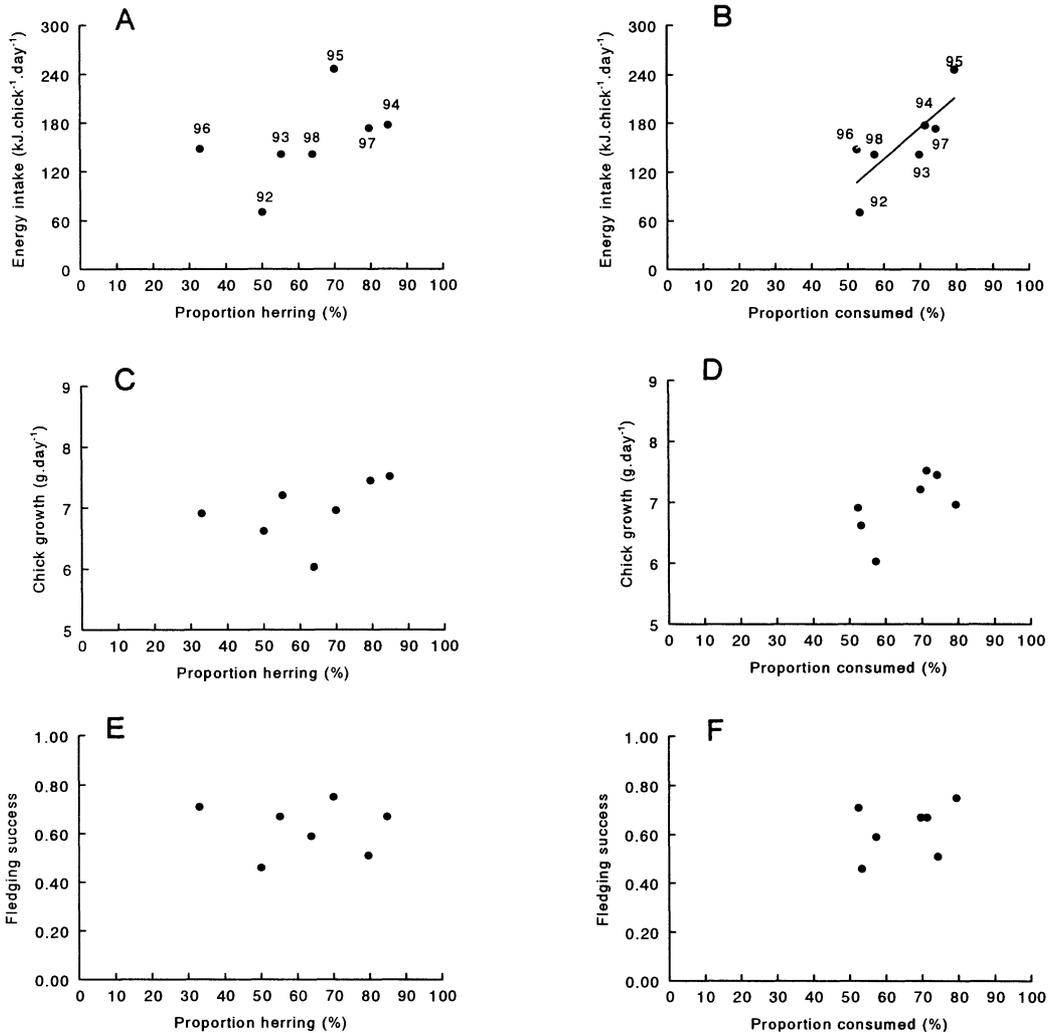
FIG. 4. Effects of yearly average diet composition and food consumption probability on average yearly daily energy intake (A–B), chick growth (C–D), and fledging success (E–F) of Sandwich Tern chicks on Griend, 1992–1998. To largely exclude effects of age, food consumption probabilities, and energy intake, rates were computed for chicks older than 15 days. A chick was assumed to have fledged when it had reached the age of 25 days. Average yearly growth was computed for first hatchlings that survived until fledging. Line represents significant relationship.

