



# Keep the chicks moving: how Sandwich terns can minimize kleptoparasitism by black-headed gulls

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(Received 6 October 1998; initial acceptance 16 November 1998;  
final acceptance 25 December 1998; MS. number: 6013)

Sandwich terns, *Sterna sandvicensis*, often nest in association with black-headed gulls, *Larus ridibundus*. The gulls provide protection against predators, but can also adversely affect the terns' reproductive success through predation and piracy of fish. To test whether leading the chicks away from the nest site is an evasive strategy used by the parents to reduce the incidence of robbery by the gulls, we kept one group of Sandwich tern chicks at their original breeding site, while, with a wire-netting enclosure, we moved another group away from the gulls. The rate of kleptoparasitism was greatly reduced when the tern chicks were moved away from the original nest site, resulting in faster growth and earlier fledging. The rate of food parasitism and chick condition were affected only during the first 5 days of the experiment. After that, the rate of kleptoparasitism no longer differed between chicks that we moved away and those remaining in the colony. A second shift of the chicks again led to less kleptoparasitism and better chick condition. In line with these findings, the condition of free-living chicks that were lured away from their nesting site by their parents also improved. In particular, chicks initially in poor condition, which apparently suffered from high rates of kleptoparasitism, left the colony site. Free-living chicks are often lured away from the robbing gulls. However, not all subcolonies provided suitable escape routes and subsequently chicks in such subcolonies suffered from high mortality rates.

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Kleptoparasitism, the stealing of already-procured food by other conspecific or heterospecific individuals, is widespread among birds (Brockmann & Barnard 1979). It often occurs among seabirds as they are generally colonial nesters and also highly aggregated when foraging (Furness 1987). Terns are especially vulnerable to kleptoparasitism. In contrast to many gulls, the majority of tern species do not swallow the fish after catching it but hold it visible in the bill when transporting it to the colony. Many studies report that terns are victims of kleptoparasitic behaviour of gulls or other terns (e.g. Hopkins & Wiley 1972; Hatch 1975; Hulsman 1976; Taylor 1979). Birds have adopted several behavioural strategies to reduce food loss through kleptoparasitism (Barnard 1984), such as retaliation or evasion. They may also tolerate losses or compensate for them by increasing their foraging effort. Evasion, the avoidance of attacks, is probably the most frequent strategy adopted and includes faster handling of prey, shifting the diet, synchronizing feeding activities and increasing the distance from the

pirates (Amat 1990). To our knowledge these behavioural strategies have not yet been reported for terns.

Sandwich terns, *Sterna sandvicensis*, almost exclusively breed together with other tern species or close to gulls (e.g. Ansingh et al. 1960; Langham 1974; Gorke 1990; Fasola & Canova 1992; Yorio & Quintana 1997). In The Netherlands they always breed in association with black-headed gulls, *Larus ridibundus* (review in Veen 1977). By seeking the proximity of the gulls, the terns benefit from the aggressive antipredator behaviour of their neighbours. Gulls actively chase away avian predators and act as a buffer against ground predators (Veen 1977). However, breeding together with black-headed gulls also involves disadvantages for the terns. The gulls themselves are important predators of tern eggs and chicks, and steal fish the parents bring to their chicks (Lind 1963; Fuchs 1977a, b; Veen 1977; Gorke 1990; Ratcliffe et al. 1997). It is generally assumed that the advantages of associative nesting outweigh the disadvantages (Lind 1963; Veen 1977). This assumption, however, is based mainly on findings during incubation and the onset of the chick-rearing period, whereas the advantages of associative nesting become less important with increasing age of the chicks. The main chick predators (black-headed gull,

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herring gull, *L. argentatus*, and lesser and great black-backed gulls, *L. fuscus* and *L. marinus*) prefer chicks of up to 2 weeks old, whereas larger chicks are much less subject to predation (Veen 1977). Thus with increasing size of the chicks there is less need to stay within the protection of the black-headed gulls. In fact, it is known that Sandwich tern parents often lead their chicks away from the nesting site (Cullen 1958; Chestney 1970; Veen 1977), which is often interpreted as a result of human disturbance (Chestney 1970; Campredon 1978) or as a mechanism to avoid infectious diseases (Cullen 1958). However, it could also be a mechanism to avoid piracy by the neighbouring gulls. Kleptoparasitism can remove a considerable part of the food brought to the chicks and can therefore have serious consequences for their daily food intake. Kleptoparasitism may thus impair the chicks' growth rate and survival. We hypothesize that leading the chicks away from the gull colonies reduces kleptoparasitism, resulting in increased growth and survival of the tern chicks. To test this hypothesis, we kept one group of Sandwich tern chicks at their original breeding site, while another group was moved away from the colony. We then compared the growth rates of these groups and free-living chicks.

## METHODS

### Study Area, Colony Structure and Meteorological Measurements

We conducted the study on the Isle of Griend, The Netherlands (53°15'N, 5°15'W) in the Dutch Wadden Sea. Griend harbours the largest colony of nesting Sandwich terns in Europe (8200 and 5600 breeding pairs in 1995 and 1996, respectively). In 1995 and 1996, the breeding population at Griend consisted of a number of subcolonies, varying in size between 140 and 1590 breeding pairs. Subcolonies were separated from each other by 25–200 m. Within a subcolony the onset of laying was highly synchronized, although some pairs settled in the colony at a later stage. Subcolonies of terns were at least partly surrounded by nesting black-headed gulls and some gulls even nested within the tern colony.

Throughout the experimental work we recorded wind speed with a calibrated cup anemometer placed within 500 m of the colony at standard meteorological level (10 m). We also recorded air temperature and rainfall, but only wind speed is considered here since this parameter is known to influence the rate of kleptoparasitism (Veen 1977).

