

Living with Gulls: The Consequences for Sandwich Terns of Breeding in Association with Black-headed Gulls

E. W. M. STIENEN^{1,2,3}, A. BRENNINKMEIJER^{1,4} AND C. E. GESCHIERE¹

¹Alterra, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

²Zoological Laboratory, University of Groningen, Kercklaan 30, NL-9750 AA Haren, The Netherlands

³Address for correspondence: Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium
Internet: eric.stienen@instnat.be

⁴Current address: Witteveen & Bos, P.O. Box 85948, NL-2508 CP Den Haag, The Netherlands

Abstract.—We studied the feeding ecology of Sandwich Terns (*Sterna sandvicensis*) in the presence of kleptoparasitising Black-headed Gulls (*Larus ridibundus*) on the Isle of Griend, The Netherlands, between 1992 and 1998. About 30% of all of the food the parents transported to the colony was lost, mainly through intervention by Black-headed Gulls. The gulls mainly took the larger fish, but showed no preference for the energetically more profitable herring. Apparently, the gulls selected for prey length or visibility of the prey, rather than for energy content of the fish. The proportion of food robbed by the gulls increased with the age of the tern chicks and was in parallel to the increase in prey length Sandwich Tern parents brought to the colony. Kleptoparasitism showed a clear pattern with time of the day, tide and wind speed. During the first few hours of the day, almost no kleptoparasitism occurred, while robbery was high around 09.00h and at dusk. This bimodal pattern in kleptoparasitism might be related to the foraging activity of the gulls. A tidal effect on food loss was less pronounced, although kleptoparasitism was significantly higher during high tide, when foraging activity of gulls for other foods was low and the number of potential pirates in the tern colony was high. Wind strength had a significant negative effect on the amount of food transported to the colony, while kleptoparasitism increased. Therefore, wind speed severely affected energy intake of the tern chicks and had strong negative effects on chick growth. During the first two weeks post-hatching, kleptoparasitism was relatively low and had only small effects on chick growth, even under unfavourable weather conditions. From then on, the negative effects of kleptoparasitism on growth became considerable. Chick growth was severely affected by strong winds. Sandwich Terns show several behavioral strategies in order to reduce the rate of food loss by the gulls and to minimize the effects on chick growth and survival. *Received 31 August 2000, accepted 27 November 2000.*

Key words.—Black-headed Gull, diurnal rhythm, chick growth, effects of wind, energy consumption, feeding ecology, kleptoparasitism, Sandwich Tern, tidal effects.

Waterbirds 24(1): 68-82, 2001

Kleptoparasitism or food piracy, the stealing of already procured food by individuals of one species from individuals of another species, is widely spread among birds (Brockmann and Barnard 1979). This is especially common in seabirds, which generally breed in dense colonies and often form aggregations when feeding (Furness 1987). In contrast with most other seabirds, nesting Sandwich Terns (*Sterna sandvicensis*) intentionally seek the proximity of potential kleptoparasites. In The Netherlands, most Sandwich Tern colonies are situated in the vicinity of or are surrounded by nesting Black-headed Gulls (*Larus ridibundus*; Veen 1977). In this way, the non-aggressive Sandwich Terns benefit from the anti-predator behavior of the gulls. By seeking the proximity of the gulls, predation on eggs and freshly

hatched chicks is greatly reduced (Lind 1963; Veen 1977). However, soon after the tern chicks hatch, some nearby breeding gulls develop into specialized kleptoparasites, resulting in serious losses of food which the tern parents bring for their offspring. As the chicks grow, the terns become less susceptible to predation, thus the advantages of associative nesting with Black-headed Gulls become less important. At the same time, the disadvantage from food robbery strongly increases (this study). Stienen and Brenninkmeijer (1999) showed by experiment that the current rate of food parasitism in the Sandwich Tern colony on the Isle of Griend, The Netherlands, had negative effects on chick growth and body condition at fledging. In this study, we give a detailed analysis of various factors influencing food parasit-

ism by gulls. A simple model is presented that shows the combined effects of kleptoparasitism and wind speed on the growth of the tern chicks on Griend. Wind speed and sea surface conditions influence the fishing ability of adult Sandwich Terns (Dunn 1973; Taylor 1983). In accordance with this, Stienen *et al.* (2000) found strong effects of wind speed on diet composition and the amount of food transported to Sandwich Tern chicks on Griend. As wind speed also influences the rate of food loss to kleptoparasitising gulls, adverse effects on chick growth were expected, although Dunn (1975) did not find an effect of wind speed on the weight increase of Sandwich Tern chicks.

METHODS

Study Area

The study was conducted on the Isle of Griend, situated in the Dutch Wadden Sea (53°15'N, 5°15'E). Griend (about 57 ha at normal high tide) consists of a low salt marsh area, partly surrounded by a somewhat higher dune ridge. The isle supports several species of colonial nesting terns and gulls. During the study period (1992-1998) 5,600-8,300 pairs of Sandwich Terns and 16,000-28,500 pairs of Black-headed Gulls nested on the island. Each year, the Sandwich Terns formed several subcolonies, which were separated from each other in space or time. Each year, a subcolony of Sandwich Terns in which hatching occurred around 1 June was chosen for study of the food transported to the nest and also kleptoparasitism. Just before hatching, 50-100 nests within the subcolony were enclosed to prevent the chicks from moving from the study site. The enclosures were made of 50 cm high wire netting of which the lower 20 cm was covered with plastic, to avoid injuries to the chick's head and bill.

Wind speed at 10 m was recorded every 5 minutes with a calibrated cup-anemometer in the vicinity of the colony. For most statistical analyses we used the average hourly wind speed. However, to analyze the effects of wind speed on the daily energy intake of the chicks we used the average wind speed during the daylight period.

Chick Observations

Within the enclosures, all chicks were banded within three days of hatching. At banding, the chicks were aged using the size of yolk sac, the length of the bill to head and feather characteristics. Each year, chicks from about 20 nests were dyed with picric acid or ink for individual recognition. The chicks were followed daily from hatching until fledging. Except in 1992 and 1995, only chicks younger than 21 days and older than 15 days, respectively, were followed. Each day, observations lasted from approximately 04.30 h to 22.30 h. If possible, the same chicks were observed each day, but when a chick died a new chick of known age was studied. Observations were performed from an elevated blind placed at

about 2 m from the enclosure. During the observations we recorded prey species, prey length and the fate of the prey (for more details see Stienen *et al.* 2000). Prey size was estimated in quarters of the parent's bill size (bill length = 5.43 ± 0.25 cm, $N = 679$). Observations were stored in data loggers with a time resolution of 1 sec. Food transported to the colony and food intake rate of the chicks were transformed into energy values according to the allometric relationships given by Stienen and Brenninkmeijer (in press).

Growth and Condition of Chicks

When weather conditions allowed it, chicks were weighed at intervals of three days to the nearest g using an electronic balance. The length of the total head (head + bill, ± 0.1 mm) was measured with a vernier caliper. When intervals between two measurements lasted less than five days, in between body mass was calculated assuming linear growth.

