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Effect of brood size and hatching sequence on prefledging mortality of Sandwich terns: why lay two eggs?

Eric W. M. Stienen · Alex Brenninkmeijer

Abstract The mortality of Sandwich tern *Sterna sandvicensis* chicks held in enclosures was studied in colonies on Griend, in the Dutch Wadden Sea, from 1992 to 1999, and on Hirsholm, in the Danish Kattegat, in 1997. Survival of chicks until fledging was 73% for chicks hatching from first-laid eggs or single-egg clutches and 59–64% for partially hatched two-egg clutches, whereas 6% of second hatchlings survived until fledging. Less than 2% of all two-chick broods actually fledged two chicks. Because 18% of the two-egg clutches only hatched one egg, 7% of fledglings of two-egg clutches originated from a second-laid egg. In nests where both eggs hatched, the number of chicks was usually reduced soon after hatching. Within five days of hatching more than 50% of the second hatchlings died of starvation or were preyed upon. It seems that overproduction commonly occurs in Sandwich terns and that investment in a surplus egg mainly serves as an insurance mechanism. On Griend and Hirsholm, chick productivity of two-egg clutches was somewhat higher than for one-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, studies suggests that Sandwich tern parents on Griend are exposed to severe food stress.

Keywords *Sterna sandvicensis* · Chick survival · Hatching asynchrony · Brood reduction

E. W. M. Stienen · A. Brenninkmeijer
Alterra, P.O. Box 47, 6700 AA Wageningen
The Netherlands

E. W. M. Stienen
Zoological Laboratory, University of Groningen,
P.O. Box 14, 9750 AA Haren, The Netherlands

Present Address:
E. W. M. Stienen (✉)
Research Institute for Nature and Forest, Kliniekstraat 25,
1070 Brussels, Belgium
e-mail: eric.stienen@inbo.be

Present Address:
A. Brenninkmeijer
Altenburg and Wymenga Ecologisch Onderzoek bv,
Spoorlaan 12, P.O. Box 32, 9269 ZR Veenwouden,
The Netherlands

Introduction

Birds often lay clutches larger than they can normally rear. The surplus eggs may enable parents to track uncertain resources or to select offspring with the highest expectation of survival, or they may serve as a food-cache for parents or for offspring (review in Forbes 1991). The extra eggs might also serve as insurance against the failure of an egg or offspring (e.g. Mock 1984; Cash and Evans 1986; Anderson 1990). Producing and incubating extra eggs can incur high fitness costs for birds, however. Experimental studies have found that increased egg production may affect egg quality (Nager et al. 2000), chick rearing capacity (Heaney and Monaghan 1995; Monaghan et al. 1998), and the future fitness (Nager et al. 2001; Visser and Lessels 2001; Kalmbach et al. 2004) of the parents. The cost of producing surplus eggs (Kalmbach et al. 2004) and the gain in terms of reproductive output may differ

between species. If the cost is smaller than the gain, parents can afford the production of extra offspring and reduce brood size if the surplus offspring is redundant.

Because seabirds are long-lived birds living in stochastic environments, they may pay an especially large fitness cost for hatching chicks synchronously and therefore, in the long term, benefit from hatching clutches asynchronously (Pijankowski 1992; Mock and Forbes 1994). Laridae produce asynchronously hatching clutches, with small final eggs, and survival of chicks within broods varies, 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; González-Solís et al. 2005, roseate tern *S. dougallii*, Nisbet 1978; Nisbet and Drury 1972; Nisbet and Cohen 1975; Burger et al. 1996; Ramos 2001, gull-billed tern *S. nilotica*, Eyler et al. 1999, and Sandwich tern *S. sandvicensis*, Langham 1974; Veen 1977). In larids both hatching asynchrony and decrease in egg size with hatching order are consistent with brood-reduction strategy (Cash and Evans 1986; Anderson 1989), but their functions are not always clearly understood (Bollinger 1994).