### Enclosures

In 1995 and 1996, we enclosed a small part of a colony, containing ca. 100 clutches, using wire netting 50 cm high. The lower 20 cm of the wire netting was covered with black plastic, to avoid injuries to the chicks' bills. In 1995, about 2 weeks after they hatched we transported nine chicks from the initial enclosure (from now on called the permanent enclosure) to an enclosure placed 50 m from the original colony site (from now on called

the moved enclosure). The remaining chicks were held in the permanent enclosure. At first, some parents had difficulties finding their chicks again in the moved enclosure, but within a few hours all but three pairs had found their chick. The three lost chicks were replaced on their original site, leaving six chicks in the moved enclosure. In 1996, the enclosure was moved stepwise to resemble more closely the natural situation in which chicks may constantly be lured away to new sites on the island. As an added advantage, it was easier for the parents to find the displaced chicks. At first the enclosure was placed 15 m from the original colony. This time all 15 pairs found their chick within a few hours. Seven days later the moved enclosure was moved 25 m further away. The direction in which the chicks were moved corresponded with the main direction in which free-living chicks moved. This was always away from the black-headed gull colony.

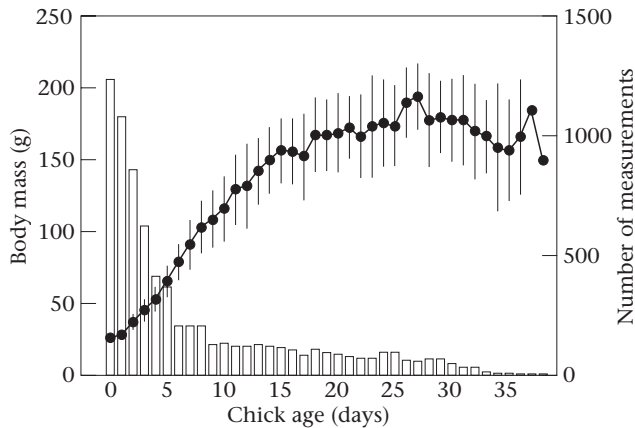
### Observation on Food Supply and Kleptoparasitism

Observations on food supply were made by the unaided eye or with binoculars (up to 10 × magnification) from a hide several metres from the enclosure. The observations were restricted to the hours around high tide. To facilitate individual recognition within the permanent enclosures, we colour marked 19 chicks in 1995, and 20 chicks in 1996, using picric acid and ink. Within the moved enclosures chick recognition was possible by individual differences in size or plumage characteristics and by location within the enclosure. We classified the fate of fish brought to the chicks as 'eaten by the chick', 'robbed by black-headed gulls' and 'other causes of loss' (such as lost from the observer's sight, rejected by the chick, left in the nest or eaten by the parent). Whenever possible, we noted the time between the arrival of a parent in the colony and the feeding of the fish. In 1996, we recorded the numbers of black-headed gulls participating in a robbery incident.

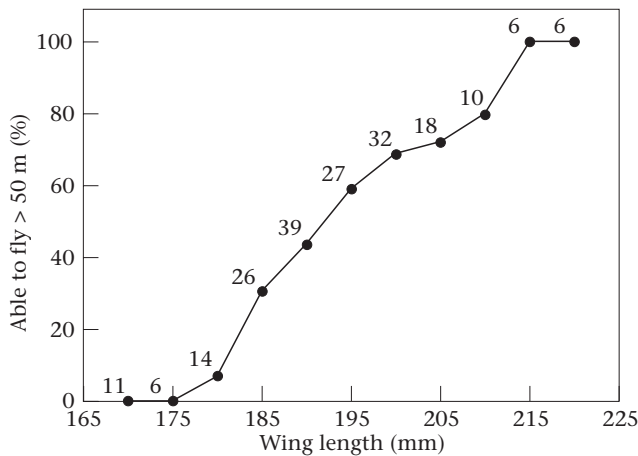
### Growth

All chicks within the enclosures were banded within 3 days of hatching. We estimated the age at ringing from the size of the yolk sac, the size of the head and plumage characteristics as a reference. Every third day (when weather permitted) the chicks were weighed to the nearest gram, and total head size (head+bill, ± 0.1 mm) and stretched wing chord (± 1 mm) were measured. Body mass on days between two measurements was computed assuming linear growth. We obtained a condition index (CI, %) by calculating the deviation of the measured body mass ( $M$ , g) from the expected body mass ( $M_{\text{exp}}$ , g) for that age (based on the mean body mass of all chicks of known age, both within and outside the enclosures, measured in 1995 and 1996; Fig. 1):

$$CI = \frac{M - M_{\text{exp}}}{M_{\text{exp}}} \times 100\% \quad (1)$$



**Figure 1.** Increase in body mass (●;  $\bar{X} \pm \text{SD}$ ) of tern chicks in 1995–1996. Bars denote the number of measurements.



**Figure 2.** Relationship between wing length and flight ability of tern chicks (●). The number of chicks processed is shown for each point.

The age of nonenclosed chicks was often unknown, which made it impossible to compute their condition index from equation (1). Therefore, we calculated an alternative condition index ( $CI^h$ ), using the mean body mass at a certain head size (instead of age) for expected body mass ( $M_{\text{exp}}$ , g). Although deviations between these two measurements of condition index were sometimes large, there was a reasonable relationship between them (Pearson regression:  $r^2=0.537$ ,  $N=289$ ,  $P<0.001$ ).  $CI^h$  was computed for chicks with heads larger than 60 mm (i.e. approximately 11 days old) as kleptoparasitism becomes obvious only when chicks are older than 10 days (unpublished data).