For each age, the expected body mass (M_{exp} , g) was computed by taking the average body mass of all study chicks which survived to fledging (i.e., >24 days old). An index for chick condition (CI) was obtained by calculating the deviation in body mass (M , g) from the expected body mass for that age:

$$CI = \frac{M - M_{\text{exp}}}{M_{\text{exp}}} \times 100\%$$

Data Analysis and Statistics

Data analyses were performed using SPSS/PC+ 4.0 statistical package (Norusis 1990). All statistical tests were performed using the Genstat statistical package (Genstat 5 Committee 1993). In all logistic regression analyses, the statistical parameters of prey species, tide, and year were treated as factor-variables. Depending on the parameter, the factor-variables were subdivided into 2-12 categories or levels. To analyze the effects prey length (in bill length units), prey energy content (in kJ), prey species (2 types, namely Herring *Clupea harengus/Sprattus sprattus* or Sandeel (sandlance) *Ammodytes tobianus/Hyperoplus lanceolatus*), wind speed (in m s^{-1}), time of day (in h), tide (12 classes, relative to high water) and year (7 categories, 1992-98), respectively. The fate of the prey brought to the colony we analyzed using a stepwise logistic regression approach. In all cases, the variables were entered into a logistic model in the order given above. Prey species, other than Clupeidae (in future called Herring) and Ammodytidae (in future called Sandeels), were omitted from all analyses since they amounted less than 1.1% of all food items supplied to the chicks (Stienen *et al.* 2000).

RESULTS

Of all Herring and Sandeels brought to the colony ($N = 16,650$) 70.7% were eaten by the Sandwich Tern chicks. Food items not eaten by the chicks were classified as follows:

1. robbed by Black-headed Gulls (18.0%),

2. eaten by the tern parent under pressure of robbing gulls (1.4%),
3. lost by the adult when out of the observer's view and parent then returned without fish (7.7%),
4. robbed by species other than Black-headed Gulls, mainly Sandwich Terns, but also some Common Terns (*Sterna hirundo*) and Common Gulls (*Larus canus*; 0.7%), and
5. other losses, such as prey which fell to the ground or eaten by the parent without intervention of gulls (1.5%).

Thus, just over 66% of the food losses could be directly linked to robbing activities of gulls (robbed by gulls or eaten by the parent under pressure of gulls). The most common event was prey robbed by a gull when a parent tern either attempted to land next to its chick or presented a fish to its chick. Loss of prey when the bird was out of the observer's view often happened, particularly when gulls chased an arriving parent tern away from the colony. However, losing prey when out of view also occurred when a chick refused food and the fish-carrying parent left the colony or when the parent was chased away from the colony by "pirates" other than Black-headed Gulls. These cases occurred rarely, thus the main reason for the loss of fish was because of intervention by gulls.

The length of the fish brought to the colony varied between 0.25 and 4.0 bill lengths. However, prey smaller than 0.75 bill lengths (0.2% of all prey) exclusively consisted of broken pieces of fish. The proportion of prey robbed by Black-headed Gulls or other species and the proportion lost when out of view significantly increased with prey length, while the proportion of food eaten by the parent and other losses decreased with prey length (Fig. 1, Table 1). Since the proportion of food robbed by Black-headed Gulls and lost out of view were by far the most important causes of food loss, the probability of consuming prey sharply decreased with prey size. If the prey species was included in the logistic regression model after prey length, it had significant effects when it concerned prey taken by Black-headed Gulls and prey

lost when out of view (Table 1). Compared with Herring, Sandeels were less often robbed by Black-headed Gulls, but more often lost while out of view. These effects annul each other, so that no significant effect was found between prey species and the probability of consuming the prey. Further, adding prey energy content to the model had no significant effects on the probability of consumption of prey (logistic regression: change in deviance = 0.2, $df = 1$, n.s.). If the prey energy content was entered into the model first, it had a significant effect on the consumption probability of a prey (logistic regression: change in deviance = 500, $df = 1$, $P < 0.001$), but removed only 2.5% of the variance, while another 2.4% was removed by then entering prey length. If the order of inclusion was reversed, prey length removed 4.9%, while only 0.002% of the variance was removed by prey energy content. So, food consumption by the tern chicks depended on the size of the fish offered rather than on its energy content.

Age of the Chicks

During the first five days post-hatching, food loss was relatively high (Fig. 2). Freshly hatched chicks were clumsy and it took them a relatively long time to handle prey. This resulted in a high proportion of the food robbed by either neighbouring terns or Sandwich Terns visiting the colony, but probably having no chicks of their own. Furthermore, freshly hatched chicks sometimes refused food. The fish was then left at the nest, consumed by the parent, or the parent left the colony still carrying the fish.

Kleptoparasitism by Black-headed Gulls gradually increased from hatching until day 15 and remained more or less constant thereafter (Fig. 2). This parallels the increase in the length of the prey brought to the colony from day 0-15 (Stienen *et al.* 2000). During the entire chick period, prey consumed by chicks were, on average, smaller than prey robbed by gulls (Fig. 3). The average size of the prey taken by the gulls increased with the age of the tern chicks. Prey of relatively small size, which were