Studies on chick survival and brood-size reduction in larids have focussed on species with maximum clutches of three eggs, with the roseate tern probably being the best studied exception. The different survival of Sandwich tern chicks has been studied in detail by Langham (1974) and Veen (1977). Although clutches of three eggs are sometimes found (probably originating from two females), Sandwich terns usually lay one or two eggs. On Griend, The Netherlands, clutch size averages 1.6 eggs, with the volume of the second egg being, on average, 7% less than that of the first (Stienen and Brenninkmeijer 1996). The second chick of two-chick broods hatches approximately 3 days after the first (Veen 1977). At our study sites on Griend and on Hirsholm, Denmark, at least, the probability of survival of the second hatchling is extremely low. In the seven years covered by this study, Sandwich terns seldom raised more than one chick to fledging. This paper analyses prefledging 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 to the terns of producing a clutch size larger than they generally rear. The reduction of the brood size is discussed with reference to the availability of food resources.

Materials and methods

The main study was carried out on the Island of Griend, situated in the Dutch Wadden Sea (53°15′N, 5°15′E), where several species of gull (mainly black-headed *L. ridibundus*, common *L. canus* and herring gull) and terns (mainly Sandwich, common, and Arctic tern *S. paradisaea*) nest. During the study period (1992–1999) the Sandwich tern population on Griend fluctuated between 5,600 and 8,300 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 the pioneer vegetation *Salicornia procumbens*, *S. europaea*, *Armeria maritima, Pucinellia 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 Kattegat (10°38′N, 57°29′E), was studied. In contrast with Griend, Hirsholm is inhabited by man, has stony undersoil and highly diverse vegetation ranging from pioneer vegetation to shrubs and trees. In 1997, 1,250 pairs of Sandwich terns nested on Hirsholm, as also did 6,500 pairs of black-headed gulls and smaller colonies of common gull, herring gull, lesser black-backed gull, 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 so that the hatching date of most chicks coincided with the peak of hatching of the entire island population. In 1993, only, another subcolony of later hatching date was studied on Griend, so that hatching dates ranged from day 140 to 172 (median hatching day=152).

Within the study sites most selected nests were marked with numbered sticks within three days of laying of the first egg. In each nest, if possible, 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. A total of 434 enclosed nests with known egg-laying sequence were selected for this study (Table 1). In 1994 on Griend hatching success and fledging success were measured in different subcolonies, so the results were not used for this study. If possible, all enclosed nests and broods were checked every three

Table 1 Clutch size, hatching success, and sample size of enclosed Sandwich tern nests on Griend and Hirsholm during the period 1992–1999

	Location								Total
Griend Year	Griend	Griend	Griend	Griend	Griend	Griend	Hirsholm	
	1992	1993	1995	1996	1997	1998	1999	1997	
1-Egg clutch									
No chick	3	3	1	7	1	6	0	4	25
One 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
Two chicks	30	27	26	11	19	32	36	10	191

Only nests for which the laying sequence of the eggs was known are listed

days and the chicks were ringed within three days of hatching. The hatching date of a chick was estimated from the state of the egg during previous monitoring, the feather characteristics of the chicks, the size of the yolk sac, total head length (i.e. head and bill), and whether or not the chick was still wet. Under favourable weather conditions the chicks' body mass (±1.0 g, using an electronic balance) and total head length (±0.1 mm, using Vernier callipers) were measured on each monitoring occasion. If a chick was missing from the enclosure it was assumed to have been preyed upon. In such circumstances the date of predation was set as the middle day between the last live measurements and the day the chick was missing from the enclosure. If the age of a missing chick exceeded 24 days, however, the chick was assumed to have fledged. At this age wing length can exceed 175 mm, which is the minimum wing length required for flying by 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 because of avian predators that either preyed on living or dead chicks (Griend and Hirsholm have no ground predators). During observations in the colony we mainly observed black-headed gulls, and occasionally common and herring gulls preying on Sandwich tern chicks. On Hirsholm in 1997 predation by herring gulls occurred more often than on Griend (personal observation). Except for avian predation there were two other reasons why chicks could be missing from the enclosures. Sometimes very young chicks (age less than five days) did not completely swallow a fish that was fed by a parent, and so part of the fish remained protruding from the chick's bill. In such circumstances it could happen that a gull tried to steal the fish while the chick was still attached to it. Consequently, the chick was transported a few meters through the air and sometimes came loose outside the enclosure. Dead chicks were occasionally removed from the enclosure by Sandwich tern parents (Stienen et al. 1997). Intra-specific removal of dead chicks and gull-enhanced transport of living chicks were very rare, however (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 for the first 25 days:

$$BC = (M - M_{exp})/M_{exp} \qquad (1)$$

Chicks were divided into five categories depending on the egg from which they hatched and the rank within the brood at hatching:

– a_1=chick from a one-egg clutch;
– a_{12}=first-hatched chick from a two-chick brood;
– b_{12}=second-hatched chick from a two-chick brood;
– a_{11}=single chick originating from the first-laid egg of a two-egg clutch of which the second egg did not hatch; and
– b_{11}=single chick originating from the second-laid egg of a two-egg clutch of which the first egg did not hatch.

Of the 434 nests listed in Table 1, 47 did not hatch any chick because of egg predation by gulls or oyster-catchers *Haematopus ostralegus*, because of addled eggs, or because some chicks died in the process of hatching. Not all chicks of the remaining 387 nests could be correctly matched to corresponding nest or egg and some very young chicks lost their metal ring. A

total of 527 hatchlings originating from 352 nests were correctly classified—141 a_1 chicks, 171 a_{12} chicks, 164 b_{12} chicks, 24 a_{11} chicks, and 27 b_{11} chicks. Because of the large size of the enclosures, coloniality was preserved, but it was impossible to measure all chicks within the enclosure on each occasion without causing unacceptably long disturbance. Eighty-two randomly chosen broods were therefore removed from the enclosures when more than 10 days old. For the 445 chicks remaining in the enclosures from hatching until fledging we observed no significant effect of hatching date on fledging viability, after controlling for the effects of year, location, and chick category (generalised linear regression analysis, deviance change=1.5, df=1, n.s.). Hatching date was not, therefore, considered in subsequent analysis.

For each period of five days, mortality was computed by dividing the number of non-surviving chicks (found dead or missing from the enclosures) by the total number of chicks present at the onset of the five-day period. Chicks that were removed from the enclosures were included in the computation of mortality until they were exiled. Dead chicks were sampled and the day of death was estimated by smell, features of the eyeball, and state of putrefaction; they were subsequently removed from the enclosures.

Statistical analysis

Generalized linear models for 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 the effects of year and location. Interaction terms were only included if they were significant. The variables location (i.e. combination of year and colony, eight levels), age category (six levels), chick category (a_1 chick, a_{12} chick etc., five levels) were entered in the analyses as factors. All generalized linear models (GLM) were corrected for overdispersion.

Results

Mortality

Mortality of Sandwich tern chicks did not differ between locations (GLM, change in deviance=118,

df=7, n.s.) but differed significantly between age categories (GLM, change in deviance=36.2, df=4, $P < 0.001$). Inclusion of chick category in the regression analysis resulted in significant effects on chick mortality (GLM, change in deviance=272.1, df=4, $P < 0.001$), and also the interaction term location×chick category had significant effects on chick mortality (GLM, change in deviance=54.6, df=27, P=0.001). Of a_1 and a_{12} chicks, respectively, 73.4 and 73.1% survived until fledging whereas only 6.2% of the b_{12} chicks survived (Fig. 1). Within five days of 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 in 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, i.e. 1.1% of all two-chick broods (n=171). Another three b_{12} chicks were removed from 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 and one b_{12} chick that was removed from the enclosure at 24 days old had an a_{12} sibling that had already fledged. If we assume this last b_{12} chick actually fledged, 1.8% of all initial two-chick broods fledged two chicks. Mortality rates were significantly higher for a_{11} (64.3% survival) and b_{11} chicks
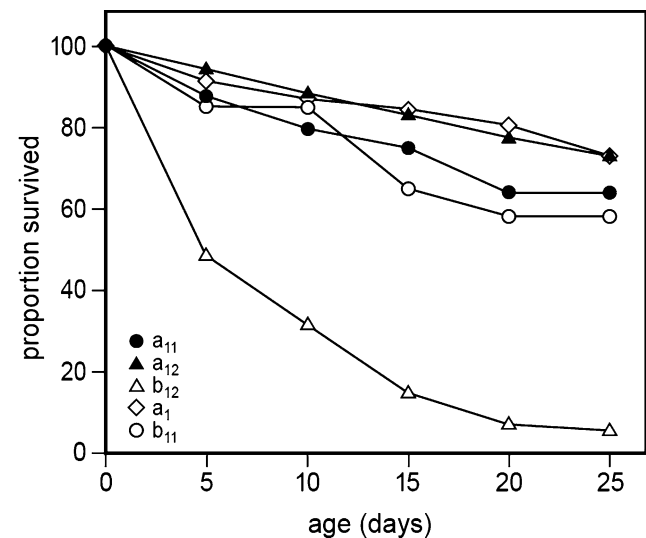
Fig. 1 Cumulative survival of Sandwich terns chicks held in enclosures on Griend in 1992–1999 and Hirsholm in 1997 in relation to laying sequence of the egg, rank within the brood, and age. a_{11}=chick originating from the first-laid egg of a partially hatched clutch, a_{12}=first-hatched chick of a two-egg clutch, b_{12}=second-hatched chick of a two-egg clutch, a_1=chick of a one-egg clutch, b_{11}=chick originating from the second-laid egg of a partially hatched clutch