To calculate age at fledging, we used data collected in 1992–1996 at Griend on flight capacity of chicks in relation to wing length (Fig. 2). Fledging was defined as being able to stay in the air for at least 50 m. For convenience, we defined fledging age as the first day when wing length exceeded 200 mm, and we calculated it assuming linear growth between the last two measurements. When wing length at the last measurement did not exceed 200 mm, the last recorded growth rate was extrapolated until wing length exceeded 200 mm ( $N=50$

chicks). The latter was done only when wing length already exceeded 175 mm. With these restrictions, fledging age of one chick in the moved enclosure in 1996 could not be estimated.

## Data Analysis and Statistics

Data analysis and all statistical tests, except for multiple and logistic regression analysis, were performed using the SPSS/PC+ 4.0 statistical package (Norušis 1990). Multiple and logistic regression analyses were performed using the Genstat statistical package (Genstat 5 Committee 1993). Daily wind speed was defined as the average wind speed during the daylight period (0400–2200 hours). Each observation bout lasted approximately 3 h during which food supply (number of fish/chick per h) was calculated. Sample sizes in this respect refer to the number of chicks. Unless stated otherwise, means are shown  $\pm$  SD.

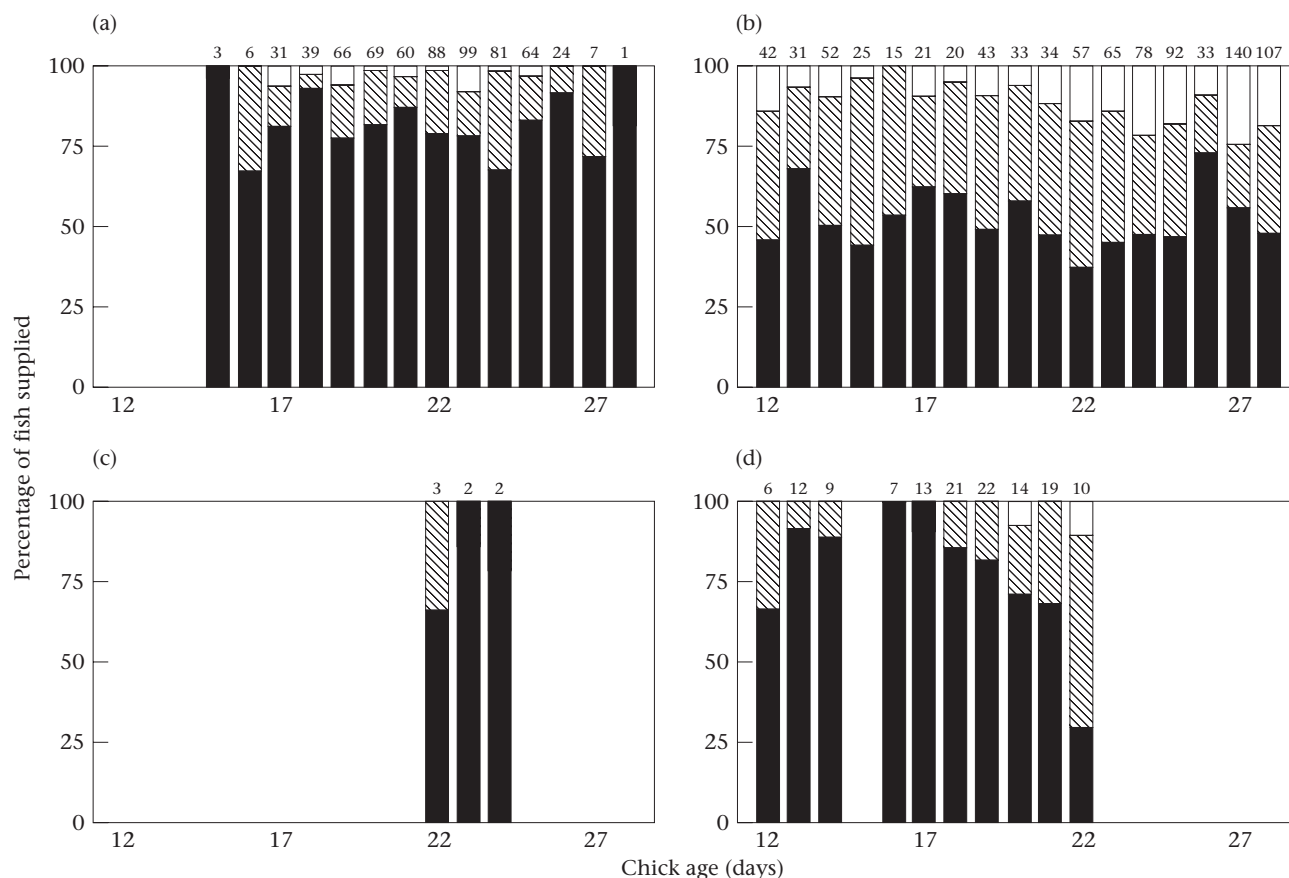
## Ethical Note

All manipulations were conducted with permission of the Dutch Ministry of Agriculture, Nature Conservation and Fisheries in The Netherlands. The chicks under study were handled carefully and their condition monitored every third day. None of the moved chicks, including those returned to the permanent enclosure, was deserted by its parents.

## RESULTS

We recorded the fate of 1701 fish brought to the colony. Of these fish 64.4% were eaten by the chicks, 25.8% were robbed by black-headed gulls and 9.8% were lost in other ways. In 1995, the number of fish supplied to the chicks did not differ from that in 1996 ( $0.60 \pm 0.29$  fish/chick per h,  $N=167$  and  $0.61 \pm 0.29$  fish/chick per h,  $N=325$ , respectively; Student's  $t$  test:  $t_{490}=0.83$ , NS). In 1995, both in the permanent and in the moved enclosure 67–100% of the supplied fish were eaten by the chicks (Fig. 3). In 1996, these figures were much lower and ranged from 44 to 73% in the permanent enclosure and from 30 to 100% in the moved enclosure.