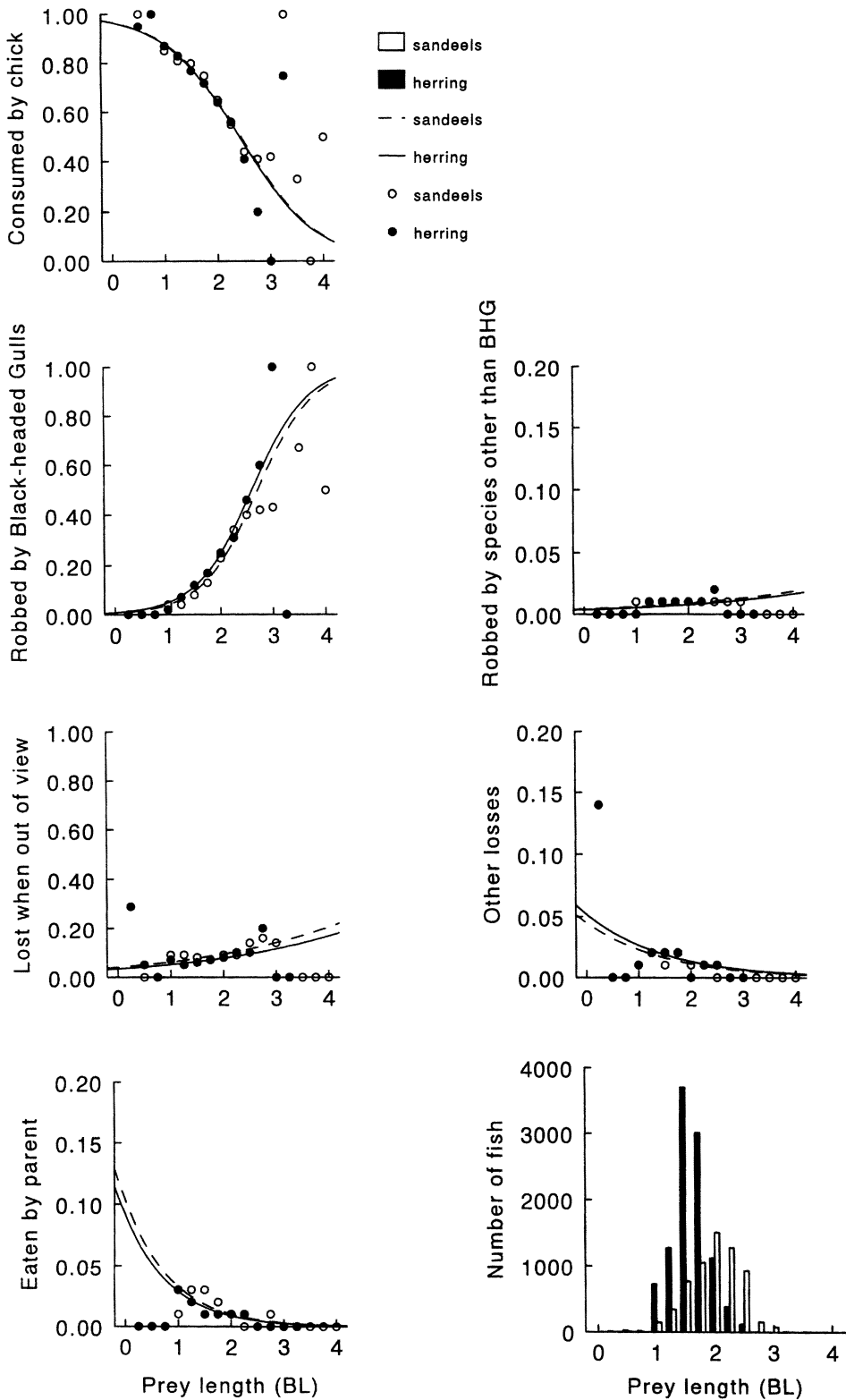


Figure 1. Fate of fish brought to Sandwich Tern chicks on Griend in 1992-98 in relation to prey length. The lines represent the regression equations given in Table 1. The lower right graph shows the number of fish considered.

Table 1. Logistic regression analyses examining the effect of prey length and prey species on the occurrence of various fates of fish (N = 16,650) brought to Sandwich Tern chicks on Griend in 1992-98. Prey length in adult bill length units.

Variable	Change in deviance	df	P-value	Estimates of coefficients \pm SE
Proportion eaten				
Constant				3.33 \pm 0.095
Prey length	989.8	1	<0.001	-1.38 \pm 0.055
Species	0.8	1	n.s.	0.036 \pm 0.044 for Sandeels
Proportion robbed by Black-headed Gulls				
Constant				-4.85 \pm 0.10
Prey length	1171.8	1	<0.001	1.87 \pm 0.059
Species	17.4	1	<0.001	-0.207 \pm 0.047 for Sandeels
Proportion lost when out of view				
Constant				-3.37 \pm 0.10
Prey length	65.3	1	<0.001	0.443 \pm 0.059
Species	10.1	1	<0.01	0.215 \pm 0.049 for Sandeels
Proportion eaten by parent				
Constant				-2.41 \pm 0.11
Prey length	40.2	1	<0.001	-1.156 \pm 0.071
Species	0.6	1	n.s.	0.120 \pm 0.058 for Sandeels
Proportion robbed by other species				
Constant				-5.64 \pm 0.12
Prey length	4.5	1	<0.05	0.393 \pm 0.073
Species	0.3	1	n.s.	0.119 \pm 0.061 for Sandeels
Proportion rest				
Constant				-2.91 \pm 0.11
Prey length (BL)	23.8	1	<0.001	-0.714 \pm 0.072
Species	1.1	1	n.s.	-0.155 \pm 0.060 for Sandeels

sometimes robbed from freshly hatched chicks, were never taken from older chicks. This suggests that gulls selected the largest prey available at that moment, rather than showing a fixed threshold of prey size, above which they made attempts to steal a fish.

Adding the age of the chicks into a logistic regression model after inclusion of prey size and species had significant effects on the probability of prey consumption (Appendix 1). In Figure 2, the difference between the expected probability of prey consumption (obtained when average prey length for a specific age is entered into the logistic curve shown in Fig. 1) and observed prey consumption is plotted against the age of the chicks. It shows that, during the first few days after hatching, consumption probabilities of both prey species were lower than expected, reflecting the high food losses to causes other than kleptoparasitism by Black-headed Gulls. From days 5-15, Sandeels were consumed more often than expected, while con-

sumption probabilities of Herring fit the expected pattern. From day 15 onwards, Sandeels were consumed less often, while Herring was consumed more often than expected on the basis of average prey length. We do not know what mechanism underlies these patterns, but it might have something to do with either a learning process by the gulls, variation in food composition, or both.

Energy provisioning to each chick increased from 62 kJ chick⁻¹ day⁻¹ at hatching to about 300 kJ chick⁻¹ day⁻¹ near fledging (Fig. 2). During the first five days after hatching, about 74% of the energy which parents brought to the colony was consumed by the chicks, decreasing to about 55% near fledging. In the week before fledging, maximum energy intake amounted to 195 kJ chick⁻¹ day⁻¹.

Effects of Wind

The proportion of food consumed by the chicks decreased from about 74% at low wind speed (≤ 5 m s⁻¹) to about 68% at high

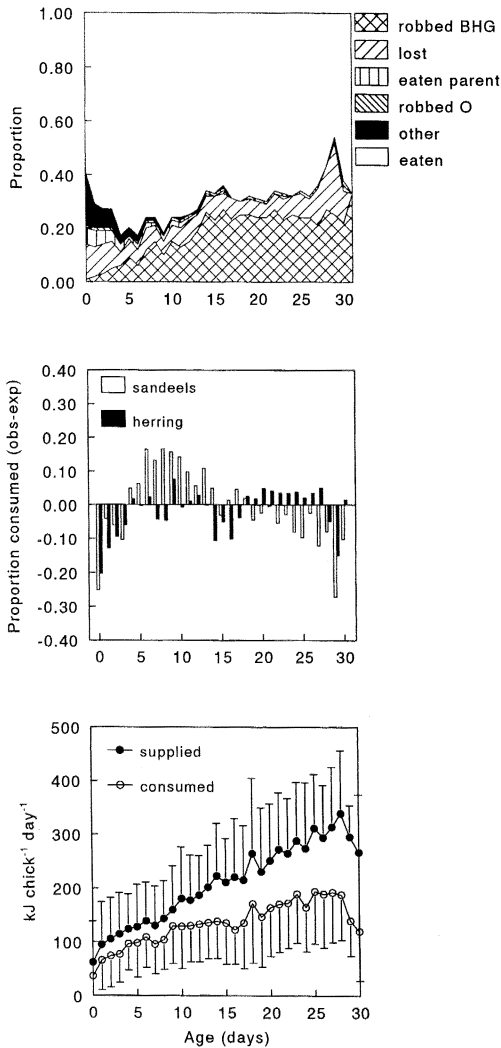


Figure 2. Top graph: fate of prey brought to the colony in relation to the age of the Sandwich Tern chicks on Griend in 1992-98. Middle graph: deviation from the expected pattern in prey consumption probabilities (i.e., observed prey consumption—consumption probability as expected from the observed prey length, see text) during the chick period. Bottom graph: the daily amount of energy brought to the colony and consumed by the tern chicks (mean ± SE) in relation to the age of the chicks. Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed O = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

wind speeds (>11 m s⁻¹; Fig. 4). This was mainly due to an increase in the proportion of food robbed by Black-headed Gulls, while the proportion of food lost out of view significantly decreased with increasing wind speed