(58.5%) than for a_1 and a_{12} chicks (Fig. 1). Of the seven b_{12} chicks which hatched after the death of the a_{12} chick 57.1% survived, very similar to the survival of b_{11} chicks.

When hatching success and fledging success are combined (Table 2) it follows that producing two-egg clutches has slight advantages for Sandwich terns in terms of chick production. Of all one-egg clutches 63% successfully raised a chick (0.63 fledglings per pair) whereas breeding success amounted to 0.69 fledglings per pair in two-egg clutches. For the two-egg clutches 82.4% of all eggs hatched successfully; somewhat lower than for one-egg clutches (85.5%), but the difference was not significant (chi-square test, $\chi^2=0.93$, n.s.). The probability of a complete hatching failure of the nest was still 6.1% lower in two-egg clutches.

Hatching mass significantly differed between a_{12} and b_{12} chicks (Table 3), 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. Early chick mortality seems, nevertheless, independent of the laying sequence of the egg. Although early mortality was much higher for b_{12} chicks than for a_{12} chicks, there was no significant difference between a_{11} and b_{11} chicks (Table 4). Early mortality of chicks in partially hatched nests (a_{11} and b_{11} chicks) was much higher than in fully hatched nests (a_{12} and a_1 chicks), but the difference was not significant.

Causes of death

The proportion of non-surviving chicks missing from the enclosure differed between locations (GLM, change in deviance=41.7, $df=7$, $P<0.001$). 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 the effects of location, the proportion of missing chicks differed significantly between age-categories (GLM, change in deviance=12.2, $df=4$, $P=0.02$). Of non-surviving chicks of ages 0–4 and 5–9 days, 52.1 and 44.4%, respectively, went 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. 2). The body condition of chicks that survived until fledging varied between –0.63 and 0.47. Body mass of chicks measured within 3 days of death (subsequently denoted "last live body mass") was usually much lower than that of surviving chicks (Fig. 2). The last live body mass of chicks that were subsequently found dead or went 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. Six percent of 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) were mainly (81.8%) b_{12} chicks (last live body condition of preyed a_{12}, a_1, a_{11}, or b_{11} chicks compared with 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, $t=0.58$, $P>0.05$).

Low food intake causing poor body condition was, apparently, an important cause of mortality of

Table 2 The effects of clutch size on hatching and breeding success of Sandwich terns on Griend and Hirsholm

Clutch size	Number of nests	Chick category	Hatching success (%)	Chick survival (%)	Breeding success (fledglings per pair)	Overall breeding success (fledglings per pair)
One egg	173	No chick	14.5		0.00	0.63
		a_1 Chick	85.5	73.4	0.63	
Two 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	

Chick survival rates were derived from Fig. 2

Table 3 Body mass and head length (mean±SD) of newly hatched Sandwich tern chicks on Griend in relation to brood size and order of hatching