supplying chicks with a sufficient amount of the more advantageous herring, energy intake (and thus growth and survival of chicks) can be improved. Our calculations suggest that by the first week after hatching, when both energy demand of the chicks and rate of kleptoparasitism are still relatively low, diet composition will have large effects on chick growth provided that one parent stays at the nest. As the season progresses, herring becomes increasingly important. But even when exclusively feeding on

herring of observed prey length, maximum growth of chicks can not be reached without parents foraging simultaneously. Parents do not seem to have much flexibility in their choice of prey species because in most years the chicks' diet did not show the expected shift towards more herring with increasing age of chicks. That suggests a limited availability of more profitable herring, so that a shift towards a less vulnerable diet could not be realized. Instead, parents tried to compensate for a poten-
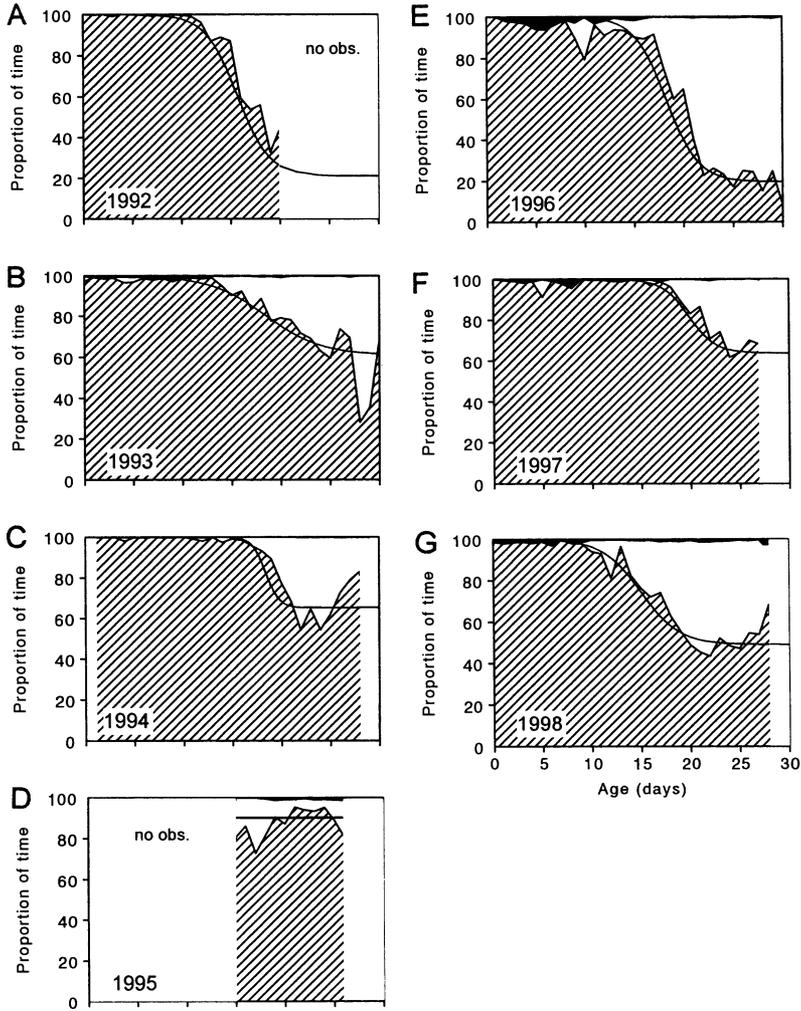
FIG. 5.   Development of parental nest attendance with the age of Sandwich Tern chicks on Griend in 1992–1998 (hatched areas = one parent present at the nest; black areas = two parents present; white areas = no parents at nest). Drawn lines are the results of least-square analysis of proportion of time the chicks were attended to by at least one parent.

tial food shortage by increasing their foraging effort, leaving the chicks unattended at the nest more often in years when food losses were high. Because food consumption probabilities were closely related to diet composition, parental effort also tended to increase with higher proportions of sandeel. In years when diet composition suggested a short supply of herring (1992, 1996), parents had to work hard. In those years, older chicks were left alone at the nest for >50% of the daylight period. In 1994, 1995, and 1997, however, the diet of chicks was dominated by herring, suggesting a relatively

high availability of that prey species. As a consequence, simultaneous parental foraging occurred at a low level, whereas chick growth was among the highest recorded in this study.