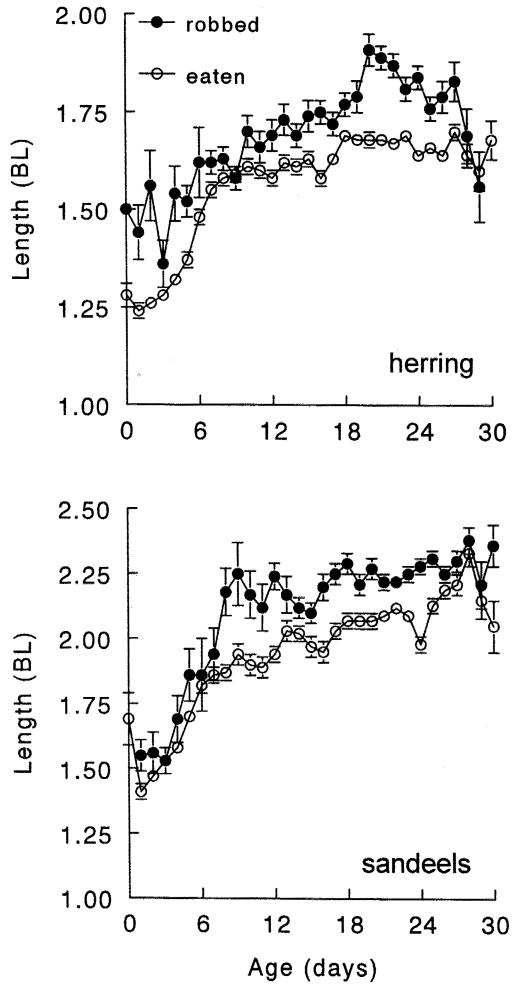


Figure 3. The length of the prey (mean ± SE) consumed by Sandwich Tern chicks on Griend in 1992-98 compared with the length of the prey (mean ± SE) lost to kleptoparasitising Black-headed Gulls in relation to the age of the chicks. BL = bill length of parent.

(Appendix 1). The decreasing proportion of food consumed by chicks with increasing wind speed is remarkable considering the decrease in prey length brought to the chicks (Stienen *et al.* 2000). The effect of wind speed on the consumption probability of a prey is even more pronounced after correcting for prey length (Fig. 4). At high wind speeds, the consumption of Sandeels was much lower than expected, while this effect was less pronounced in Herring (Fig. 4).

Wind speed had a strong effect on the amount of energy supplied to the chicks. Highest inputs were found with wind speed

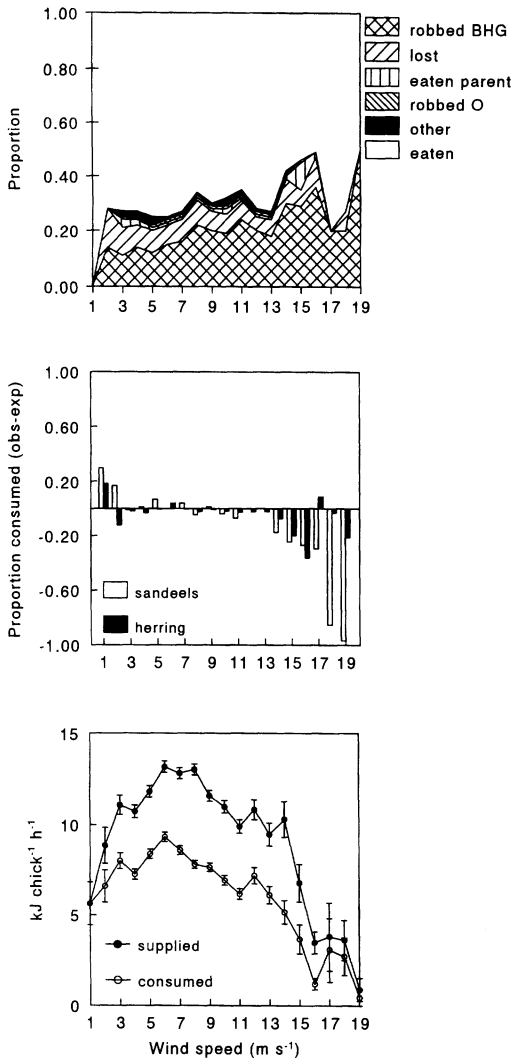


Figure 4. Top graph: the effect of wind speed on the fate of food brought to Sandwich Tern chicks on Griend in 1992-98. Middle graph: the deviation from the expected pattern in prey consumption probabilities (i.e., observed prey consumption—consumption probability as expected from the observed prey length, see text) in relation to wind speed. Bottom graph: the amount of energy brought to the colony and consumed by the chicks (mean \pm SE) in relation to wind speed. Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed O = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

around 7 m s^{-1} , while energy supply strongly decreased at speeds higher than 8 m s^{-1} (Fig. 4). At high wind speeds, the low transport rate coincided with high food losses, thus the energy intake rate of the chicks was severely affected.

Diel Pattern in Kleptoparasitism

During the first few hours of the day, almost all food brought to the colony was eaten by the chicks (Fig. 5). At that time, the gulls showed almost no interest in the fish brought to the colony. Until 09.00 h, robbing activity of the gulls increased, resulting in an increasing proportion of the food being robbed by the gulls and of the proportion of the food lost when out of view, and a decreasing proportion of the food being consumed by the chicks (Appendix 1). The highest losses were found around 09.00 h and at the end of the day. This typical bimodal pattern was found in all years, although the exact timing varied somewhat from year to year. Since prey length did not vary much during the day (Stienen *et al.* 2000), a correction for prey length gave almost identical results (Fig. 5).

Energy transport rate to the colony peaked around 06.00 h (Fig. 5). At that time, food loss to robbing gulls was still low, resulting in high energy intake rates by the chicks. In contrast, the peak in energy transport at the end of the day coincided with high proportions of food loss, so that no peak in energy intake rate was found at the end of the day. Energy intake rate of chicks was lowest around 09.00 h, when low rates of food transport coincided with high proportions of food loss.

Tidal Effects

Tidal influences on the probability of food consumption were significant (Appendix 1), but the effect was much smaller than the effect of chick age, wind speed and time of day. Relatively high proportions of food loss were found near high water (Fig. 6). At that time, Sandeels brought to the colony were relatively long (Stienen *et al.* 2000), which to some extent might explain the high rates of kleptoparasitism. When prey length was taken into account, food loss of both Sandeels and Herring was somewhat higher than expected at high tide (Fig. 6). The high rate of food loss around high tide coincided with a peak in energy transport to the colony, so that energy intake rate of the chicks showed only small fluctuations during the tidal cycle (Fig. 6).