	Number of chicks	Body mass (g)	Head size (mm)
a_1	31	27.05±2.53 (b_{12})	37.60±1.18
a_{12}	21	26.98±2.10 (b_{12})	38.03±1.05
b_{12}	32	25.00±2.45	37.59±1.26

Text within parentheses denotes significant differences (Scheffé-test, $F_{2,82}$=7.62 and 1.11, $P<0.001$ and n.s., respectively)

Table 4 Mortality of Sandwich tern chicks during the first five days after hatching in relation to chick category

Chick category	Number of chicks	Mortality
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)

The number of non-surviving chicks is shown in parentheses. Mortality for chick category b_{12} was significantly different from that for all the other chick categories ($P<0.05$ by means of chi-square or Fisher's exact test)

enclosed Sandwich tern chicks at Griend and Hirsholm. One might, therefore, expect that having two chicks is disadvantageous for their growth and that the time 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 five categories according to their age at the moment the b chick died. Indeed, the time of death of the b chick significantly affects the survival of the a chick (GLM, having controlled for effects of *location* and *age category*, change in deviance=13.6, *df*=4, $P<0.01$), but the direction was unexpected (Fig. 3). In nests where the b chick died 0–4 days after hatching of the a chick, the a chick had relatively low chances of survival (64.5% survived until fledging, so very much the same as for a_{11} chicks and somewhat higher than for b_{11} chicks). If the b chick survived the first five days but died afterwards, survival chances of the a chick ranged from 80.8 to 84.0%. In the few nests where the b chick survived until fledging, survival 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, $P=0.02$). Where a decrease in fledging condition with increasing duration of the time two chicks were present was expected, however, an increase is found (Fig. 4).
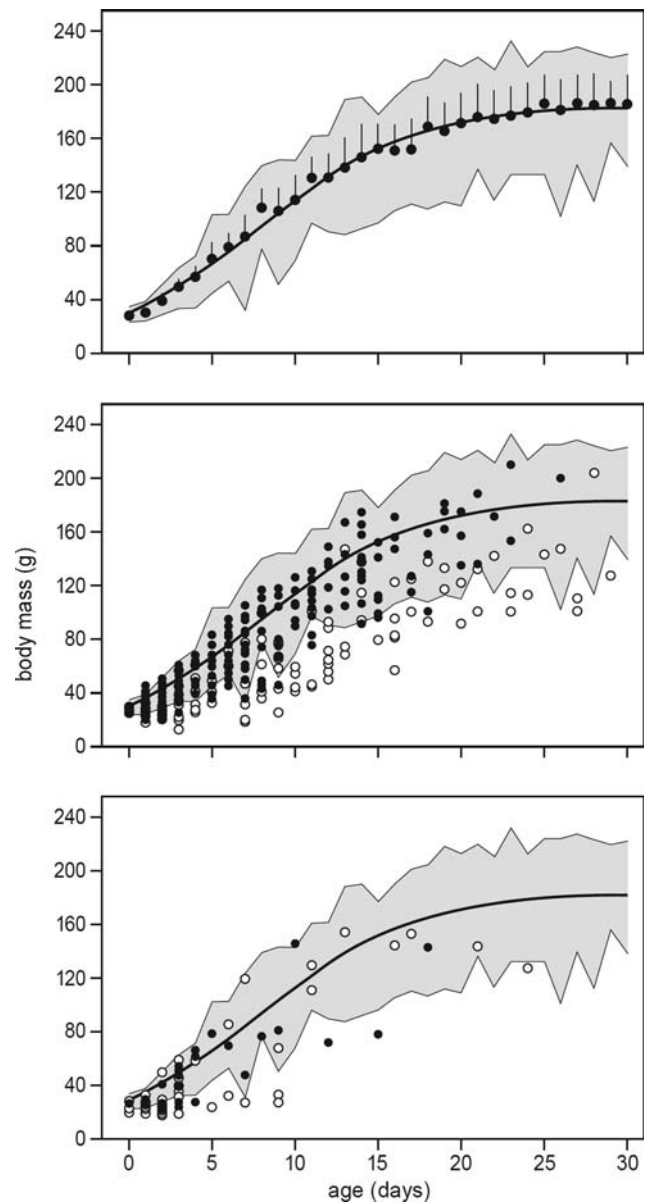

