

Consequences of brood size and hatching sequence for prefledging mortality in Sandwich Terns: why lay two eggs?

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ABSTRACT

Mortality of Sandwich Tern *Sterna sandvicensis* chicks held in enclosures was studied in colonies on Griend, Dutch Wadden Sea, from 1992-1999 and Hirsholm, Danish Kattegat, in 1997. Survival until fledging of chicks amounted to 73% for chicks hatching from first-laid eggs or single egg clutches and 59-64% for partially hatched 2-egg clutches, whereas 6% of the second hatchlings survived until fledging. Less than 2% of all 2-chick broods actually fledged 2 chicks. Because 18% of the 2-egg clutches only hatched one egg, still 7% of the fledglings of 2-egg clutches originated from a second-laid egg. In nests where both eggs hatched, the number of chicks was generally reduced soon after hatching. Within 5 days from hatching, more than 50% of the second hatchlings died of starvation or were preyed upon. It appears that overproduction commonly occurs in Sandwich Terns and that it mainly serves as an insurance mechanism. On Griend and Hirsholm, chick productivity of 2-egg clutches was somewhat higher compared to 1-egg clutches. Undernourishment was an important cause of death, either directly by starvation or by selective predation of chicks in poor condition. This in combination with earlier published studies suggests that Sandwich Tern parents on Griend are exposed to a high food stress.

INTRODUCTION

Birds often lay clutches larger than they normally can rear. The surplus eggs may allow parents to track uncertain resources, to select offspring with the highest survival expectations, or they may serve as food-cache for parents or offspring (review in Forbes 1991). Also, the extra eggs might serve as an insurance against the failure of an egg or offspring (e.g. Mock 1984; Cash and Evans 1986; Anderson 1990). Producing surplus offspring requires that parents are able to efficiently reduce brood size if the surplus offspring is redundant, otherwise they may increase rather than decrease reproductive variance (Forbes 1991). Birds adopting a brood reduction strategy are thought to facilitate this process by producing a small final egg (Slagsvold *et al.* 1984) and by asynchronous hatching of the eggs (Cash and Evans 1986, Anderson 1989).

Being long-lived birds living in stochastic environments, seabirds may pay an especially large fitness cost for hatching chicks synchronously and therefore benefit from hatching clutches asynchronously in the long term (Pijankowski 1992, Mock & Forbes 1994). Laridae produce asynchronously hatching clutches, small final eggs and show differential survival of chicks within broods, with the last-hatched chick in a brood having the lowest probability of survival to fledging (e.g. Herring Gull *Larus argentatus*, Parsons 1970, Lesser Black-backed Gull *L. fuscus*, Royle and Hamer 1998, Kittiwake *Rissa tridactyla*, Coulson and Porter 1985, Common Tern *Sterna hirundo*, Langham 1972; Nisbet 1978; Nisbet and Cohen 1975; Bollinger *et al.* 1990, Roseate Tern *S. dougallii*, Nisbet 1978; Nisbet and Drury 1972; Nisbet and Cohen 1975; Burger *et al.* 1996, Gull-billed Tern *S. nilotica*, Eyler *et al.* 1999 and Sandwich Tern, Langham 1974; Veen 1977). Both hatching asynchrony and the decrease in egg size with hatching order in larids are consistent with the brood reduction strategy, but their functions are not always clearly understood (Bollinger 1994).

Studies on chick survival and brood size reduction in larids focussed on species with maximum clutches of three eggs, with the Roseate Tern probably being the best studied exception. Differential survival of Sandwich Tern chicks has been studied in detail by Langham (1974) and Veen (1977). Although sometimes clutches of three eggs can be found (probably originating from two females), Sandwich Terns generally lay one or two eggs. On Griend clutch size averages 1.6 eggs, with the volume of the second egg being on average 7% smaller than the first egg (Stienen and Brenninkmeijer 1996). The second chick of 2-chick broods hatches about three days after the first (Veen 1977). At least at our study sites on Griend, The Netherlands, and on Hirsholm, Denmark, the survival probability of the second hatchling is extremely low. In seven years covered by the present study, Sandwich Terns seldom raised more than one chick to fledging. This paper analyses pre-fledging mortality of Sandwich Tern chicks held in enclosures on Griend and Hirsholm in relation to egg sequence and rank within the brood. We will discuss possible benefits for the terns of producing a clutch size larger than they generally rear. The reduction of the brood size is discussed in the light of the availability of food resources.

MATERIALS AND METHODS

The main study was carried out on the Isle of Griend, situated in the Dutch Wadden Sea (53°15'N, 5°15'E), where several species of gulls (mainly Black-headed *Larus ridibundus*, Common *L. canus* and Herring Gull *L. argentatus*) and terns (mainly Sandwich, Common *S. hirundo* and Arctic Tern *S. paradisaea*) nest. During the study period (1992-99) the population of Sandwich Terns on Griend fluctuated between 5600 and 8300 breeding pairs, each year consisting of several subcolonies. The island consists of a sandy ridge that was constructed in 1988 to protect the lower marshy inner part of the original island. The salt marsh is dominated by a pioneer vegetation of *Salicornia procumbens*, *S. europaea*, *Armeria maritima*, *Puccinellia maritima* and *Limonium vulgare*. The higher parts are dominated by *Halimione portulacoides*, *Matricaria maritima*, *Atriplex littoralis* and grasses (mainly *Elymus farctus*, *E. repens*, *Leymus arenarius* and *Festuca rubra*). For comparison in 1997 a Sandwich Tern colony on Hirsholm, Danish Kattégat (10°38'N, 57°29'E), was studied. In contrast to Griend, Hirsholm is inhabited by man, has a stony under-soil and highly diverse vegetation ranging from pioneer vegetation to shrubs and trees. In 1997, 1250 pairs of Sandwich Terns nested on Hirsholm as well as 6500 pairs of Black-headed Gulls and smaller colonies of Common Gull, Herring Gull, Lesser Black-backed Gull *L. fuscus* and Arctic Tern.