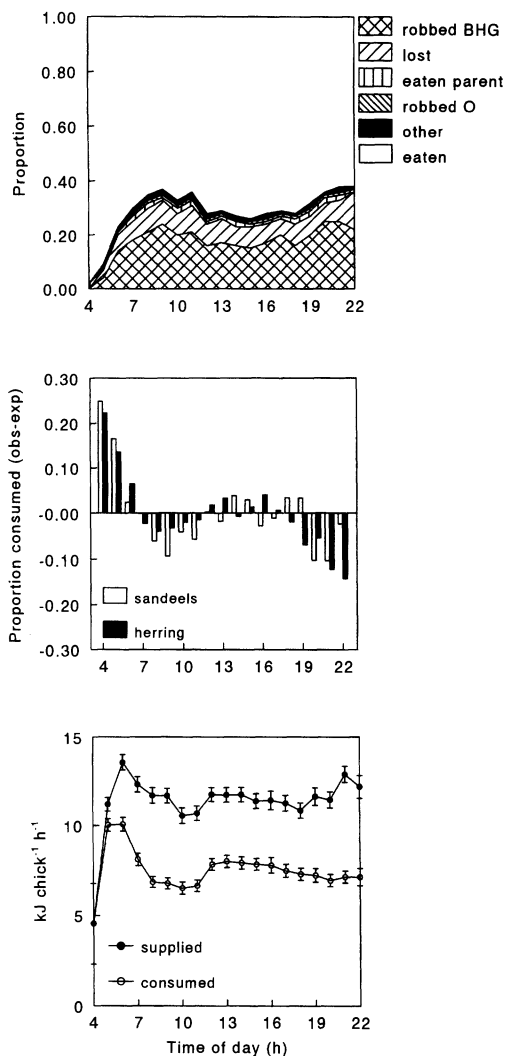


Figure 5. Top graph: variation in the fate of the prey brought to the colony during the course of the day. Middle graph: the deviation from the expected diel pattern in prey consumption probabilities (i.e., observed prey consumption—consumption probability as expected from the observed prey length, see text). Bottom graph: fluctuations in the amount of energy brought to the colony and consumed by the tern chicks (mean ± SE) during the day. Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed O = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

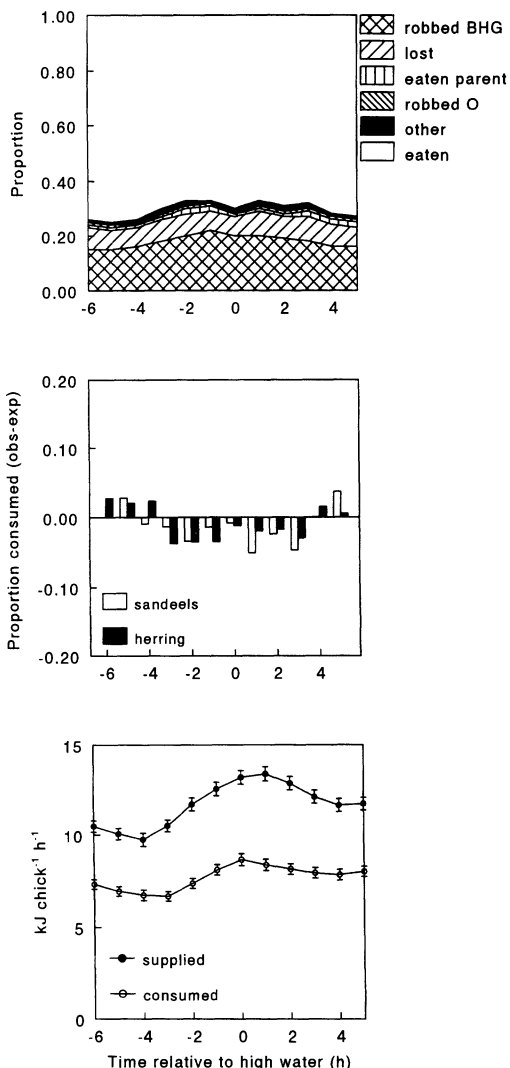


Figure 6. Upper graph: tidal effects on the fate of the prey supplied to the colony. Middle graph: the deviation from the expected pattern in prey consumption probability (i.e., observed prey consumption—consumption probability as expected from the observed prey length, see text) during a tidal cycle. Lower graph: tidal influence on the amount of energy brought to the colony and consumed by the chicks (mean ± SE). Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed O = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

Effects on Chick Growth

In this paragraph, we will analyze to what extent food losses influence body mass growth of the chicks. Also, the effects of wind speed are included in the analyses, as wind

speed has strong effects on both the amount of food brought to chicks and the proportion of food actually consumed by chicks. In all years, most of the fluctuations in chick condition closely followed the fluctuations in wind speed (Fig. 7). With strong winds,