Fig. 2 Body mass in relation to age (means±SD and ranges) of enclosed Sandwich tern chicks on Griend and Hirsholm that survived until fledging (*upper graph*), that were later found dead (*middle graph*), or that went missing from the enclosures when not yet able to fly (*lower graph*). *Drawn lines* are logistic growth curves fitted through the data for fledged chicks (body mass (g)=183.3/(1+5.08×exp(−0.212×age)), *n*=1,532, r^2=0.87). *Black dots* denote body mass >3 days before death or before they were missing from the enclosure, *open dots* denote body mass within 3 days of death or going missing

## Discussion

Overproduction and brood reduction

Brood reduction is rather commonplace in birds and is thought to be facilitated by producing a small final egg (Slagsvold et al. 1984) and by asynchronous hatching of
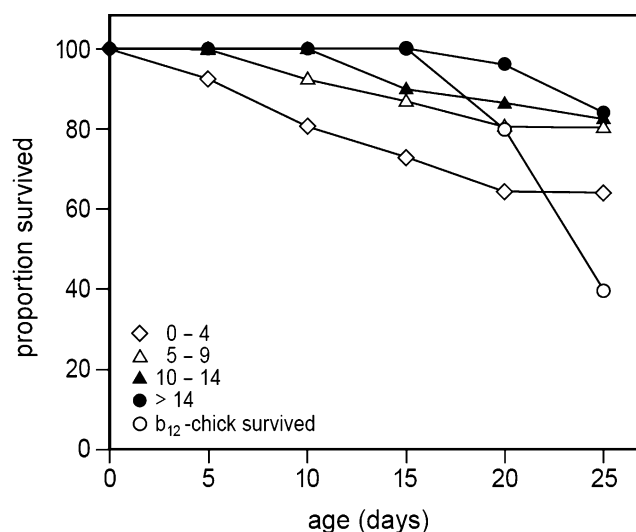
Fig. 3 Cumulative survival of first hatched Sandwich tern of two-chick broods in relation to the time the second hatchling was present. *0–4* Second hatched chick died between day 0 and day 4 from hatching of the first chick, etc.

the eggs (Anderson 1989; Cash and Evans 1986). Overproduction and brood reduction in birds may serve various functions (review in Mock and Parker 1998):

1 it may enable parents to select the fittest offspring;
2 it may serve as a mechanism for resource tracking (extra offspring may be affordable in the event of unpredictable improvement of the food situation);
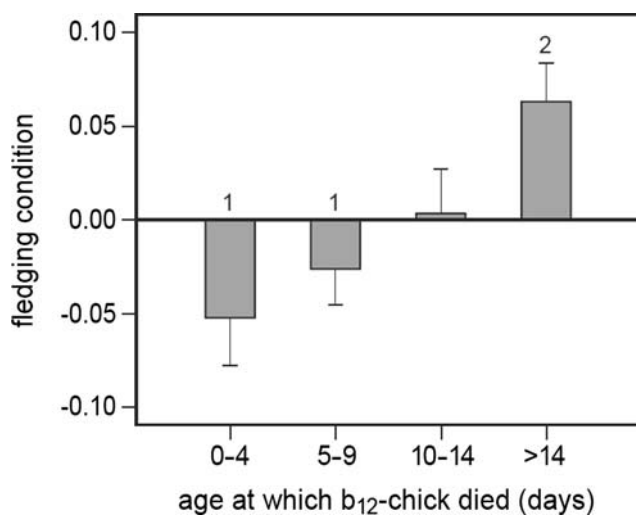
Fig. 4 Fledging condition of first-hatched Sandwich tern chicks in relation to the time of death of the second hatchling. *0–4* Second hatched chick died between day 0 and day 4 from hatching of the first chick, etc. *Numbers* above bars indicate that the fledging condition of chicks of which the b_{12} chick died at an age of more than 2 weeks significantly differed from that in the two categories where the b_{12} chick died when < 10 days

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 failure of an egg or defective offspring (see also Clark and Wilson 1981).