Enclosures

Each year on Griend and on Hirsholm in 1997 a part of a subcolony containing 50-100 nests was selected for further study. To reduce possible effects of hatching date, the subcolonies under study were chosen in a way that the hatching date of most chicks coincided with the peak of hatching of the entire island population. Only in 1993, an additional subcolony of later hatching date was studied on Griend, so that hatching dates ranged from day 140-172 (median hatching day = 152).

Within the selected study sites, most nests were marked with numbered sticks within 3 days after laying of the first egg. If possible, in each nest the eggs were marked in sequence of laying with a permanent marker. A few days before hatching of the first eggs, part of the selected study site was enclosed with wire netting. In total 434 enclosed nests with known laying sequence of the eggs were selected for this study (Table 7.1). In 1994 on Griend, hatching success and fledging success were measured in different subcolonies, so that the results were not used for this study. If possible, all enclosed nests and broods were checked every three days and the chicks were ringed within 3 days after hatching. The hatching date of a chick was estimated from the state of the egg during the previous control, feather characteristics of the chicks, the size of the yolk sac, total head length (*i.e.* exposed culmen length) and whether or not the chick was still wet. Under favourable weather conditions the chicks' body mass, total head length and stretched wing chord were measured during each control. If a chick was missing from the enclosure it was presumed to be preyed upon. In such case the date of predation was set as the middle day between last live measurement and the day that the chick was missing.

Table 7.1. Clutch size, hatching success and sample size of enclosed Sandwich Tern nests on Griend and Hirsholm in the period 1992-1999. Only nests of which laying sequence of the eggs was known are listed.

Location: Year:	Griend 1992	Griend 1993	Griend 1995	Griend 1996	Griend 1997	Griend 1998	Griend 1999	Hirsholm 1997	Total
1-egg clutch									
No chick	3	3	1	7	1	6	0	4	25
1 chick	15	24	11	41	27	6	17	7	148
2-egg clutch									
No chick	0	3	1	4	5	5	1	3	22
a-chick	3	5	2	1	4	6	2	3	26
b-chick	5	1	1	2	5	5	2	1	22
2 chicks	30	27	26	11	19	32	36	10	191

from the enclosure. If the age of a missing chick exceeded 24 days, however, the chick was presumed to have fledged. At this age wing length can exceed 175 mm, which is the minimum wing length required for flying in Sandwich Tern chicks (Stienen and Brenninkmeijer 1999). A chick was categorised as dead if it was found dead or when it was missing from the enclosure when still not able to fly. The latter losses were mainly due to avian predators that either preyed upon living or dead chicks (both Griend and Hirsholm hold no ground predators). During observations in the colony, we mainly observed Black-headed Gull, and occasionally Common and Herring Gull preying upon Sandwich Tern chicks. On Hirsholm in 1997, predation by Herring Gulls occurred more often than on Griend (own observation). Except for avian predation, there were two other reasons why chicks could be missing from the enclosures. Sometimes very young chicks (age < 5 days) did not completely swallow a fish that was fed by a parent, thus part of the fish was sticking out of the chick's bill. In such case it could happen that a gull tried to rob the fish while the chick was still attached to it. Consequently, the chick was transported a few meters through the air and sometimes came lose outside the enclosure. Occasionally dead chicks were removed from the enclosure by Sandwich Tern parents (Stienen *et al.* 1997). However, the intra-specific removal of dead chicks and gull-enhanced transport of living chicks were very rare events (own observations) and have only small effects on the results of this study.

Body condition (BC) of the chicks was defined as the proportional deviation of the measured body mass (M , g) from the average body mass (M_{exp} , g) of chicks of the same age that survived the first 25 days:

$$BC = \frac{M - M_{\text{exp}}}{M_{\text{exp}}} \quad \text{equation 1}$$

Chicks were divided into the following five categories dependent on the egg from which it hatched and the rank within the brood at hatching: a_1 = chick from a 1-egg clutch, a_{12} = first-hatched chick from a 2-chick brood, b_{12} = second-hatched chick from a 2-chick brood, a_{11} = single chick originating from the first-laid egg of a 2-egg clutch of which the second egg did not hatch and b_{11} = single chick originating from the second-laid egg of a 2-egg clutch of which the first egg did not hatch.

Of the 434 nests listed in Table 7.1, 47 did not hatch any chick because of egg predation by gulls or Oystercatcher *Haematopus ostralegus*, addled eggs or chicks that died in the process of hatching. Not all chicks of the remaining 387 nests could correctly be matched to corresponding nest or egg and some very young chicks lost their metal ring. In total 527 hatchlings originating from 352 nests could be justly classified of which 141 a_1 -chicks, 171 a_{12} -chicks, 164 b_{12} -chicks, 24 a_{11} -chicks and 27 b_{11} -chicks. Through the large size of the enclosures coloniality was preserved, but it was impossible to measure all chicks within the enclosure at each occasion without causing an unacceptably long disturbance. Therefore, 82 randomly chosen broods were put out of the enclosures when more than 10 days old. For the 445 remaining chicks that were held in enclosures from hatching until fledging, we found no significant effect of hatching date on the fledging probability after controlling for effects of year, location and chick category (Table 7.2). Therefore, hatching date will not be considered in further analyses.