On Griend, average annual growth rates varied between 6.0 and 7.5 g day^{-1}, thus most chicks in our study grew at a rate well below that of chicks fed *ad libitum* (12.8 g day^{-1}; Klaassen et al. 1992). So also in favorable years, chicks grew at a rather slow rate, whereas parents could theoretically have increased their foraging effort to achieve faster growth. Fast growth, however, results in relatively high en-
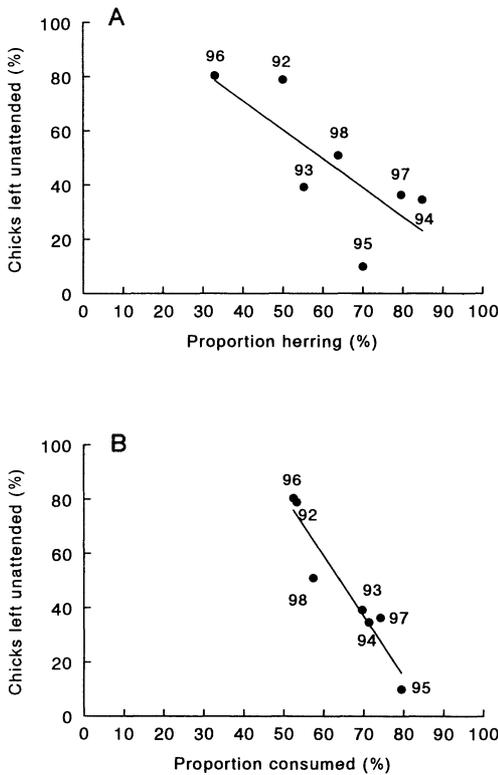
FIG. 6.   Parental nest attendance (asymptotic values of the proportion of time parents left the chicks unattended at the nest, Fig. 5) in relation to diet composition (A, Pearson regression, $r^2 = 0.55$, $n = 7$, $P = 0.06$) and food consumption probability (B, Pearson regression, $r^2 = 0.84$, $n = 7$, $P = 0.004$), Griend, 1992–1998.
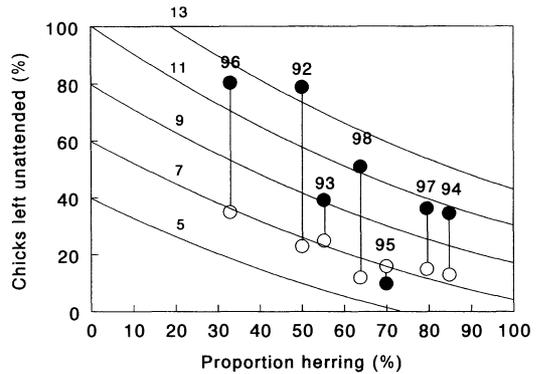
FIG. 7.   Proportion of time a Sandwich Tern chick must be left unattended to achieve peak energy intake rates at different growth rates of the chick in relation to diet composition (drawn lines) and assuming that only one chick is present in the nest. Numbers above lines indicate growth rate. Peak energy requirements of chicks are computed using the relationship between growth rate and maximum gross energy intake (GEI_{MAX}) from figure 5 in Klaassen et al. (1992): $GEI_{MAX} = 157 + 17.8 \times$ growth. Energy intake rate of the chicks (GEI) was computed assuming that only average observed sized prey was fed to the chicks (1.6 and 2.0 BL, respectively, in herring and sandeel, corresponding with daily intake rates of 272 and 176 kJ): $GEI = (1 + \%CU/100) \times (PH/100 \times 272 + (1-PH/100) \times 176)$, where $\%CU =$ proportion of time the chick is left unattended at the nest and PH = proportion of herring. Dots = average observed yearly proportion of time the chicks were left unattended. Circles = prediction of the proportion of time the chicks are left unattended, given the average observed growth rate and diet composition.