To examine the effect of enclosure type on the probability that a fish was eaten, robbed or lost, we first controlled for possible effects of year (two levels), age, wind speed and any interactions between these parameters, before entering enclosure type (two levels) into a logistic regression model. In 1996, the probability that a fish was eaten by the chick was lower than in 1995 and decreased with increasing wind speed (Table 1). Neither age nor any of the interaction terms proved to have significant effects. Adding enclosure type to the model resulted in a significant change in deviance. So, controlling for the effects of year and wind, the proportion of fish eaten by the chicks was higher in the moved enclosure than in the permanent enclosure, and the proportion of fish robbed was higher in the permanent enclosure than in the moved enclosure. Controlling for the effects of year and age of the chicks, the proportion of



**Figure 3.** Fate of fish delivered to tern chicks of various age in the permanent enclosure in 1995 (a) and 1996 (b) and in the enclosures moved away from the original colony in 1995 (c) and 1996 (d). ■: Fish eaten; ▨: fish robbed; □: otherwise lost. The number of fish observed is shown above the bars.

fish lost otherwise was also lower in the moved enclosure than in the permanent enclosure. The latter can be explained because the category 'lost otherwise' also partly depended on the robbing behaviour of the gulls. This category is predominantly formed by fish lost from the observer's sight (unpublished data), which happened mainly when a gull chased a fish-carrying parent away from the colony after which the tern returned without the fish. In conclusion, the incidence of robbery and losing a fish decreased when the chicks were moved away from their original nest site, resulting in the chicks consuming more of the food.

The number of gulls participating in kleptoparasitism had large effects on the proportion of food eaten by the tern chicks (Fig. 4; logistic regression:  $r^2=0.272$ , deviance<sub>1,220</sub>=82.72,  $P<0.001$ ). In the permanent enclosure, the chicks ate all the fish when no gull attempted to rob but none when 10 gulls participated in robbing actions. Significantly more black-headed gulls tried to rob a fish from the arriving parents in the permanent enclosure than in the moved enclosure ( $3.18 \pm 1.95$  and  $1.30 \pm 1.51$  gulls, respectively; loglinear regression: deviance<sub>1,325</sub>= 103.58,  $P<0.001$ ). The average number of robbing gulls in the moved enclosure ranged from 0.4 to 2.3. This coincides with consumption rates of 75.2–94.5%, close to the figures presented in Table 2.

When a parent arrived in the colony with a fish, it usually made several loops before landing next to its chick. The time a parent spent flying above the colony before successfully delivering the fish was highly variable and ranged from 0 to 26 min. Unsuccessful deliveries lasted 0–35 min. Delivery time depended on the number of black-headed gulls trying to rob the fish. When no gulls were present, it took a parent approximately 2 min to deliver the fish to its chick, increasing to more than 6 min when five gulls were present. When even more gulls were present a parent unsuccessfully tried to feed its chick after 6–7 min of flying above the colony. There was no difference in delivery time between successful and unsuccessful deliveries (multiple regression:  $t_1=0.86$ ,  $P=0.39$ ).

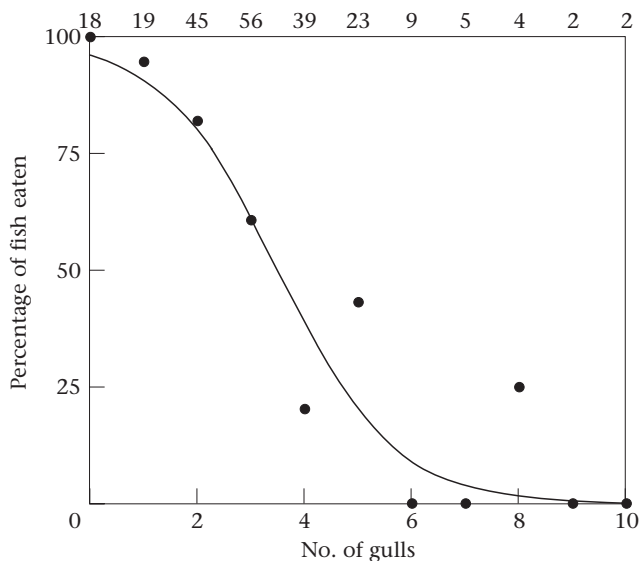
Examining the proportion of fish consumed by the chicks for the days on which simultaneous observations were available (Table 2) suggests that during the first 5 days of the experiment, consumption rate in the moved enclosure was about 30% higher than in the permanent enclosure. After day 5 the difference dropped markedly and from day 7 onwards it no longer existed. Owing to strong wind on the first day after the second move, consumption rates were relatively low in both enclosure types. Nevertheless, the second move again resulted in a more than 30% higher consumption rate compared with that of the chicks in the permanent enclosure, although