For each period of 5 days, mortality rate was computed by dividing the number of non-surviving chicks (found dead and missing from the enclosures) by the total number of chicks present at the onset of the 5-day period. Chicks that were put out of the enclosures were included in the computation of mortality rate until they were exiled. Dead chicks were sampled, their body mass and total head length were measured, and the day of death was estimated by smell, features of the eyeball and state of putrefaction and were subsequently removed from the enclosures.

Table 7.2. Generalised linear regression analysis examining the effect of location, chick category and hatching date on the fledging probability of 445 Sandwich Tern chicks that were held in enclosures from hatching until fledging on Griend (1992-1999) and Hirsholm (1997).

Variable	(change in) Deviance	df	P-value
Null model	609.6	444	
Final model	351.0	407	
Location	31.9	7	< 0.001
Chick category	176.7	4	< 0.001
Location*chick category	48.3	25	0.003
Hatching date	1.5	1	n.s.

Statistical analyses

Generalized linear models for the analysis of mortality rates (using binomial distribution) were performed with the Genstat statistical package (Genstat 5 Committee 1993). For data analysis and all other statistical tests we used the SPSS/PC+ 4.0 statistical package (Norusis 1990). We report differences at a probability level of $P < 0.05$ as significant. To compare mortality rates between groups of chicks we first controlled for effects of year and location. Interaction terms were only included if they were significant. The parameters location (*i.e.* a combination of year and colony, 8 levels), age category (6 levels), chick category (a_1 -chick, a_{12} -chick etc., 5 levels) were entered in the analyses as factor variables. All generalized linear models were corrected for overdispersion.

RESULTS

Mortality rate

Mortality rates of Sandwich Tern chicks did not differ between Griend and Hirsholm, but significantly differed between age categories (Table 7.3). Further adding of chick category to the regression analysis resulted in significant effects on chick mortality rates and also the interaction term location*chick category had significant effects on chick mortality rates. Of a_1 - and a_{12} -chicks, respectively 73.4% and 73.1% survived until fledging, while only 6.2% of the b_{12} -chicks survived (Fig. 7.1). Within five days from hatching, more than 50% of the b_{12} -chicks had died and in some years this figure was even higher. In total, only nine b_{12} -chicks survived until fledging. Of these chicks, four originated from nests of which the a_{12} -chick had died before hatching of the b_{12} -chick. Of the remaining five surviving b_{12} -chicks, three had a more slowly growing a_{12} -sibling that eventually died. Thus only two nests actually fledged two chicks, corresponding with 1.1% of all 2-chick broods ($n = 171$). Another three b_{12} -chicks were put out of the enclosure before fledging. Of these chicks, two had an a_{12} -sibling that had died by the time the b_{12} -chick was exiled, while one b_{12} -chick that was put out of the enclosure at 24 days old had an a_{12} -sibling sibling that had already fledged. If we assume that the latter b_{12} -chick has

Table 7.3. Generalised linear regression analysis examining the effect of location, age and chick category on the mortality rate of enclosed Sandwich Tern chicks on Griend and Hirsholm.

Variable	(change in) Deviance	df	P-value
Null model	609.0	175	
Final model	234.4	133	
Location	11.8	7	n.s.
Age category	36.2	4	< 0.001
Chick category	272.1	4	< 0.001
Location*chick category	54.6	27	0.001

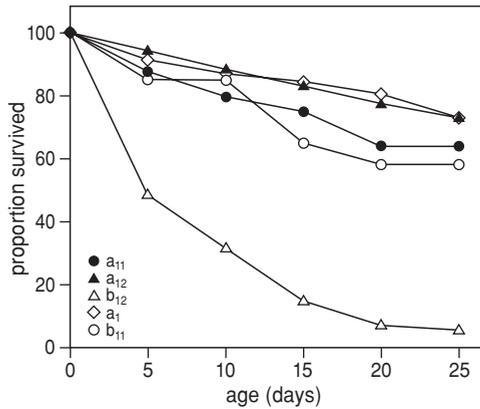


Figure 7.1. Cumulative survival of Sandwich Terns chicks held in enclosures on Griend in 1992-1999 and Hirsholm in 1997 in relation to laying sequence of the egg, rank within the brood and age. A₁₁ = chick originating from the first-laid egg of a partially hatched clutch, a₁₂ = first-hatched chick of a 2-egg clutch, b₁₂ = second-hatched chick of a 2-egg clutch, a₁ = chick of a 1-egg clutch, b₁₁ = chick originating from the second-laid egg of a partially hatched clutch.

actually fledged, 1.8% of all initial 2-chick broods fledged two chicks. A₁₁- (64.3% survival) and b₁₁-chicks (58.5%) experienced significantly higher mortality rates than a₁- and a₁₂-chicks (Fig. 7.1). Of the 7 b₁₂-chicks of which the a₁₂-chick died before hatching of the b-chick 57.1% survived, very similar to the survival of b₁₁-chicks.

When hatching success and fledging success are combined (Table 7.4) it follows that producing 2-egg clutches has slight advantages for Sandwich Terns in terms of chick production. Of all 1-egg clutches 63% successfully raised a chick, whereas breeding success amounted to 0.69 fledglings per pair in 2-egg clutches. Of the 2-egg clutches 82.4% of all

Table 7.4. The effects of clutch size on hatching and breeding success of Sandwich Terns on Griend and Hirsholm. Chick survival rates were derived from figure 2.

Clutch size	Number of nests	Chick category	Hatching success	Chick survival	Breeding success (fledgling per pair)	Overall breeding success (fledgling per pair)
1 egg	173	no chick	14.5%		0.00	0.63
		a ₁ chick	85.5%	73.4%	0.63	
2 eggs	261	no chick	8.4%		0.00	0.69
		a ₁₁ chick	10.0%	64.3%	0.06	
		b ₁₁ chick	8.4%	58.5%	0.05	
		a ₁₂ chick	73.2%	73.1%	0.54	
		b ₁₂ chick	73.2%	6.2%	0.05	

eggs hatched successfully; somewhat lower than in 1-egg clutches (85.5%), but the difference was not significant (chi-square test, $\chi^2 = 0.93$, n.s.). Still, the probability of a complete hatching failure of the nest was 6.1% lower in 2-egg clutches.