ergy demands of the chicks (Klaassen et al. 1994). On the other hand, fast growth might improve survival chances of a chick, but in Sandwich Terns chick survival was almost not affected above a growth rate of 7 g day^{-1} (E. W. M. Stienen unpubl. data). Thus, increased foraging efforts would probably not lead to a large increase of reproductive output, unless some parents might have been able to raise two chicks, which occurred rarely. Even when the diet contains only herring, it would be impossible for an average parent to raise two chicks growing >7 g day^{-1} to fledging (Fig. 7). That is in accordance with the very few pairs (0.7%) that fledged two chicks during the study period. Other fitness costs might be that unattended chicks are more vulnerable to predation, as is frequently observed in seabird colonies (e.g. Hamer et al. 1991, Bukacinski et al. 1998), al-

though in the Sandwich Tern chick predation is relatively low towards the end of chick-rearing (Veen 1977). Moreover, unattended tern chicks provoke serious attacks of neighboring gulls and terns, which sometimes results in the death of a chick (E. W. M. Stienen and A. Brenninkmeijer pers. obs.). Nevertheless, fledging success in our study was not correlated with parental nest attendance (Pearson regression, $r^2 = 0.18$, $P = 0.34$). On the other hand, increased parental foraging might involve fitness costs for the parents. Effects of parental effort on subsequent fecundity have been demonstrated in a wide variety of bird species (e.g. Røskaft 1985, Smith et al. 1987, Gustafsson and Sutherland 1988, Verhulst 1995, Wernham and Bryant 1998). An effect of increased parental effort on subsequent survival is more difficult to demonstrate, but evidence is growing that such

effects occur (Daan et al. 1996, Golet et al. 1998). Life-history theory predicts that individuals should strive for maximization of lifetime reproductive success. Long-lived species like Sandwich Terns should, therefore, reduce their current breeding effort rather than jeopardize their residual reproductive value (Drent and Daan 1980). In Herring Gulls (*Larus argentatus*; Pons and Migot 1995) and puffins (*Fratercula arctica*; Wernham and Bryant 1998), variation in food availability indeed affects clutch size and reproductive output, but not adult (local) survival. In the kittiwake (*Rissa tridactyla*), however, reproductive costs do affect survival (Golet et al. 1998), thus also in long-lived species parents sometimes trade their own survival for that of their offspring.

Energy intake of chicks is a product of food delivery rate to the colony, length distribution, and consumption probability of the food. Prey delivery rate can be adapted by parents foraging simultaneously to fit energy demands of the chicks and to counteract variation in food availability and consumption rates caused by factors other than prey length (e.g. wind speed, Veen 1977). In this study, average yearly proportion of time the chicks were left unattended correlated very well with average yearly energy intake per parent (Pearson regression, $n = 7$, $r^2 = 0.86$, $P = 0.003$). Apparently, in most years parental buffering was sufficient to keep actual energy intake of chicks >140 kJ day^{-1} and to avoid negative effects on chick growth and survival (Fig. 4). The model presented in Figure 7 depicts that only in most unfavorable years, when no herring is available, parents would not be able to fully compensate for the high losses inflicted by gulls. To achieve a growth rate of 7 g day^{-1}, which was the average growth rate of surviving chicks in this study (see above), we expected biparental foraging to occur between 10 and 36% of the time, given average annual proportions of herring observed. However, proportion of time chicks were left unattended varied between 10 and 80% of the time. Except for 1995, our computations yielded a conservative prediction (Fig. 7), which might have several reasons. First, energy requirements of the chicks were measured under laboratory conditions. In the field, chicks have higher costs for thermoregulation and activity, so that gross energy requirements will be somewhat higher than shown in Figure 1. Sec-

TABLE 3. Daily energy provisioning per parent (kJ chick^{-1} day^{-1} parent^{-1}) and daily energy intake rate per parent (kJ chick^{-1} day^{-1} parent^{-1}) of Sandwich Tern chicks older than 15 days on Griend in 1992–1998. Daily energy provisioning to the chicks (DEP, kJ chick^{-1} day^{-1}) and daily energy intake rate (DEI, kJ chick^{-1} day^{-1}) were corrected for the proportion of time the chicks were left unattended (%CU) as follows: DEP^{cor} = 100% $\times$ DEP/(100 + %CU) and DEI^{cor} = 100% $\times$ DEI/(100 + %CU).