**Table 1.** Logistic regression analysis of the proportion of food eaten by the tern chicks, robbed by black-headed gulls and lost in other ways

| Variable                         | Change in deviance | df  | P      | Estimates of coefficients $\pm$ SE     |
|----------------------------------|--------------------|-----|--------|----------------------------------------|
| <b>Proportion eaten</b>          |                    |     |        |                                        |
| Constant                         |                    | 488 |        | 2.538 $\pm$ 0.320                      |
| Year                             | 112.8              | 1   | <0.001 | -1.443 $\pm$ 0.153 for 1996            |
| Wind speed                       | 15.4               | 1   | <0.001 | -0.139 $\pm$ 0.035                     |
| Enclosure type*                  | 45.7               | 1   | <0.001 | 1.370 $\pm$ 0.274 for moved enclosure  |
| <b>Proportion robbed</b>         |                    |     |        |                                        |
| Constant                         |                    | 488 |        | -2.936 $\pm$ 0.326                     |
| Year                             | 50.5               | 1   | <0.001 | 1.075 $\pm$ 0.154 for 1996             |
| Wind speed                       | 21.2               | 1   | <0.001 | 0.1562 $\pm$ 0.036                     |
| Enclosure type*                  | 17.4               | 1   | <0.001 | -0.896 $\pm$ 0.268 for moved enclosure |
| <b>Proportion lost otherwise</b> |                    |     |        |                                        |
| Constant                         |                    | 488 |        | -4.851 $\pm$ 0.475                     |
| Year                             | 48.2               | 1   | <0.001 | 1.434 $\pm$ 0.222 for 1996             |
| Age                              | 24.1               | 1   | <0.001 | 0.073 $\pm$ 0.019                      |
| Enclosure type*                  | 13.1               | 1   | <0.001 | -1.692 $\pm$ 0.544 for moved enclosure |

Only significant parameters are shown.

\*Chicks were kept in enclosures either in the colony or moved away from the colony.

**Figure 4.** The percentage of food eaten by tern chicks in the permanent enclosure in the colony in relation to the number of black-headed gulls participating in robbing. The number of observations is shown.

the difference was not significant at the 0.05 level owing to the large variation. The same pattern can be seen in the difference in the number of robbing gulls between the two enclosure types (Table 2). In 1996, during the first 5 days of the experiment, a parent arriving in the permanent enclosure was on average attacked by 2.4–3.2 black-headed gulls, while in the moved enclosure only 0.4–0.5 gulls participated in kleptoparasitism. On day 7, the difference in the number of robbing gulls was almost zero. The second move again resulted in a difference of 2.8 gulls between the two enclosures.

## Effects on Growth and Survival

At the start of the experiment, age and condition index of the chicks did not differ significantly between the two enclosure types (Student's *t* test: age: 1995:  $t_{23}=1.35$ ; 1996:  $t_{35}=0.54$ ; condition: 1995:  $t_{23}=0.73$ ; 1996:  $t_{35}=0.44$ ; NS in all cases), although in both years chick condition was on average lower in the moved enclosure than in the permanent enclosure. In line with the findings that consumption rates improved during the first 5 days after the shift, chick condition in the moved enclosure greatly improved in this period (Fig. 5). All steps resulted in a considerable increase in  $\Delta$  condition (i.e. the difference in chick condition between the moved and permanent enclosure) during the first 5 days after moving. In all cases the change in chick condition during the first 5 days of the experiment differed significantly between the two enclosure types (Table 3). After this period,  $\Delta$  condition either stabilized or decreased. The decrease in  $\Delta$  condition in 1995 can be explained to a large extent by the majority of chicks in the moved enclosure being close to the theoretical maximum body mass, thus further improvement of their condition was not possible. At the same time chick condition in the permanent enclosure increased as a result of improved weather, thus reducing  $\Delta$  condition. After day 13, the first chicks flew out of the enclosures, sometimes resulting in considerable changes in average chick condition.

To analyse the daily changes in chick condition, we carried out a multiple regression analysis separately for the permanent and the moved enclosure with independent variables condition index at first measurement ( $CI^1$ ), average wind speed on the day before the measurement ('wind'), year of observation ('year' two levels) and time after onset of the experiment ('time' two levels: 1–5 days and >5 days). In the permanent enclosures, daily change in chick condition depended on  $CI^1$ , wind speed and year

**Table 2.** Logistic regression analysis of the percentage of the fish eaten ( $\bar{X} \pm \text{SE}$ ) by the chicks in the permanent and moved enclosures

| Year | Days after start | $\Delta$ gull | Percentage of fish consumed |                 | Deviance | <i>P</i> |
|------|------------------|---------------|-----------------------------|-----------------|----------|----------|
|      |                  |               | Permanent                   | Moved           |          |          |
| 1995 | 8                |               | 78.4 $\pm$ 10.3             | 80.0 $\pm$ 19.9 | 0.70     | NS       |
| 1996 | 4                | 2.0           | 67.5 $\pm$ 8.8              | 94.1 $\pm$ 5.9  | 11.30    | <0.001   |
|      | 5                | 2.6           | 53.6 $\pm$ 12.3             | 88.2 $\pm$ 6.8  | 6.45     | <0.02    |
|      | 7                | 0.6           | 65.7 $\pm$ 8.0              | 63.5 $\pm$ 10.2 | 0.01     | NS       |
|      | 1*               | 2.8           | 32.1 $\pm$ 11.3             | 63.9 $\pm$ 10.5 | 3.20     | 0.06     |

Days after start: Days after the moved enclosure was placed around the chicks;  $\Delta$  gull: difference in the number of robbing gulls between the two enclosure types.

\*One day after the enclosure was moved a second time. See text for details.

of observation (Table 4). In the moved enclosures,  $CI^1$  and year had significant effects on the change in condition. Controlling for these variables and in contrast to the findings in the permanent enclosure, the time after onset of the experiment had a significant effect on the change in chick condition, showing that chick condition improved during the first 5 days after the shift.

In 1995, all chicks in the permanent and in the moved enclosure survived until fledging. In 1996, in the permanent enclosure 16 chicks fledged (80%), while in the moved enclosure 13 chicks survived (87%). The difference is, however, not significant (Fisher's exact test: NS). The age at fledging was related to both year and enclosure type, and differed by 4 days between the earliest and latest group (Table 5). Chicks in the moved enclosure fledged 1–2 days sooner than the chicks in the permanent enclosure.