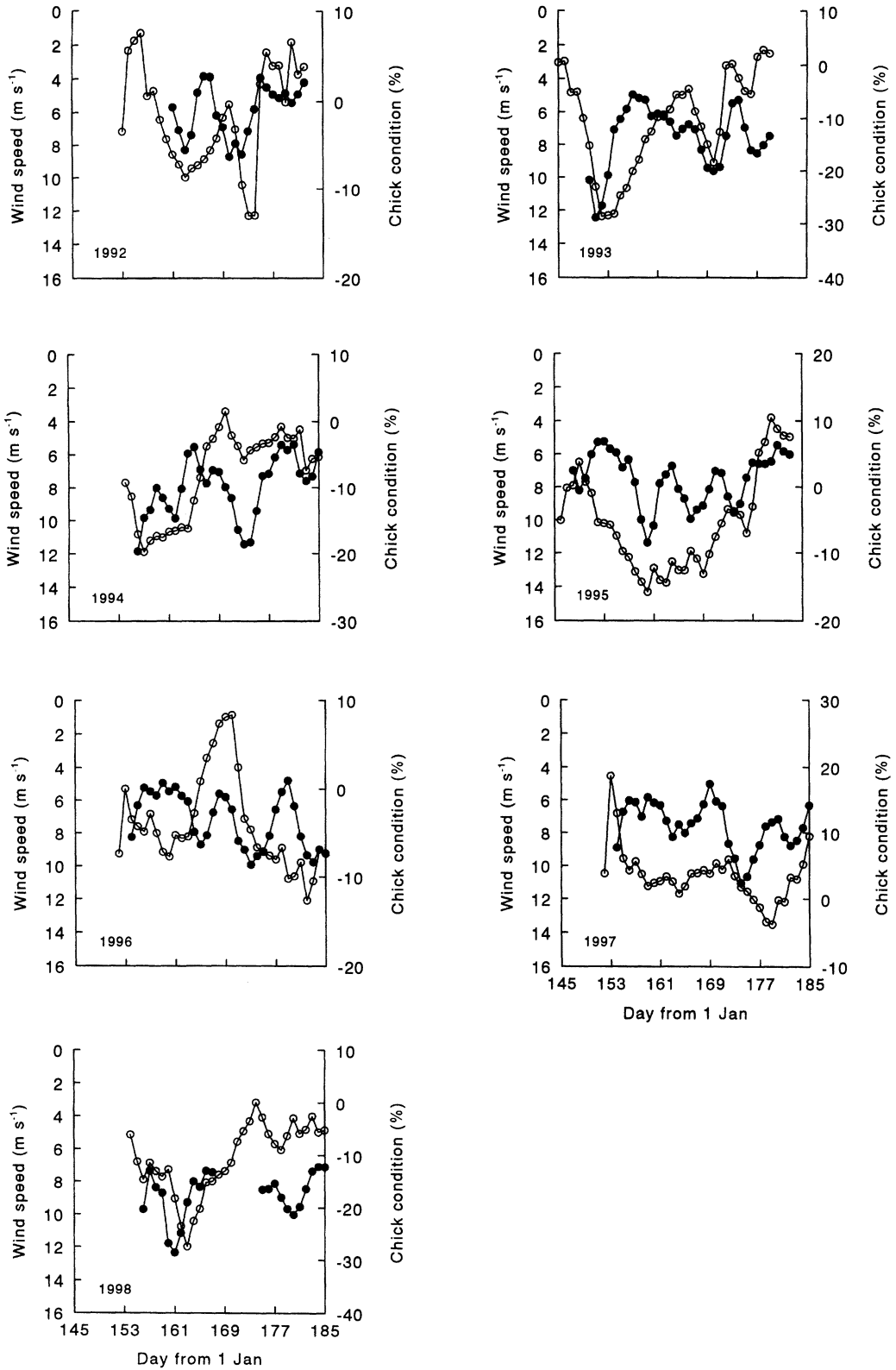


Figure 7. Development of the condition of Sandwich Tern chicks (dots, right axis) on Griend in 1992-98 in relation to wind speed (circles, left axis).

the average condition of the chicks rapidly decreased, but when weather conditions improved, body condition of surviving chicks increased again.

To investigate to what extent the loss of food to Black-headed Gulls affected growth of the tern chicks, a curve was fitted describing body mass growth in relation to the age of the chicks and daily gross energy intake:

$$\text{GR} = 8.07 \pm 0.59 - 0.32 \pm 0.09 * \text{age} - 0.0040 \pm 0.0030 * \text{age}^2 + 0.024 \pm 0.0020 * \text{GEI}$$

(N = 1,093 chick measurements, $R^2 = 0.28$, $F_{3,1090} = 152$, $P < 0.001$),

where GR is the daily growth of a chick (g day^{-1}), age is the age of the chick in days and GEI is the daily gross energy intake rate (kJ day^{-1}).

Subsequently, the effects of wind speed on energy transport to the colony and energy intake rate of the chicks were computed:

$$\text{GET} = 66.3 \pm 20.1 + 7.42 \pm 0.28 * \text{age} + 16.36 \pm 5.04 * \text{wind speed} - 1.30 \pm 0.30 * \text{windspeed}^2$$

(N = 1,583, $R^2 = 0.33$, $F_{3,1579} = 287$, $P < 0.001$)

$$\text{GEI} = 88.5 \pm 16.5 + 4.01 \pm 0.22 * \text{age} + 5.24 \pm 4.16 * \text{wind speed} - 0.70 \pm 0.25 * \text{wind speed}^2$$

(N = 1,583, $R^2 = 0.19$, $F_{3,1579} = 124$, $P < 0.001$),

where GET is the daily amount of energy transported to a chick (kJ day^{-1}), GEI is the daily amount of energy consumed by a chick (kJ day^{-1}), age is the age of the chick in days and wind speed is the average daily wind speed (m s^{-1}).

Using these formulae, we computed two estimates of chick growth, namely:

- 1) Assuming that all food transported to the chick was actually eaten by the chick, and
- 2) When food loss (i.e., all food that is not consumed by the chick) is taken into account.

Furthermore, we modeled growth in calm and in windy weather conditions (wind speed 5 m s^{-1} and 15 m s^{-1} , respectively). Second hatched chicks were omitted from this exercise and maximum body mass growth was set at 13 g day^{-1} (i.e., maximum growth rate recorded in the laboratory; Klaassen *et al.* 1992). The results are shown in Figure 8.

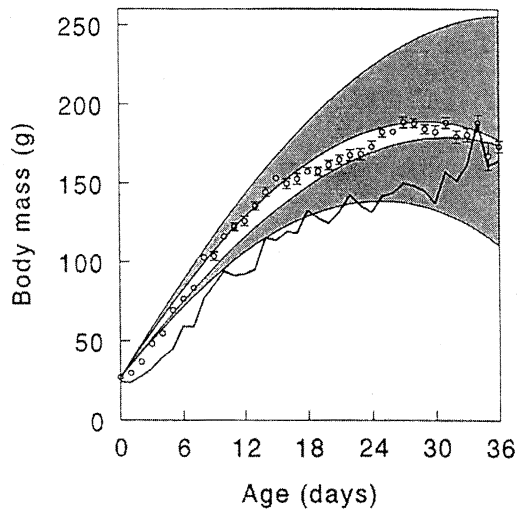


Figure 8. Body mass growth (circles, mean \pm SE) of first-hatched and single Sandwich Tern chicks on Griend in 1992-98. The line represents the average of the five lowest measurements of body mass of surviving chicks (i.e., chicks which reached an age of at least 25 days). The two shaded areas show a model of body mass growth that incorporates effects of kleptoparasitism and wind speed (see text). The upper shaded area encloses the maximum body mass growth (i.e., assuming that all food brought to the colony is actually consumed by the chicks) and normal body mass growth (i.e., accounting for prey losses) under favourable weather conditions (i.e., wind speed 5 m s^{-1}); the lower shaded area encloses the maximum and minimum body mass growth of the chicks under stormy weather conditions (i.e., wind speed 15 m s^{-1}).

Under favourable weather conditions and in the absence of Black-headed Gulls, the chicks would theoretically reach a maximum body mass of 256 g at day 36. If, however, food loss is taken into account, maximum body mass would be reached when the chicks are 29 days old, but maximum body mass would be 186 g, a decrease of 27% compared with the situation without food loss. The prediction of growth under these conditions (wind speed = 5 m s^{-1} and accounting for food loss) closely follows the observed growth of the chicks (Fig. 8). This is not surprising, since during our study the wind speed averaged $7.7 \pm 2.4 \text{ m s}^{-1}$, close to 5 m s^{-1} used in the model. Under persistent windy conditions (wind speed 15 m s^{-1}) maximum body mass would be 179 g at day 31, assuming that all food brought to the colony is actually consumed by the chicks. However, since kleptoparasitism is high under stormy conditions,

growth would cease at day 25. At that time, maximum body mass would be only 139 g, which is below the body mass of the four slowest growing chicks Klaassen *et al.* (1992) raised in the laboratory under a restricted food regime. Also, it is close to the minimum body mass of surviving chicks on Griend (Fig. 8). The model further predicts that chicks older than 25 days would quickly lose weight under stormy conditions and would fall behind the minimum body mass recorded on Griend. Adverse wind conditions affect chick growth during the first two weeks post-hatching, but the effects are not disastrous for the average chick. Even when strong winds blow for a long period, most first hatchlings would survive the first two weeks after hatching. However, for chicks older than 25 days, such conditions would seriously affect growth and the chicks would starve to death.