Year	Energy provisioned (mean ± SE)	Energy intake (mean ± SE)	Number of chick days
1992	128.7 ± 14.3	58.7 ± 8.0	32
1993	181.6 ± 6.7	115.2 ± 4.9	207
1994	221.2 ± 6.8	147.7 ± 5.6	212
1995	299.6 ± 8.4	225.5 ± 7.4	143
1996	177.2 ± 4.6	88.4 ± 3.7	163
1997	213.5 ± 5.6	147.0 ± 4.7	152
1998	190.6 ± 6.6	101.0 ± 4.4	172

ond, some parents had to feed two chicks during the last week before fledging, whereas the predictions assume that only one chick is present. Also, predictions are based on length-specific food transport rates and food-consumption rates mainly measured in relatively favorable years (1993 and 1994). However, magnitude of the deviation differs from year to year, with relatively high parental effort measured in 1992, 1996, and 1998, and low effort in 1995. That variation is due to yearly differences in energy intake rate caused by differences in provisioning rate, prey length, and robbing intensity. In 1992, only 129 kJ day^{-1} was provided to chicks per parent (Table 3). In combination with low proportions of herring and high prey losses, that resulted in low energy intake per parent, even when considering that in that year chicks were only followed until 21 days old. In 1996 and 1998, at least one of the two prey items were relatively short compared to other years (Stienen et al. 2000). Still, robbery was high resulting in low rates of energy intake per parent. In contrast, in 1995 provisioning rates were high and food losses exceptionally low, resulting in high intake rates per parent and accordingly low parental effort.

There are indications that food availability around Griend was much better in the past than in the 1990s. In 1966, under normal weather conditions, individual chicks were fed 15 fish per day and by age 5 they were fed 38 g fish per day (Veen 1977), corresponding with an energy

intake of 192–199 kJ day^{-1}. In the 1990s, however, chicks at that age were fed only 7.1 ± 4.2 fish day^{-1} ($n = 91$), corresponding with an energy intake of 97.7 ± 63.9 kJ day^{-1}. Chick mortality was, however, almost equal in the two periods (E. W. M. Stienen unpubl. data). Thus, it seems likely that chicks grew faster and parental nest attendance was higher than in the 1990s, but unfortunately no data on growth and parental effort are available for 1966. A low availability of herring might explain why the population on Griend only partly recovered from collapse in the 1960s caused by poisoning of the Dutch coastal waters with pesticides (Koeman and Van Genderen 1966, Brenninkmeijer and Stienen 1992). The current population size on Griend (on average ~7,000 pairs in the 1990s) is less than half the size prior to the collapse, which is not compensated for by an increase in other parts in The Netherlands (Brenninkmeijer and Stienen 1992). The pesticide incident was followed by an extremely low stock size and recruitment rate of North Sea herring in the 1970s (Corten 1990). Following the collapse in the 1960s, there probably was a period with highly unfavorable food composition, resulting in maximum working levels of parents. That might have affected reproductive output and the number of pairs that actually started breeding on Griend, but no studies are available that can support that. However, many studies found that changes in bird numbers are related to changes in food supplies (Newton 1998). Also, in terns it has often been suggested that food availability directly influences the number of pairs that attempt to breed (Monaghan & Zonfrillo 1986, Crawford & Dyer 1995, Phillips et al. 1996). Such might also be the case in Sandwich Terns. Indeed, we found a strong positive correlation between the number of pairs nesting on Griend in the period 1992–1996 and the proportion of herring in the chicks' diet (Pearson regression, $n = 5$, $r^2 = 0.88$, $P = 0.02$). Until 1997, Griend supported all Sandwich Terns nesting in the Dutch Wadden Sea. From 1997 onwards, other large colonies were established in the area and the correlation between number of pairs nesting on Griend and diet composition was no longer valid. Nevertheless, the fewer breeding attempts in poor years might have indirectly improved breeding success if mainly "high quality" individuals started breeding. Those individuals might be able to spend more time on foraging and counterbalance the expected negative effects on growth and survival of their offspring.

Foraging decisions.—The optimal foraging theory predicts a selective prey choice depending on encounter rate of the prey (Stephens and Krebs 1986). When a tern encounters a small prey item, it can choose between catching the prey or continue searching for a larger prey. The theory of central place foraging predicts that the acceptance of a prey depends on availability of higher-ranked prey. If insufficient numbers of highly ranked prey are available, the diet will be broadened through inclusion of lesser-ranked prey. There is growing evidence that birds incorporate additional constraints, like kleptoparasitism, in their consideration of which prey to catch (Thompson and Barnard 1984, Tuckwell and Nol 1997). Taking kleptoparasitism into account, herring would by far be the most profitable prey species for Sandwich Terns on Griend. However, the encounter rate of the most profitable size seems low, because the majority of all herring brought to the ternery were much smaller than the most profitable size (2.9 bill lengths). The main foraging area of Sandwich Terns nesting on Griend is situated between the isles of Vlieland and Terschelling, 10–12 km Northwest of Griend (Veen 1977). Those waters support mainly small herring (Fonds 1978, Corten 1996), thus narrowing the food choice of Sandwich Terns on Griend.