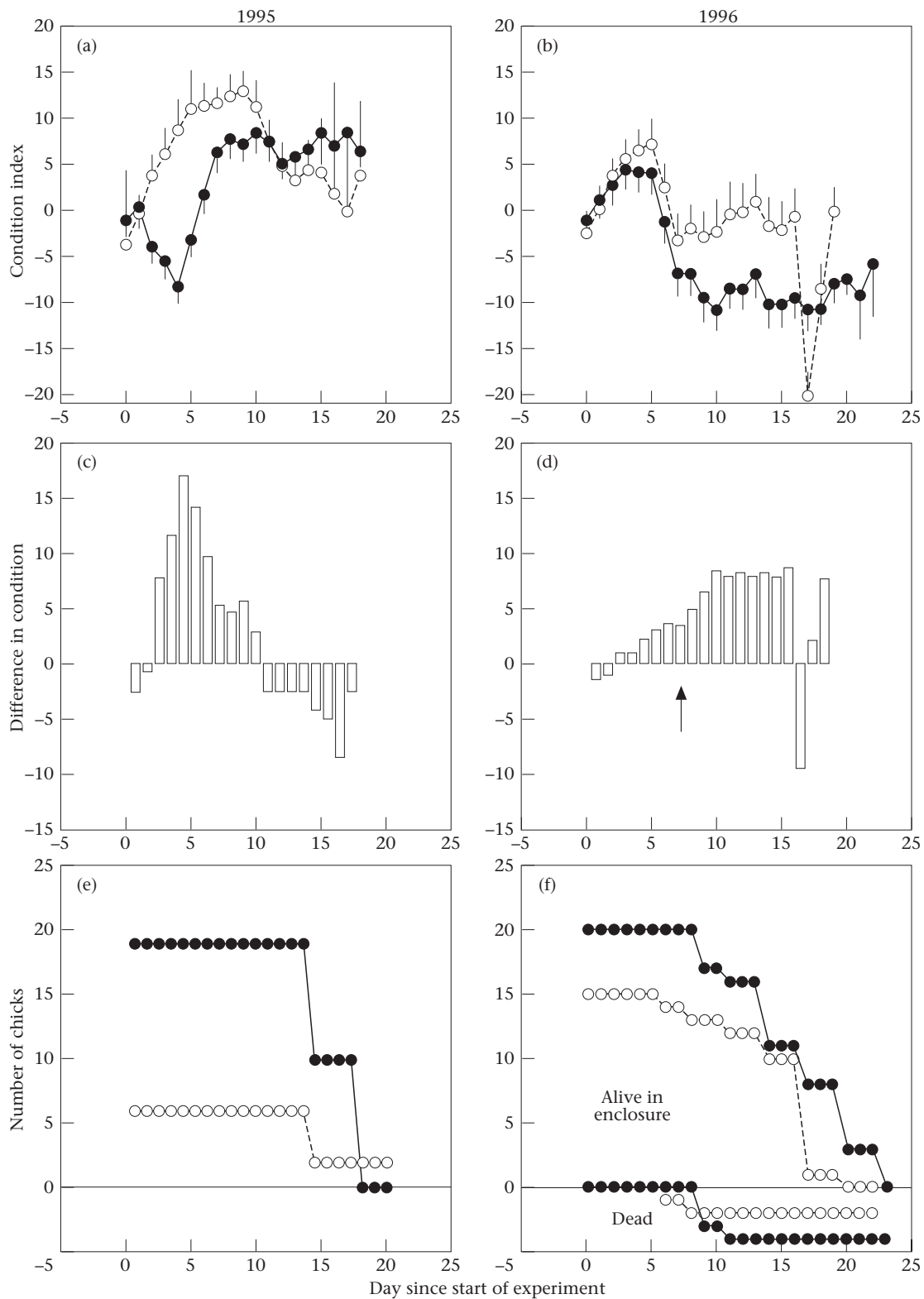
### Condition of Free-living Chicks

In accordance with our findings in the enclosure experiments, the condition of free-living chicks was significantly higher in 1995 ( $6.14 \pm 12.89$ ,  $N=362$ ) than in 1996 ( $-0.87 \pm 16.84$ ,  $N=589$ ; ANOVA:  $F_{1,949}=45.44$ ,  $P<0.001$ ). Furthermore, the condition of chicks recaptured outside their colony of birth ( $2.15 \pm 13.42$ ,  $N=194$ ) did not differ from the condition of chicks that did not leave the colony site ( $1.73 \pm 16.40$ ,  $N=737$ ; ANOVA:  $F_{1,949}=0.26$ , NS), which seems to contradict our results found in the experiments. The discrepancy can be explained if chicks in especially poor condition leave the colony site. Thus, when they are recaptured outside the colony area their condition, although probably improved, is still low. We therefore selected chicks that were captured inside the colony of birth and recaptured within 4 days outside the colony site. Only 11 chicks met these conditions (Table 6). Their condition index at first capture was indeed lower than the condition of chicks that did not leave the colony site (one-tailed  $t$  test:  $t_{146}=1.93$ ,  $P<0.05$ ). At recapture, the condition index of the moved chicks was improved by 0.11, while that of chicks captured twice within the same colony improved by only 0.01 (one-tailed  $t$  test:

$t_{146}=2.63$ ,  $P<0.01$ ). Of the chicks that left the colony site, 81.8% were in better condition when recaptured, while an improvement was measured for only 46.7% of the chicks captured twice in the same colony ( $\chi^2_1=5.02$ ,  $P<0.05$ ).