In Sandwifch terns, overproduction serving resource tracking (2) seems rather costly, because in 10 years (1992–2001; data from this study and unpublished data) almost no pair was able to fledge two chicks on Griend. Given that Sandwich terns can live more than 25 years, however, and if the costs involved in producing an extra offspring are relatively low, it might be affordable to produce two eggs even if "good" years occur at a very low frequency. There is however, growing evidence that egg production incurs high fitness costs in larids (Heaney and Monaghan 1995; Monaghan and Nager 1997; Monaghan et al. 1998; Nager et al. 2000, 2001), so the resource-tracking hypothesis does not seem applicable to Sandwich terns. The current food situation and the high rates of kleptoparasitism cause food stress for Sandwich tern parents on Griend (Stienen and 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 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 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 two-egg clutches only 1 egg hatched, 7.2% of the fledglings of two-egg clutches originated from second-laid eggs and parents that laid two eggs had a somewhat higher breeding success (Table 2). A similar reproductive strategy is found in *Eudyptes* penguins, which lay two eggs of different sizes and always reduce their brood to one chick (Warham 1975; Massaro and Davis 2004), although in penguins the function of the smaller egg remains unclear (e.g. St. Clair 1998). Obligate brood reducers presumably can afford the production of a second egg because the involved fitness costs are smaller than the reproductive gain. In

seabirds that always lay a single egg, the cost of producing an extra egg is probably larger than the gain. In facultative brood reducers the balance between cost and gains may depend on food resources. In facultative brood-reducing penguins the initial size hierarchy of siblings and hatching asynchrony are variable and may thus be adjustable to food abundance (Seddon and van Heezik 1991; Williams and Croxall 1991). In contrast, short-lived passerines lay large clutches with relatively large final eggs to minimise initial size differences between siblings and to promote the survival of the entire brood (Clark and Wilson 1981; Slagsvold et al. 1984).

Reproductive output

Sandwich tern 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 a high chance of survival 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. Chances of survival of their chicks were somewhat lower (mainly because of high chick mortality during the first 5 days), but fledging condition was comparable with that of the first category. These may be young birds that produce poor quality eggs (Gonzáles-Solís et al. 2004) and of which the eggs are more prone to predation (Veen 1977). Unlike in common terns where chick-rearing ability is affected by the age of the parents (González-Solís et al. 2005), young, inexperienced Sandwich terns seem to experience no more difficulties in feeding offspring than older birds (Veen 1977). In a third category of Sandwich tern parents brood size was reduced in an early phase and the remaining chick also had poor chances of survival. Their chicks were in relatively poor body condition. These parents apparently had no difficulty protecting their eggs and chicks from predators, but had difficulty providing enough food for the chicks. In common terns, these low quality parents are birds in poor body condition that participate in breeding but have consistently poor chick-rearing capacity (Wendeln and Becker 1999). 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 time 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 achieved high survival rates for their a_{12} chick and even had a small chance of rearing two chicks to fledging. If laying two eggs and, sometimes during their lifetime, raising two chicks is a consistent trait of high-quality individuals, this would imply a great fitness gain for those birds and cause strong selection pressures on laying a two-egg clutch.

A reproductive output of less than one fledgling per breeding pair and poor survival of second hatchlings are not unique to Griend or Hirsholm, but seem rather commonplace for Sandwich terns. In a Sandwich tern colony at Zeebrugge, Belgium, no pair was able to fledge two chicks in any of the five years from 2001 to 2005 (own observations in enclosed subcolonies). Isenmann (1975) mentions that in the Camarque, France, only 7% of all pairs had two chicks close to fledging. All other measurements of breeding productivity in Sandwich terns in the literature are doubtful, because 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. These studies, nevertheless, rarely observed a breeding success much higher than one fledged chick per pair (Schmidt 1969; Chestney 1970; Langham 1974; Walsh et al. 1990). Only Campredon (1978) mentions breeding success of more than 1.7 fledglings per pair, and he based this figure on the number of dead chicks found in the colony (which would have excluded losses because of predators, if any). At first sight, Veen (1977) also observed 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 with our study, however, in which 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, mortality in the 1970s is comparable with that in the 1990s when 83.5 and 15.2%, respectively, of a_{12} and b_{12} chicks survived the first two weeks posthatching (Fig. 2).