Hatching mass significantly differed between a_{12} - and b_{12} -chicks (Table 7.5), in accordance with the generally smaller size of the second-laid egg (Stienen and Brenninkmeijer 1996). Hatching mass of a_1 -chicks was similar to that of a_{12} -chicks. Structural size (total head length) did not differ between these groups, thus b_{12} -chicks hatched with lower body reserves. Nevertheless, early chick mortality seems independent of the laying sequence of the egg. Although b_{12} -chicks experienced a much higher early mortality rate than a_{12} -chicks, there was no significant difference between a_{11} - and b_{11} -chicks (Table 7.6). Early mortality rate of chicks of partially hatched nests (a_{11} - and b_{11} -chicks) was much higher than that of fully hatched nests (a_{12} - and a_1 -chicks), but the difference was not significant.

Causes of death

The proportion of non-surviving chicks that was missing from the enclosure differed between locations (Table 7.7). It was extremely low on Griend in 1995 (< 5% were not found) and highest on Hirsholm where 70.6% of all non-surviving chicks were missing from the enclosure. Controlling for effects of location, the proportion of missing chicks significantly differed between age-categories (Table 7.7). Of non-surviving chicks in the age of 0-4 and 5-9 52.1% and 44.4%, respectively, was missing from the enclosure. The proportion of missing chicks decreased to 20.0-20.8% for chicks between 10 and 19 days and was only 11.8% for chicks of 20-24 days.

The body mass of Sandwich Tern chicks was highly variable (Fig. 7.2). The body condition of chicks that survived until fledging varied between -0.63 and 0.47. Body mass of chicks measured within three days from death (further called last live body mass), generally was much lower than that of surviving chicks (Fig. 7.2). The last live body mass of chicks that were found dead or were missing from the enclosures averaged 31.9% and 22.6%, respectively, below the average body mass of surviving chicks. Of these groups 47.9% and 43.5%, respectively, had a last live body mass that was even lower than the minimum recorded body mass of surviving chicks. This suggests that most non-surviving chicks suffered from undernourishment and ultimately starved to death or were taken by predators. Still, 6.0% of the chicks that were found dead ($n = 119$) and 21.7% of the missing chicks ($n = 46$) had last live body conditions that were higher than or equal to the average body condition of surviving chicks. Most (80.0%) of the missing chicks in good body condition ($BC \geq 0.0$) were a_{12} -, a_1 -, a_{11} - or b_{11} -chicks, whereas missing chicks in poor condition ($BC < -0.1$) mainly (81.8%) concerned b_{12} -chicks (last live body condition of preyed a_{12} -, a_1 -, a_{11} - or b_{11} -chicks vs. b_{12} -chicks, -0.02 (SD 0.18, $n = 17$) and -0.34 (SD 0.24, $n = 29$), Student's t-test: $t = 4.75$, $P < 0.001$). The last live body condition of missing a_{12} -, a_1 -, a_{11} - and b_{11} -chicks did not differ significantly from the body condition of surviving chicks (-0.02, SD 0.18, $n = 17$ and 0.00, SD 0.10, $n = 185$, respectively, $t = 0.58$, $P > 0.05$).

Table 7.5. Body mass and head length (mean \pm SD) of freshly hatched Sandwich Tern chicks on Griend in relation to brood size and hatching position. Text within brackets denotes significant differences (Scheffé-test, $F_{2,82} = 7.62$ and 1.11 , $P < 0.001$ and n.s., respectively).

Chick category	Number of chicks	Body Mass (g)	Head size (mm)
a ₁	31	27.05 \pm 2.53 (b ₁₂)	37.60 \pm 1.18
a ₁₂	21	26.98 \pm 2.10 (b ₁₂)	38.03 \pm 1.05
b ₁₂	32	25.00 \pm 2.45	37.59 \pm 1.26

Table 7.6. Mortality rate of Sandwich Tern chicks during the first five days after hatching in relation to chick category. The number of non-surviving chicks is shown between brackets. Differences in mortality between groups were tested by means of chi-square or Fisher's exact test. Only significant differences ($P < 0.05$) are shown.

Chick category	Number of chicks	Mortality	Differences
a ₁₂	171	0.05 (9)	
a ₁	141	0.09 (12)	
a ₁₁	24	0.13 (3)	
b ₁₁	20	0.15 (3)	
b ₁₂	171	0.51 (87)	1,2,3,4

Table 7.7. Logistic regression analysis examining the effect of location and age of Sandwich Tern chicks on the proportion of non-surviving chicks that were missing from the enclosures.