The advantage of a herring-dominated diet for Sandwich Terns breeding on Griend can not be translated to other areas and might even be restricted to the research period because it totally depends on the length-specific encounter rate and consumption probability. In fact, on the Farne Islands in the early 1960s, the prey of Sandwich Terns consisted of 74% sandeel, whereas chick growth was much higher than in our study (Pearson 1968). However, sandeel provided to chicks were smaller (on average ~2.5 g) and fishing trips lasted shorter (1.03 h) than in our study (3.5 g and 1.2 h). Sandeel availability around the Farne Islands might have been higher or sandeel was found closer to the colony. Also, the rate of kleptoparasitism on the Farne Islands was probably extremely low, because at that time the Farne Islands held only a few pairs of Black-headed Gulls (1–2 pairs). Diet composition cannot be generally used as an indicator for reproductive success.

Parental effort on the other hand seems a good candidate to serve as a general indicator of energy intake in Sandwich Terns.

LITERATURE CITED

BRENNINKMEIJER, A., AND E. W. M. STIENEN. 1992. Ecologisch profiel van de Grote Stern (*Sterna sandvicensis*) RIN-rapport 92/17. DLO-Institute for Forestry and Nature Research, Arnhem, The Netherlands.

BROCKMANN, H. J., AND C. J. BARNARD. 1979. Kleptoparasitism in birds. Animal Behaviour 27:487–514.

BUKACINSKI, D., M. BUKACINSKA, AND A. L. SPAANS. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the Lesser Black-backed Gull *Larus fuscus*. Ibis 140:422–430.

CAMPREDON, P. 1978. Reproduction de la sterne caugec, *Thalasseus sandvicensis* Lath., sur le Banc d'Arguin (Gironde). Aperçu de sa distribution hivernale. L'Oiseau et R.F.O. 48:123–150, 263–279.

CHARNOV, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

CORTEN, A. 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. Netherlands Journal of Sea Research 25:227–235.

CORTEN, A. 1996. Ecoprofiel haring. RIVO/DLO-rapport CO59/95. DLO-Rijksinstituut voor Visserij Onderzoek, Ijmuiden, The Netherlands.

CRAWFORD, R. J. M., AND B. M. DYER. 1995. Responses by four seabird species to a fluctuating availability of cape anchovy *Engraulis capensis* off South Africa. Ibis 137:329–339.

DAAN, S., C. DEERENBERG, AND C. DIJKSTRA. 1996. Increased daily work precipitates natural death in the Kestrel. Journal of Animal Ecology 65:539–544.

DRENT, R. H., AND S. DAAN. 1980. The prudent parent: Energetic adjustments in avian breeding. Ardea 68:225–252.

FONDS, M. 1978. The seasonal distribution of some fish species in the western Dutch Wadden Sea. Pages 42–77 in Fishes and Fisheries of the Wadden Sea (N. Dankers, W. J. Wolff and J. J. Zijlstra, Eds.). Stichting Veth tot steun aan Waddenonderzoek, Leiden, The Netherlands.

FUCHS, E. 1977. Kleptoparasitism of Sandwich Terns *Sterna sandvicensis* by Black-headed Gulls *Larus ridibundus*. Ibis 119:183–190.

GENSTAT 5 COMMITTEE. 1993. GENSTAT 5 Reference Manual. Clarendon Press, Oxford.

GOLET, G. H., D. B. IRONS, AND J. A. ESTES. 1998. Survival costs of chick rearing in Black-legged Kittiwakes. Journal of Animal Ecology 67:827–841.

GORKE, M. 1990. Die Lachmöwe (*Larus ridibundus*) in Wattenmeer und Binnenland. Seevögel 11:1–48.

GUSTAFSSON, L., AND W. J. SUTHERLAND. 1988. The costs of reproduction in the Collared Flycatcher *Fidecula albicollis*. Nature 335:813–815.