### DISCUSSION

Leading young Sandwich terns away from the original colony site reduced the incidence of food piracy by black-headed gulls. By avoiding the robbing gulls, the chicks lost 30% less food. Moreover, as delivery time of the fish decreased when the gulls were avoided, parents could achieve a 5% higher delivery rate. Thus parents that adopt such evasive behaviour can improve their chicks' growth rate and their body condition and reduce the prefledging period. However, leaving the colony site also involves costs. Manoeuvring one's chick through and along colonies of breeding terns and gulls provokes serious attacks by the territory owners. We sometimes observed wandering chicks being pecked to death by neighbouring terns and gulls. It is therefore not surprising that, in particular, chicks in poor condition had moved to other sites on the island. Apparently these chicks suffered from high rates of kleptoparasitism and consequently their parents took the risk of guiding them to better spots. During observations in the enclosures it appeared that parents that lost their fish to robbing gulls several times in succession were restless and tried to lure their chick away to better sites (which was impossible as those chicks were enclosed). Abandoning the nest site is therefore likely to occur in colonies where the rate of kleptoparasitism is high. In colonies other than Griend, movements of broods away from the nesting area have been observed, but have always been ascribed to factors other than food parasitism such as human disturbance or avoidance of infectious diseases (Cullen 1958; Chestney 1970; Campredon 1978). On Griend, human disturbance is kept to a minimum and although seabirds are often heavily infected with ectoparasites or ants (Converse et al. 1976; Feare 1976; King et al. 1977; Spendelov 1982; Nisbet & Welton 1984; Boulinier & Danchin 1996) this has never been observed on Griend, leaving kleptoparasitism by



**Figure 5.** (a, b) Variation in chick condition ( $\bar{X} \pm SE$ ) for the permanent (●) and moved (○) enclosures throughout the experiment in 1995 and 1996. The arrow indicates when the enclosure was moved 25 m further away. (c, d) Difference in average condition index between the two enclosure types. Positive values indicate that the chicks in the moved enclosure were in better condition than those in the permanent enclosure. The arrow indicates when the enclosure was moved 25 m further away. (e, f) Number of chicks alive in the enclosure and number of chicks found dead.

**Table 3.** The mean of each chick's change in condition  $\pm$  SE over the first 5 days of the experiment

| Experiment  | Permanent        | Moved            | $t^*$ | $df$ | $P^*$  |
|-------------|------------------|------------------|-------|------|--------|
| 1995 step 1 | $-2.05 \pm 1.38$ | $14.72 \pm 3.29$ | 5.50  | 23   | <0.001 |
| 1996 step 1 | $5.21 \pm 1.57$  | $9.64 \pm 2.21$  | 1.68  | 33   | 0.05   |
| 1996 step 2 | $-5.53 \pm 1.46$ | $0.67 \pm 2.64$  | 2.18  | 26   | 0.02   |

Chicks were kept in enclosures either in the colony or moved away from the colony in one (1995) or two (1996) steps.

\*One-tailed Student's  $t$  test.

**Table 4.** Multiple regression analyses examining the effect of previous condition ( $CI^1$ ), wind speed, year and time after onset of the experiment on the daily change in chick condition

| Variable                   | Estimate $\pm$ SE            | Variance ratio | $P$    |
|----------------------------|------------------------------|----------------|--------|
| <b>Permanent enclosure</b> |                              |                |        |
| Constant                   | $5.02 \pm 0.84$              |                |        |
| $CI^1$                     | $-0.10 \pm 0.02$             | 16.11          | <0.001 |
| Wind speed                 | $-0.49 \pm 0.09$             | 21.47          | <0.001 |
| Year                       | $-1.75 \pm 0.36$ for 1996    | 22.84          | <0.001 |
| Time after onset           | $-0.63 \pm 0.37$ for >5 days | 2.93           | NS     |
| <b>Moved enclosure</b>     |                              |                |        |
| Constant                   | $6.59 \pm 1.26$              |                |        |
| $CI^1$                     | $-0.10 \pm 0.02$             | 16.19          | <0.001 |
| Wind speed                 | $-0.38 \pm 0.13$             | 1.28           | NS     |
| Year                       | $-2.47 \pm 0.56$ for 1996    | 6.14           | 0.01   |
| Time after onset           | $-3.34 \pm 0.51$ for >5 days | 43.64          | <0.001 |

black-headed gulls as the best explanation for the observed movements of the chicks.

Published data show considerable variation in the incidence of food piracy (e.g. Fuchs 1977a; Veen 1977; Ratcliffe et al. 1997; Garthe & Kubetzki 1998). Although

**Table 5.** Age at fledging  $\pm$  SD in the permanent and moved enclosures in 1995 and in 1996

| Year | Enclosure type | Age at fledging  | Number of chicks |
|------|----------------|------------------|------------------|
| 1995 | Permanent      | $29.63 \pm 1.38$ | 19               |
|      | Moved          | $28.67 \pm 0.82$ | 6                |
| 1996 | Permanent      | $32.81 \pm 3.31$ | 16               |
|      | Moved          | $30.50 \pm 2.97$ | 12               |

Multiple regression analysis revealed a significant effect of year ( $F_{1,49}=12.73$ ,  $P<0.001$ ) and enclosure type ( $F_{1,49}=5.91$ ,  $P<0.05$ ).