Variable	(change in) Deviance	df	P-value
Null model	101.7	35	
Final model	47.8	44	
Location	41.7	7	< 0.001
Age category	12.2	4	0.02

Low food intake rate causing poor body condition apparently was an important cause of chick mortality in enclosed Sandwich Tern chicks at Griend and Hirsholm. Therefore one might expect that having two chicks is disadvantageous for their growth and that the duration that two chicks are present in the brood has consequences for survival of the first hatchling or at least for its body condition. To test these assumptions, a-chicks were divided into 5 categories according to their age at the moment the b-chick died. Indeed, the time of death of the b-chick significantly affects survival rate of the a-chick (Table 7.8), but the direction was unexpected (Fig. 7.3). In nests where the b-chick died 0-4

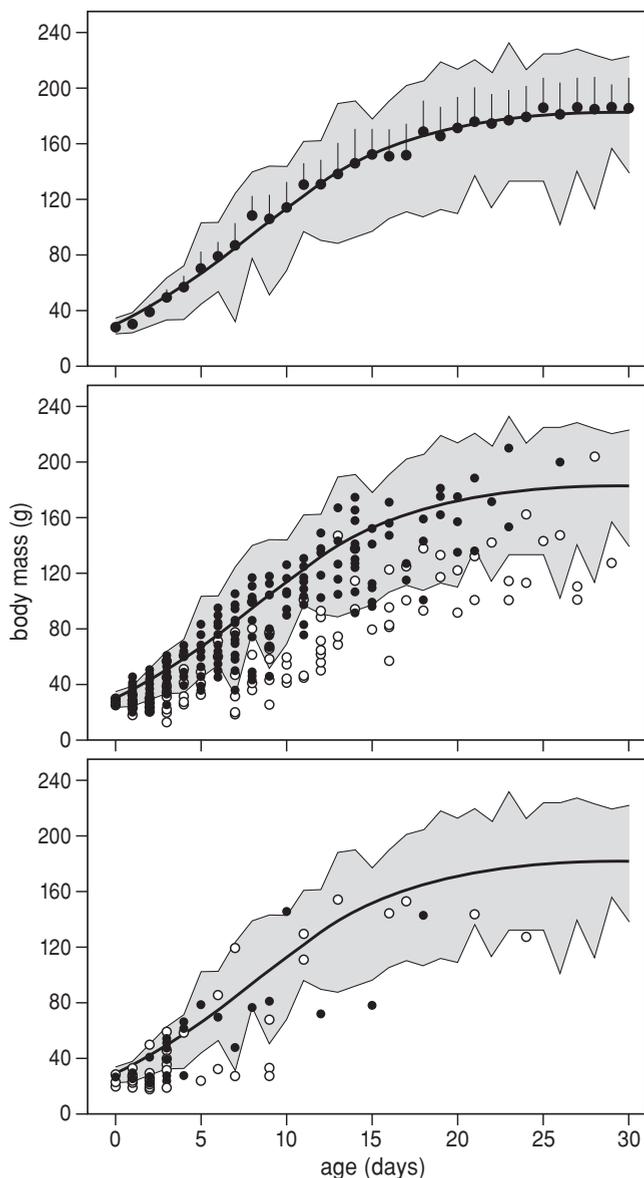


Figure 7.2. Body mass (means + SD and ranges) of enclosed Sandwich Tern chicks on Griend and Hirsholm that survived until fledging (upper graph) and body mass of chicks that were found dead (middle graph) or were missing from the enclosures when not yet able to fly (lower graph) in relation to age. Drawn lines represent logistic growth curve fitted through data of fledged chicks (body mass (g) = $183.3/(1+5.08*\exp(-0.212*age))$, $n = 1532$, $r^2 = 0.87$). Black dots = body mass > 3 days before death or before they were missing from the enclosure, open circles = body mass within 3 days from death or missing.

Table 7.8. Logistic regression analysis examining the effect of location and age category on the mortality rate of a_{12} -chicks in relation to the age at which the b_{12} -chick died (5 levels: died when a_{12} -chick was 0-4, 5-9, 10-14 or > 14 days, and b_{12} -chick survived until fledging).

Variable	(change in) Deviance	df	P-value
Null model	124.0	75	
Final model	50.5	60	
Location	13.5	7	n.s.
Age category	46.4	4	< 0.001
Age of death	13.6	4	< 0.01

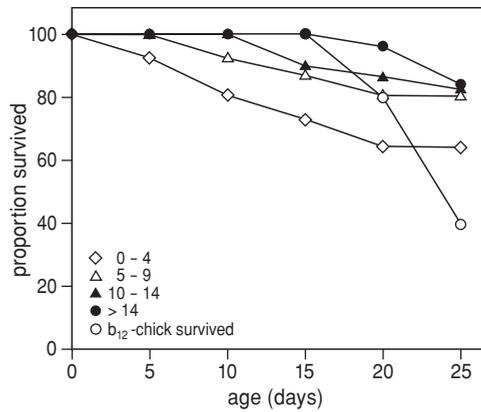


Figure 7.3. Cumulative survival of first hatched Sandwich Tern of 2-chick broods in relation to the time the second hatchling was present. 0-4 = second hatched chick died between day 0 and day 4 from hatching of the first chick, etc.

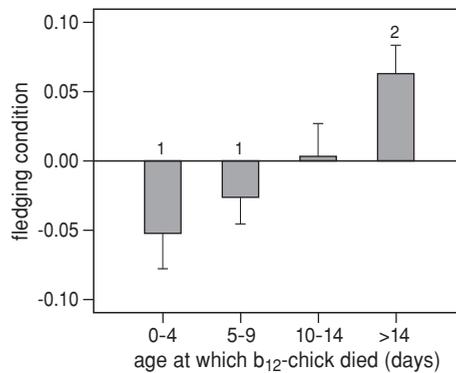


Figure 7.4. Fledging condition of first-hatched Sandwich Tern chicks in relation to the time of death of the second hatchling. 0-4 = second hatched chick died between day 0 and day 4 from hatching of the first chick, etc. Numbers above bars denote significant differences.

days after hatching of the a-chick, the a-chick had relatively low survival chances (64.5% survived until fledging, so very much the same as a₁₁-chicks and somewhat higher than b₁₁-chicks). If the b-chick survived the first five days but died afterwards, survival chances of the a-chick ranged from 80.8–84.0%. In the few nests where the b-chick survived until fledging survival rate of a-chicks was only 40.0%. The fledging condition (*i.e.* average BC of the chick when older than 24 days) depended on the time of death of the b-chick (ANOVA, $F_{3, 82} = 3.7$, $P = 0.02$). However, where a decrease in fledging condition with increasing duration of the time that two chicks were present was expected an increase is found (Fig. 7.4).