DISCUSSION

In the first two weeks after hatching, food loss to Black-headed Gulls was low and had no major effects on the growth of Sandwich Tern chicks. From two weeks old, the length of the prey brought to the tern chicks was at a maximum and kleptoparasitism was high. At this time, the effects of kleptoparasitism on the growth of Sandwich Tern chicks can be considerable. However, chick mortality can be very high in the first week after hatching (Langham 1974; Stienen and Brenninkmeijer, in press a). This reflects a high mortality of second hatched chicks, as they receive almost no food from their parents (Stienen *et al.* 2000). The peak in mortality of first hatchlings between day 20-24 as observed on Griend (E. Stienen and A. Brenninkmeijer, unpublished data) probably is a combined effect of peak energy demands being reached (Klaassen *et al.* 1992) and high rates of kleptoparasitism. At that time, some subcolonies of Sandwich Terns on Griend become almost totally deserted, as parents lure their chicks to other sites on the island. Stienen and Brenninkmeijer (1999) argued that leaving the colony site could be an evasive behavior to avoid high prey losses to the gulls and to improve the chicks' survival chances. Leaving

the colony site to avoid kleptoparasitism by the neighboring gulls becomes even more important during windy weather, when food transport to the colony is low. If under such conditions, the terns cannot avoid the kleptoparasitising gulls (in the current study because the chicks were enclosed or in natural situations because the subcolony is surrounded by thick vegetation), growth is severely curtailed and can even become negative. Nevertheless, tern chicks have wide margins within which they can survive (Klaassen *et al.* 1992; E. Stienen and A. Brenninkmeijer, unpublished data) and only when a long lasting period of windy weather occurred was large scale chick mortality observed (Veen 1977). Dunn (1975) did not find any effects of wind speed on the body mass growth of Sandwich Tern chicks. However, Dunn's study (1975) covered wind speeds ranging from 0.9 m.s⁻¹, while the adverse effect of wind on the energy intake of chicks only become obvious at higher wind speeds. Also, the number of Black-headed Gulls nesting on Coquet Island, where Dunn (1975) did his study, were much lower than on Griend, and kleptoparasitism might have been accordingly low.

Economics of Black-headed Gulls

In the present study, we found that the loss of food positively correlated with the length of the prey supplied to the chicks. As the gross energy content of fish exponentially increases with its length, larger fish are far more profitable for the gulls than small ones. Several studies show that both the chance of being attacked by pirating gulls and the probability of losing a fish to them increases with the length of the fish (Hopkins and Wiley 1972; Hulsman 1976; Ratcliffe *et al.* 1997), although very large fish are sometimes avoided by kleptoparasites (Dunn 1972). Such increase would be expected if the pirates prefer larger and therefore more profitable prey or if larger prey simply are more conspicuous to kleptoparasites. However, in contrast to what we might expect from economic reasoning, prey length was a better predictor of the rate of prey loss than the energy content of the prey.

Herring of a specific size were robbed as often as Sandeels of the same length, whereas Herring has a much higher energy content (Stienen and Brenninkmeijer, in press). Assuming that robbing success does not depend on prey length (but see Dunn 1972), this finding suggests that Black-headed Gulls selected for prey length or visibility of the prey rather than for energy content of the prey. Similar results were found in a Sandwich Tern colony at the Sands of Forvie (Scotland), where Black-headed Gulls selected terns carrying large Sandeels, but virtually ignored birds carrying shorter, but more profitable gadoids or clupeids (Fuchs 1977).

Patterns in Kleptoparasitism

Dunn (1973) showed that the robbing intensity of Roseate Terns *Sterna dougallii* increases with the number of hosts present at a certain moment. In contrast, in interactions between Sandwich Terns and Black-headed Gulls, there seems to be no relationship between the number of host terns and the rate of kleptoparasitism. In the early morning, the pirating gulls, although present, showed no interest in the potential food resource provided by the terns. Furthermore, food supply peaked around 06.00 h, while the rate of food loss was highest three hours later. Moreover, the variation in diet composition during the day did not provide an explanation for the observed diel pattern in kleptoparasitism. The proportion of Herring in the diet is high during the crepuscular hours and relatively low around 12.00 h (Stienen *et al.* 2000). Since the relatively short Herring are subjected less to kleptoparasitism, one would expect food piracy to be highest just before noon and then gradually decreasing towards dusk, which was not the case. Light conditions can be excluded as a factor determining the diel pattern in kleptoparasitism, because although the incidence of robbery was low in the early morning, it was relatively high at dusk. Apparently other factors are important. From an energetic point of view, it might be expected that kleptoparasitism would be especially high during the first hours after sunrise. After a night without

food, the hunger of the gull chicks would urge the parents to get sufficient food and thus one may expect an increased intensity of food piracy in the early morning. On the other hand, if gull parents start to search for food at sea, kleptoparasitism would be particularly low in the early morning. There are, however, specialists and occasional pirates among the gulls (Veen 1977; Gorke 1990). The number of specialized pirates is relatively low and their activity tends to be constant during the course of the day (Veen 1977). The number of occasional pirates, however, greatly outnumber the specialists, and their presence in the colony can greatly vary during the day (Veen 1977). Only when occasional pirates cannot find sufficient food elsewhere, they visit the ternery to rob the terns (Veen 1977; Monaghan *et al.* 1989; Oro 1996). The diurnal pattern in foraging activity of Black-headed Gulls shows a bimodal pattern, with most activity in the early morning and in the late afternoon (Glutz von Blotzheim and Bauer 1982), which might explain the typical pattern in kleptoparasitism. Veen (1977) also found that the number of fish-stealing Black-headed Gulls present in the tern colony varied with the state of the tide. During high tide, when the main feeding grounds of the gulls are out of reach and foraging activity of the gulls is low (Gorke 1990), the number of pirating gulls present in the colony is relatively high (Veen 1977). As a result, we found a high rate of kleptoparasitism around high tide. Kleptoparasitism decreased towards low tide, when the gulls resume feeding on the tidal flats. Weather conditions may influence the robbing behavior of the gulls in the same way. With strong winds the mud flats are less exposed during low tide and moreover, the gulls may have difficulties while searching for food in flight. So the high rates of food loss with strong winds probably result from high numbers of occasional pirates present in the tern colony.