the rate of kleptoparasitism in this study is within the range reported in the literature, it might have been slightly overestimated because our observations were restricted to the hours around high tide, when the number of robbing gulls is highest (Veen 1977). The large between-year difference in the incidence of robbery was not caused by differences in chick age or weather conditions, and although the supplied fish were longer in 1996 ( $1.94 \pm 0.33$  and  $2.01 \pm 0.37$  bill lengths, respectively, in 1995 and 1996; Student's  $t$  test:  $t_{1515}=4.97$ ,  $P<0.01$ ) the difference seems too small to explain the large difference in kleptoparasitism. A less favourable food situation for the breeding gulls may have played an important role in this. Several authors mention that kleptoparasitism in terns occurs more frequently when alternative food for the pirates is scarce (Veen 1977; Monaghan et al. 1989; Gorke 1990; Oro 1996). Another factor in this respect may be the occurrence of a specialized pirate. Gorke (1990) clearly illustrated that there are

**Table 6.** Average condition indexes ( $CI \pm SE$ ) of chicks that stayed in their natal colony and of those that walked away from the colony

| Recapture site    | $CI$ at capture  | $CI$ at recapture | Change           | No. of chicks | No. improved* |
|-------------------|------------------|-------------------|------------------|---------------|---------------|
| Within colony     | $2.54 \pm 1.23$  | $3.31 \pm 1.44$   | $0.77 \pm 1.05$  | 137           | 64            |
| Outside of colony | $-6.06 \pm 3.85$ | $4.84 \pm 3.21$   | $10.90 \pm 3.48$ | 11            | 9             |

Chicks were recaptured within 4 days.

\*Number of chicks whose condition improved.

**Table 7.** The percentage of chicks of known fate that fledged in relation to the presence of suitable escape routes in the subcolony concerned

| Subcolony | No. of breeding pairs | Suitable escape routes present | Percentage fledged | N   | Differences between subcolonies* |
|-----------|-----------------------|--------------------------------|--------------------|-----|----------------------------------|
| 1         | 161                   | Yes                            | 100                | 6   | 2,3,4,5,6                        |
| 2         | 807                   | Yes                            | 78.5               | 149 | 1,3,4,5,6                        |
| 3         | 1776                  | No                             | 24.3               | 423 | 1,2,4,5                          |
| 4         | 1374                  | Almost none                    | 43.6               | 236 | 1,2,3                            |
| 5         | 227                   | Almost none                    | 42.1               | 38  | 1,2,3                            |
| 6         | 478                   | Yes                            | 40.0               | 15  | 1,2                              |
| Total     | 4823                  |                                | 43.8               |     |                                  |

\*The percentage of chicks fledging is significantly different ( $P < 0.05$ ) from that of the other subcolonies shown; chi-square or Fisher's exact test.

specialists and generalists among the black-headed gulls. If the number of specialized pirates was higher in 1996 this also could explain the observed difference in consumption rate.

Veen (1977) described learning by black-headed gulls with respect to predation of eggs laid out near the colony. Over the first few days when the eggs were exposed to the gulls 'the gulls reacted with fear to the eggs'. Only after 10 days were the first eggs preyed upon. At that time, 'some gulls developed into experienced egg-predators'. Our results suggest that the same holds for kleptoparasitism, since it apparently took some time for the black-headed gulls surrounding the moved enclosure to learn that the more or less continuous supply of fish could be harvested. At first, the gulls showed almost no interest in this potential food resource. After a while, some gulls started to kleptoparasitize the terns and probably also attracted others. After 5 days, the rate of kleptoparasitism no longer differed between the permanent and the moved enclosures. However, on the first day after the second shift in 1996, the number of robbing gulls in the moved enclosure was relatively high and as a consequence the proportion of fish consumed by the chicks was low (Table 2). Wind was strong on this day, which may have attracted some occasional pirates to the enclosures, since the number of robbing gulls in the permanent enclosure was unusually high and consumption rates were extremely low. Unfortunately, we did not record the number of robbing gulls during the next few days when wind conditions improved. However, as the consumption rates improved (more than 50% eaten by the chicks 2 days later), the number of kleptoparasites probably diminished.

In natural situations, without enclosures, piracy may be even more reduced. In our experiment, the chicks were forced to stay at one location for at least 7 days. Outside the enclosures, parents can in theory react to piracy by black-headed gulls at any time by leading their youngsters to a new site. By abandoning an occupied site 5 days after settlement, or even sooner when robbing exceeds a certain threshold, terns can reduce piracy to a minimum, provided the new site has better opportunities for feeding their offspring. However, not all subcolonies provide suitable escape routes for chicks. In some subcolonies on

Griend parents were forced to stay at the original breeding site, simply because their chicks were trapped in a natural enclosure formed by dense vegetation. In 1996, half of the subcolonies on Griend were in locations where escape was impossible or difficult. Piracy was extremely severe in these subcolonies; we observed hundreds of black-headed gulls on guard here. The high rate of kleptoparasitism and the absence of suitable escape routes resulted in high rates of chick mortality in these subcolonies (Table 7); more than half of the ringed chicks of known fate were found dead before fledging. Since these subcolonies comprised 70% of the total population, reproductive success of the entire colony was extremely low in 1996. In this case, for many parents the decision to seek the gulls' protection proved fatal.

### Acknowledgments

We thank Piet van Tienen, Hans Schekkerman and the many occasional guests for their assistance in the field and the Vereniging Natuurmonumenten for allowing us to work on Griend. Logistic support was provided by Jan van Dijk, Dirk van Holk, Dirk Kuiper and the 'Rijkspolitie te Water Harlingen'. We are grateful to Hilko van der Voet for his statistical help. Jan Veen is thanked for giving us the opportunity to do research on Griend and for his scientific support. Nico van den Brink, Rudi Drent, Hans Schekkerman and Arie Spaans offered valuable suggestions on the manuscript. Further helpful suggestions were offered by Juan A. Amat, Angela K. Turner and an anonymous referee.

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