DISCUSSION

Reproductive output

Parents in this study that produced only one egg took the risk of losing the egg before hatching. If, however, the egg hatched successfully, the chick had high survival chances and fledged in average body condition (fledging condition did not differ between chick-categories; ANOVA, $F_{4, 190} = 0.1$, n.s.). A second category of parents produced two eggs, but hatched only one. Survival chances of their chicks were somewhat lower (mainly because of high chick mortality during the first five days), but fledging condition was comparable to the first category. For unknown reasons, the eggs and chicks of these parents were more prone to predation, but the parents apparently had no difficulties with providing enough food to their chick. A third category in which brood size was reduced in an early phase and whose surviving chick had poor survival changes as well. Their chicks were in relatively poor body condition at fledging. These parents apparently had no difficulties in protecting their eggs and chicks from predators, but had difficulties with providing enough food to the chicks. Finally, there was a small group of high quality parents that were able to hatch two eggs and keep two chicks alive for a relatively long period and to raise a fledgling that was in good body condition. Obviously, these parents invested more energy in the production of eggs and the rearing of their chicks than other parents, but reached high survival rates of their a₁₂-chick and even had a small chance to rear two chicks to fledging.

A reproductive output of less than one chick per breeding pair and a poor survival of second hatchlings are not unique for Griend or Hirsholm, but rather seem commonplace in Sandwich Terns. In a Sandwich Tern colony at Zeebrugge, Belgium, no pair was able to fledge 2 chicks in any of the 4 years during the period 2001-2004 (own observations in enclosed subcolonies). Isenmann (1975) mentions that in the Camarque, France, only 7% of all pairs had 2 chicks close to fledging. All other measurements of breeding productivity in Sandwich Terns in the literature are doubtful, as either only counts of 'large' chicks were made or breeding success was estimated from the numbers of dead chicks found. Sometimes, no method is described at all. Nevertheless, these studies hardly ever found a breeding success much higher than 1 fledged chick per pair (Schmidt 1969;

Chestney 1970; Langham 1974; Walsh *et al.* 1990). Only Campredon (1978) mentions a breeding success of more than 1.7 fledglings per pair, but he based this figure on the number of dead chicks found in the colony (which would have excluded losses due to predators, if any). At first sight, Veen (1977) also found higher survival rates on Griend in the period 1971-1972. He suggests that up to 84% (49.3-83.8%) of the a_{12} -chicks and up to 20% (11.8-20.0%) of the b_{12} -chicks survived until fledging. In contrast, however, to our study where fledging age was set at 25 days, Veen defined chicks older than 14 days as fledglings. If we use the same definition of fledging as Veen did, mortality rate in the 1970s is comparable to that in the 1990s when 83.5% and 15.2%, respectively of the a_{12} - and b_{12} -chicks survived the first two weeks posthatching (Fig. 7.2).

It remains puzzling to what extent our results can be compared to that of studies where chicks were not held in enclosures. After all, by preventing the chicks to move away from the colony site by retaining them in enclosures they suffer from increased rates of kleptoparasitism and consequently mortality rates might have been higher than in natural situations (Stienen & Brenninkmeijer 1999). On the other hand, one would expect that enclosing chicks would only affect older chicks, because (1) also in natural situations very young chicks stay in the vicinity of the nest and (2) kleptoparasitism by Black-headed Gulls is still rather low during the first week after hatching (Stienen *et al.* 2001). In our study, however, most b_{12} -chicks died in an early stage of life when possible negative effects of the enclosures are not yet to be expected. In non-enclosed subcolonies on Griend and Hirsholm we also found many dead b_{12} -chicks of less than 1 week old and during observations of Sandwich Terns parents feeding fledglings at the beaches around Griend we very rarely observed more than one fledgling per parent, suggesting a generally low survival rate of second hatchlings.

Overproduction and brood reduction

The extremely low survival rate of b_{12} -chicks is surprising when considering that Sandwich Terns on Griend on average produce 1.6 eggs per nest (Stienen and Brenninkmeijer 1996). Apparently Sandwich Terns produce more eggs than they normally can raise chicks and often the brood size is reduced in an early stage if both eggs hatch successfully. Overproduction is widely spread among plants and animals (including several seabirds) and may serve various functions (review in Mock and Parker 1998): (1) it may allow parents to select the fittest offspring, (2) it may serve as a mechanism for resource-tracking (extra offspring may be affordable in the case of unpredictable improvement of the food situation), (3) it may facilitate sibling survival (if extra offspring serve as helpers or meals for other siblings) or (4) it may be an insurance against accidental failure of an egg or defective offspring.

In Sandwich Terns, overproduction serving resource tracking (2) seems rather costly as in 10 years time (1992-2001; data from this study and non-published data) almost no pair was able to fledge 2 chicks on Griend. However, given that Sandwich Terns can become more than 25 years old, and if the costs involved in producing an extra offspring are relatively low (but see Heaney and Monaghan 1995), it might be affordable to pro-

duce two eggs even if 'good' years occur at a very low frequency. The present food situation around Griend and the high rates of kleptoparasitism causes a lot of food stress for Sandwich Terns parents (Stienen & Brenninkmeijer 2002) and undernourishment is an important cause of death for Sandwich Tern chicks (this study). This suggests that resources were low during the 1990s. Sibling facilitation (3) in terms of the youngest sibling helping or serving as an extra meal for the first hatchling does not occur in Sandwich Terns. There might be a small advantage of having a younger sibling, because parents that have two chicks increase the rate of food transport to the nest. This would be temporarily advantageous to the first hatchling, namely during the first few days when the first hatchling consumes almost all food brought to the brood (Stienen *et al.* 2000). The extra egg serving as an insurance (4) in combination with selection of the fittest offspring (1) seems to be the most plausible explanation for overproduction in Sandwich Terns. The failure of the first egg or the death of the first chick in an early stage occurred relatively often in our study plots. In 18.4% of the 261 2-egg clutches only 1 egg hatched, 7.2% of the fledglings of 2-egg clutches originated from second-laid eggs and parents that laid two eggs had a somewhat higher breeding success (Table 7.4).