Adaptive Strategies against Kleptoparasites

Birds that are victims of kleptoparasites have adopted several behavioral strategies to reduce food loss. Barnard (1984) distin-

guishes three forms of behavioral strategies against kleptoparasites, namely retaliation, evasion and increased effort. Probably the most obvious thing to do when suffering from high rates of kleptoparasitism is simply to avoid the pirates. As mentioned, Sandwich Terns appear to lure their chicks away from the robbing gulls. In this way, the terns can improve food intake, resulting in faster growth and improved survival of the chicks (Stienen and Brenninkmeijer 1999). When Sandwich Terns are not able to escape from the gulls, the birds have other strategies to reduce the impact of pirating gulls. A common strategy is for a parent to mask a feeding event by forming a shield around the chick with its wings, while the partner feeds the youngster. Some tern parents have developed an uncommon strategy to diminish the chance of robbery and, unlike most Sandwich Terns, they hold the fish longitudinally in the bill, almost invisible to the gulls. Retaliation is sometimes practiced by Sandwich Terns, but the effectiveness of this behavior is low. Another way to diminish kleptoparasitism would be to shift towards a Herring dominated diet, as this prey species is less vulnerable to kleptoparasitism than sandeels. However, in most years, parents did not supply more Herring with increasing age of the chicks (Stienen and Brenninkmeijer, in press b), suggesting that the availability of this prey species is limited. Instead, the parents compensated for the prey losses by increasing their foraging effort. So by adopting a wide range of behavioral strategies Sandwich Terns are usually able to live with the kleptoparasitising gulls, from which anti-predator behavior they benefit during the egg and early chick stage.

ACKNOWLEDGMENTS

We like to thank all the persons who helped gathering the data for this paper. Especially, Teun Baarspul, Peter van Beers, John Habraken, Maaike Raaijmakers and Piet van Tienen spent many hours in a hide, watching how the precious fish were robbed from the terns. Logistic support was provided by the crew members of 'het Griltje' and the 'Phoca', and the 'Rijkspolitie te water, Harlingen'. Rudi Drent, Arie Spaans and Jan Veen made valuable comments on an earlier draft of this paper. Further Dr. J. C. Coulson and two anonymous referees commented on the manuscript.

LITERATURE CITED

- Barnard, C. J. 1984. The evolution of food-scrounging strategies within and between species. Pages 95-126 in *Producers and scroungers: strategies of exploitation and parasitism* (C. J. Barnard, Ed.). Croom Helm, London.
- Brockmann, H. J. and C. J. Barnard. 1979. Kleptoparasitism in birds. *Animal Behaviour* 27: 487-514.
- Dunn, E. K. 1972. Studies on terns, with particular reference to feeding ecology. Unpublished Ph. D. Thesis, Durham University, Durham.
- Dunn, E. K. 1973. Changes in fishing ability of terns associated with windspeed and sea surface conditions. *Nature* 244: 520-521.
- Dunn, E. K. 1973. Robbing behavior of Roseate Terns. *Auk* 90: 641-651.
- Dunn, E. K. 1975. The rôle of environmental factors in the growth of tern chicks. *Journal of Animal Ecology* 44: 743-754.
- Fuchs, E. 1977. Kleptoparasitism of Sandwich Terns *Sterna sandvicensis* by Black-headed Gulls *Larus ridibundus*. *Ibis* 119: 183-190.
- Furness, R. W. 1987. Kleptoparasitism in seabirds. Pages 77-100 in *Seabirds feeding ecology and the role in marine ecosystems* (J. P. Croxall, Ed.). Cambridge University Press, Cambridge.
- Genstat 5 Committee. 1993. *Genstat 5 Reference Manual*. Clarendon Press, Oxford.
- Glutz von Blothheim, U. N. and K. M. Bauer. 1982. *Handbuch der Vögel Mitteleuropas. Band 8/2: Charadriiformes III*. Akademische Verlagsgesellschaft, Wiesbaden.
- Gorke, M. 1990. Die Lachmöwe (*Larus ridibundus*) in Wattenmeer und Binnenland. *Seevögel* 11: 1-48.
- Hopkins, C. D. and R. H. Wiley 1972. Food parasitism and competition in two terns. *Auk* 89: 583-594.
- Hulsman, K. 1976. The robbing behaviour of terns and gulls. *Emu* 76: 143-149.
- Klaassen, M., B. Zwaan, P. Heslenfeld, P. Lucas and B. Luijckx. 1992. Growth rate associated changes in the energy requirements of tern chicks. *Ardea* 80: 19-28.
- Langham, N. P. E. 1974. Comparative breeding biology of the Sandwich Tern. *Auk* 91: 255-277.
- Lind, H. 1963. Nogle sociale reaktioner hos ternene. *Dansk Ornithologisk Forenings Tidsskrift* 57: 155-175.
- Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine and J. Blackwood. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. *Journal of Animal Ecology* 58: 261-274.
- Norušis, M. J. 1990. *SPSS/PC+ 4.0. Base Manual*. SPSS, Chicago.
- Oro, D. 1996. Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. *Ibis* 138: 218-221.
- Ratcliffe, N., D. Richardson, R. Lidstone 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.
- 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 sandvicensis*. *Ardea* 88: 33-49.
- Stienen, E. W. M. and A. Brenninkmeijer. In press. Foraging decisions of Sandwich Terns in the presence of kleptoparasitising gulls. *Auk*.
- Taylor, I. R. 1983. Effect of wind on foraging behaviour of Common and Sandwich Terns. *Ornis Scandinavica* 14: 90-96.
- 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.

Appendix 1. Estimates of coefficients (\pm SE) of a logistic regression analysis examining the effects of prey length (in adult bill length units), prey species (2 levels), chick age, wind speed, time of day, tide (12 levels) and year of observation (7 levels) on the fate of the fish brought to the tern chicks on Griend (N = 16,650). Estimates are printed bold if the added effect of a variable resulted in a significant change in deviance ($P < 0.05$). In cases of significant factor-variables (prey species, tide and year) estimates are printed bold for all levels. Robbed other sp. = robbed by species other than Black-headed Gulls, age² = quadratic function of age, wind speed² = quadratic function of wind speed, etc.

Variable	Fate of the fish
	Eaten by chick ($R^2 = 0.08$)
Constant	16.4 \pm 1.03
Prey length	-1.60 \pm 0.068
Prey species for <i>Sandeels</i>	0.19 \pm 0.052
Age	0.065 \pm 0.011
Age ²	-0.0020 \pm 0.0004
Wind speed	-0.0045 \pm 0.034
Wind speed ²	-0.00264 \pm 0.00205
Time of day	-3.99 \pm 0.36
Time of day ²	0.45 \pm 0.044
Time of day ³	-0.021 \pm 0.0023
Time of day ⁴	0.00035 \pm 0.00004
Tide	
for tidal hour -5	0.071 \pm 0.10
for tidal hour -4	0.015 \pm 0.10
for tidal hour -3	-0.15 \pm 0.10
for tidal hour -2	-0.25 \pm 0.10
for tidal hour -1	-0.22 \pm 0.093
for tidal hour 0	-0.16 \pm 0.094
for tidal hour 1	-0.32 \pm 0.094
for tidal hour 2	-0.29 \pm 0.10
for tidal hour 3	-0.36 \pm 0.10
for tidal hour 4	-0.14 \pm 0.10
for tidal hour 5	-0.019 \pm 0.10
Year	
for 1993	-0.65 \pm 0.13
for 1994	-0.77 \pm 0.13
for 1995	0.17 \pm 0.15
for 1996	-0.87 \pm 0.13
for 1997	-0.66 \pm 0.13
for 1998	-0.79 \pm 0.14