HAMER, K. C., R. W. FURNESS, AND R. W. G. CALDOW. 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. Journal of Zoology 223:175–188.

KLAASSEN, M., B. ZWAAN, P. HESLENFELD, P. LUCAS, AND B. LUIJCKX. 1992. Growth rate associated changes in the energy requirement of tern chicks. Ardea 80:19–28.

KLAASSEN, M., B. HABEKOTTÉ, P. SCHINKELSHOEK, E. STIENEN, AND P. VAN TIENEN. 1994. Influence of growth rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks. Ibis 136:197–204.

KOEMAN, J. H., AND H. VAN GENDEREN. 1966. Some preliminary notes on residues of chlorinated hydrocarbon insecticides in birds and mammals in the Netherlands. Journal of Applied Ecology 3:99–106.

KREBS, J. R. 1973. Behavioral aspects of predation. Pages 73–111 in Perspectives in Ethology (P. P. G. Bateson and P. H. Klopfer, Eds.). Plenum Press, New York.

LESSELS, C. M., AND D. W. STEPHENS. 1983. Central place foraging: Single-prey loaders again. Animal Behaviour 31:238–243.

MONAGHAN, P., AND B. ZONFRILLO. 1986. Population dynamics of seabirds in the Firth of Clyde. Proceedings of the Royal Society of Edinburgh, Series B 90:363–340.

NEWTON, I. 1998. Population Limitation in Birds. Academic Press Limited, London.

NORUŜIS, M. J. 1990. SPSS/PC+ 4.0. Base Manual. SPSS Inc., Chicago.

ORIANS, G. H., AND N. E. PEARSON. 1979. On the theory of central place foraging. Pages 154–177 in

Analysis of Ecological Systems (D. J. Horn, R. D. Mitchell, and G. R. Stairs, Eds.). Ohio State University Press, Columbus.

PEARSON, T. H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology 37:521–552.

PHILLIPS, R. A., R. W. G. CALDOW, AND R. W. FURNESS. 1996. The influence of food availability on the breeding effort and reproductive success of Arctic Skua *Stercorarius parasiticus*. Ibis 138:410–419.

PONS, J.-M., AND P. MIGOT. 1995. Life-history strategy of the Herring Gull: Changes in survival and fecundity in a population subjected to various feeding conditions. Journal of Animal Ecology 64:592–599.

RATCLIFFE, N., D. RICHARDSON, R. L. SCOTT, P. J. BOND, C. WESTLAKE, AND S. STENNETT. 1997. Host selection, attack rates and success rates for Black-headed Gull kleptoparasitism of terns. Colonial Waterbirds 20:227–234.

RØSKAFT, E. 1985. The effect of enlarged brood size on future reproductive potential of the Rook. Journal of Animal Ecology 54:255–260.

SCHOENER, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

SMITH, H. G., H. KÄLLANDER, AND J. Å. NILSSON. 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. Auk 104:700–706.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.

STIENEN, E. W. M., AND A. BRENNINKMEIJER. 1999. Keep the chicks moving: How Sandwich Terns can minimize kleptoparasitism by Black-headed Gulls. Animal Behaviour 57:1135–1144.

STIENEN, E. W. M., P. W. M. VAN BEERS, A. BRENNINKMEIJER, J. M. P. M. HABRAKEN, M. H. J. E. RAAIJMAKERS, AND P. G. M. VAN TIENEN. 2000. Reflections of a specialist: Patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna Sandvichensis*. Ardea 88:33–49.

THOMPSON, D. B. A., AND C. J. BARNARD. 1984. Prey selection by plovers: Optimal foraging in mixed-species groups. Animal Behaviour 32:554–563.

TUCKWELL, J., AND E. NOL. 1997. Intra- and inter-specific interactions of foraging American Oystercatchers on an oyster bed. Canadian Journal of Zoology 75:182–187.

VEEN, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). Behaviour (Supplement)20:1–193.

VERHULST, S. 1995. Reproductive decisions in Great Tits. An optimal approach. Ph.D. dissertation, University of Groningen, Groningen, The Netherlands.

WERNHAM, C. V., AND D. M. BRYANT. 1998. An experimental study of reduced parental effort and future reproductive success in the puffin, *Fratercula arctica*. Journal of Animal Ecology 67:25–40.

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