As 2-egg clutches seem to be slightly more productive, one might expect that Sandwich Terns on Griend nowadays tend to lay larger clutch than in the past. There is, however, no evidence for this. Brouwer (1930) mentions a clutch size of 1.75 in 1929 on Griend, in 1970-72 clutch size averaged 1.81 (Veen 1977) and in the 1980s clutch size averaged 1.6 (Brenninkmeijer & Stienen 1992). The apparent advantages of producing a 2-egg clutch thus might be nullified by parental reproductive costs involved in producing and rearing a large clutch.

It is thought that birds adopting a brood reduction strategy may facilitate this process by producing a small final egg (Slagsvold *et al.* 1984) and by asynchronous hatching of the eggs (Anderson 1989; Cash & Evans 1986) as is the case in Sandwich Terns (Veen 1977; Stienen & Brenninkmeijer 1996). Experimental studies on other Laridae suggest that lower survival rate of the last-hatched chick is primarily caused by hatching asynchrony while egg size difference is less important (Parsons 1975; Bollinger 1994; Royle & Hamer 1998), which is also suggested by our results (Table 7.6). In an experimental study in the Caspian Sea, Gauzer (1989) found that 73.9% of synchronously hatched Sandwich Terns broods produced 2 fledglings, compared to 23.3% in the control group that hatched chicks asynchronously. Gauzer (1989) found that Sandwich Terns were even able to raise three chicks to fledging provided that in the experimentally enlarged clutch the three eggs hatched synchronously. Although we were not able to extract Gauzer's (1989) definition of fledging, the study demonstrated that asynchronous hatching of the eggs facilitates brood reduction in Sandwich Terns. It also appears that the food situation in Gauzer's study area was much more profitable than on Griend and Hirsholm. In our study hatching asynchrony results in a knock-out race and facilitates the death of the youngest sibling. If both chicks would have hatched synchronously periods of food stress might very well result in the death of both siblings.

Food availability

Stienen & Brenninkmeijer (2002) showed that in the presence of kleptoparasitising gulls food availability on Griend is not sufficient to rear two chicks to fledging. This study confirms that undernourishment resulting in a decrease in body condition that finally leads to starvation was an important cause of death in enclosed Sandwich Tern chicks on Griend and Hirsholm. A large proportion of the chicks that were missing from the enclosures lagged behind in body mass as well. The high proportion of missing chicks on Hirsholm (70.6% of all non-surviving chicks were missing) is probably the result of high removal rates of both living and dead chicks by Herring Gulls (own observation). On Griend, predominantly Black-headed Gulls preyed upon Sandwich Tern chicks. Despite large differences in the proportion chicks that were missing from the enclosures, survival rates did not differ between Griend and Hirsholm. Although this study does not differentiate between predation and starvation, the results suggest that predators selectively took smaller chicks in poor body condition (mainly b₁₂-chicks) that would otherwise have died from starvation and/or they removed chicks that had starved to death. Selective predation on chicks in poor condition was also found in Common Terns (Nisbet 1975) and was earlier described in Sandwich Terns on Griend by Veen (1977).

In conclusion, in most pairs of Sandwich Terns on Griend and Hirsholm the brood was reduced to only one chick at an early stage mainly through starvation of the second hatchling. Also for first hatchlings and singletons starvation was an important cause of death, suggesting a high degree of food stress. Earlier studies on Griend (Stienen *et al.* 2001, Stienen & Brenninkmeijer 2002) show that this is a combined effect of a poor food situation and high rates of kleptoparasitism. This gives the terns little leeway during periods of bad weather when feeding conditions deteriorate and food loss to the gulls increases.

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REFERENCES

- Anderson, D.J. 1989. The role of hatching asynchrony in siblicidal brood reduction of two booby species. *Behavioral Ecology and Sociobiology* 25: 363-368.
- Anderson, D.J. 1990. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. *American Naturalist* 135: 334-350.
- Bollinger, P.B. 1994. Relative effects of hatching order, egg size variation and parental quality on chick survival in Common Terns. *Auk* 111: 263-273.
- Bollinger, P.B., Bollinger, E.K. and Malecki, R.A. 1990. Test of three hypotheses of hatching asynchrony in the Common Tern. *Auk* 107: 696-706.
- Brenninkmeijer, A. and Stienen, E.W.M. 1992. Ecologisch profiel van de Grote Stern (*Sterna sandvicensis*). RIN-rapport 92/17. DLO-Institute for Forestry and Nature Research, Wageningen.
- Brouwer, G.A. 1930. Waarnemingen in 1929, verzameld door de Club van Trekwaarnemers. *Ardea* 19: 20-66.
- Burger, J., Nisbet, I.C.T., Safina, C. and Gochfeld, M. 1996. Temporal patterns in reproductive success in the endangered Roseate Tern (*Sterna dougallii*) nesting on Long Island, New York, and Bird Island, Massachusetts. *Auk* 113: 131-142.
- 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, 263-179.
- Cash, K.J. and Evans, R.M. 1986. Brood reduction in the American white pelican. *Behavioural Ecology and Sociobiology* 18: 413-418.
- Chestney, R. 1970. Notes on the breeding habits of common and Sandwich Terns on Scolt Head Island. *Transactions Norfolk Norwich Naturalists Society* 21: 353-363.
- Coulson, J.C. and Porter, J.M. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* 127: 450-466.
- Cullen, J.M. 1958. Some adaptations in the nesting behaviour of terns. *Proceedings XII International Ornithological Congress*: 153-157.
- Eyler, T.B., Erwin, R.M., Stotts, D.B. and Hatfield, J.S. 1999. Aspects of hatching success and chick survival in Gull-billed Terns in coastal Virginia. *Waterbirds* 22: 54-59.
- Forbes, L.S. 1991. Insurance offspring and brood reduction in a variable environment: the costs and benefits of pessimism. *Oikos* 62: 325-332.
- Gauzer, M.Y. 1989. Asynchronous hatching of chicks as a factor of juvenile mortality of Sandwich Tern, *Sterna sandvicensis*. *Zool. Zhurnal* 68: 103-112.
- Genstat 5 Committee 1993. *Genstat 5 Reference Manual*. Clarendon Press, Oxford.
- Heaney, V. and Monaghan, P. 1995. A within-clutch trade-off between egg production and rearing in birds. *Proceedings Royal Society London* 261: 361-365.
- Isenmann, P. 1975. Über einen Versuch zur Messung der Fütterungshäufigkeit von fat flüggen Jungvögel bei der Brandseeschwalbe (*Sterna sandvicensis*) in der Camarque (Süd-Frankreich). *Vogelwarte* 28: 159-160.
- Langham, N.P.E. 1972. Chick survival in terns (*Sterna* spp.) with particular reference to the Common Tern. *Journal of Animal Ecology* 41: 385-395.
- Langham, N.P.E. 1974. Comparative breeding biology of the Sandwich Tern. *Auk* 91: 255-277.
- Mock, D.W. 1984. Infanticide, siblicide and avian nestling mortality. In: (Hausfater, G. and Hrdy, S.B. (eds.), *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp. 3-30.
- Mock, D.W. and Forbes, L.S. 1994. Life-history consequences of avian brood reduction. *Auk* 111: 115-123.
- Mock, D.W. and Parker, G.A. 1998. Siblicide, family conflict and the evolutionary limits of selfishness. *Animal Behaviour* 56: 1-10.
- Nisbet, I.C.T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. *Nature* 241: 141-142.
- Nisbet, I.C.T. 1975. Selective effects of predation in a tern colony. *Condor* 77: 221-226.
- Nisbet, I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, *Sterna hirundo* and *S. dougallii*. *Ibis* 120: 207-215.

- Nisbet, I.C.T. and Cohen, M.E. 1975. Asynchronous hatching in Common and Roseate Terns, *Sterna hirundo* and *S. Dougallii*. *Ibis* 117: 374-380.
- Nisbet, I.C.T. and Drury, W.H. 1972. Measuring breeding success in Common and Roseate Terns. *Bird Banding* 43: 97-106.
- Norusis, M.J. 1990. SPSS/PC+ 4.0. Base Manual. SPSS, Chicago.
- Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). *Nature* 228: 1221-1222.
- Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. *Ibis* 117: 517-520.
- Pijankowski, B.C. 1992. A revision of Lack's brood reduction hypothesis. *American Naturalist* 139: 1270-1292.
- Royle, N.J. and Hamer, K.C. 1998. Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. *Journal of Avian Biology* 29: 266-272.
- Schmidt, G.A.J. 1969. Ein vogelkundlicher Bericht über fünf Jahre Schutzarbeit (1965-1969) in sieben Reservaten des Vereins Jordsand. *Jordsand Mitteilungen* 5: 2-62.
- Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, Ö. and Husby, M. 1984. On the adaptive value of intr-clutch egg-size variation in birds. *Auk* 101: 685-687.
- Stienen, E.W.M. and Brenninkmeijer, A. 1996. Variatie in legselgrootte en eivolume bij de Noordse Stern *Sterna paradisaea*, Visdief *S. hirundo* en Grote Stern *S. sandvicensis*. *Limosa* 69: 37-46 (with English summary).
- Stienen, E.W.M. and Brenninkmeijer, A. 1999. Keep the chicks moving: how Sandwich Terns can minimize kleptoparasitism by black-headed gulls. *Animal Behaviour* 57: 1135-1144.
- Stienen, E.W.M. and Brenninkmeijer, A. 2002. Foraging decisions of Sandwich Terns in the presence of kleptoparasitising gulls. *Auk* 119: 473-486.
- Stienen, E.W.M., Brenninkmeijer, A. and Geschiere, K.E. 2001. Living with gulls: the consequences for sandwich Terns of breeding in association with Black-headed Gulls. *Waterbirds* 24: 68-82.
- Stienen, E.W.M., Brenninkmeijer, A. and van Tienen, P.G.M. 1997. Grote Sterns *Sterna sandvicensis* verwijderen eierschalen en dode kuikens uit de kolonie. *Sula* 11: 26 (with English summary).
- Stienen, E.W.M., van Beers, P.W.M., Brenninkmeijer, A., Habraken, J.M.P.M., Raaijmakers, M.H.J.E. and van Tienen, P.G.M. 2000. Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*. *Ardea* 88: 33-49.
- Thomas, C.S. 1983. The relationships between breeding experience, egg volume and reproductive success of Kittiwake *Rissa tridactyla*. *Ibis* 125: 567-574.
- Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). *Behaviour* 20 (Supplement): 1-193.
- Walsh, P.M., Sears, J. and Heubeck, M. 1990. Seabird numbers and breeding success in 1989. *Nature Conservancy Council CSD report* 1235.