The extent to which our results can be compared with those from studies in which chicks were not held in enclosures remains puzzling. After all, by preventing the chicks from moving away from the colony site by retaining them in enclosures they suffer from increased kleptoparasitism and, consequently, mortality rates might have been higher than in natural situations (Stienen and Brenninkmeijer 1999). On the other hand, one would expect that enclosing chicks would only affect older chicks, because:

1 in natural situations very young chicks stay in the vicinity of the nest; and

2 kleptoparasitism by black-headed gulls is rather low during the first week after hatching (Stienen et al. 2001).

In our study, however, most b_{12} chicks died at 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 less than 1 week old and during observations of Sandwich tern parents feeding fledglings on beaches around Griend we very rarely observed more than one fledgling per parent, suggesting a usually low survival of second hatchlings.

Food availability

Stienen and Brenninkmeijer (2002) have shown that in the presence of kleptoparasitising gulls food availability on Griend is not sufficient to rear two chicks to fledging. The current study confirms that undernourishment resulting in a decrease in body condition that finally leads to starvation was an important cause of death of enclosed Sandwich tern chicks on Griend and Hirsholm. A large proportion of the chicks that were missing from the enclosures also lagged behind in body mass. The high proportion of missing chicks on Hirsholm (70.6% of all non-surviving chicks were missing) is probably the result of removal of large numbers of living and dead chicks by herring gulls (own observation). On Griend, predominantly black-headed gulls preyed upon Sandwich tern chicks. Despite large differences between the proportion of chicks 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 b_{12} 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 for common terns (Nisbet 1975) and was earlier described for Sandwich terns on Griend by Veen (1977).

In an experimental study in the Caspian Sea, Gauzer (1989) found that 73.9% of synchronously hatched Sandwich terns broods produced two fledglings, compared with 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 if, in the experimentally enlarged clutch, the three eggs hatched synchronously. Although we were not able to find Gauzer's (1989) definition of fledging, the study revealed that asynchronous hatching of the

eggs facilitates brood reduction in Sandwich terns. It also seems that the food situation in Gauzer's study area was much more favourable than on Griend and Hirsholm. In our study hatching asynchrony resulted in a knock-out race and facilitated the death of the youngest sibling. If both chicks had hatched simultaneously periods of food stress might very well have resulted in the death of both siblings.

In conclusion, for most pairs of Sandwich terns on Griend and Hirsholm the brood was reduced to only one chick at an early stage, mainly by starvation of the second hatchling. Starvation was also an important cause of death for first hatchlings and singletons, suggesting severe food stress. Earlier studies on Griend (Stienen et al. 2001; Stienen and Brenninkmeijer 2002) showed 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 gulls increases.

Zusammenfassung

Konsequenzen von Gelegegröße und Schlüpffolge für die Mortalität von Küken der Brandseeschwalbe: Warum in Zweiergelege investieren?

Wir untersuchten Sterblichkeit und Wachstum von Küken der Brandseeschwalbe *Sterna sandvicensis* innerhalb umzäunter Nester in Kolonien auf den Inseln Griend im Niederländischen Wattenmeer (1992–1999) und Hirsholm im Dänischen Kattegat (1997). Der Ausfliegeerfolg von Küken aus Einergelegen oder von Küken aus erstgelegten Eiern komplett geschlüpfter Zweiergelege betrug 73%, von Küken aus teilweise geschlüpften Zweiergelegen 59–64%. Dagegen überlebten nur 6% der letztgeschlüpften Küken von Zweierbruten bis zum Ausfliegen. Da in 18% der Zweiergelege nur ein Ei schlüpfte, stammten weitere 7% der aus Zweiergelegen hervorgegangenen Flüglinge aus einem zweiten Ei. Zweierbruten wurden normalerweise innerhalb weniger Tage auf einen Jungvogel reduziert. Mehr als die Hälfte der zweitgeschlüpften Küken verhungerte oder wurde erbeutet, bevor sie ein Alter von 5 Tagen erreicht hatten. Dass Brandseeschwalben trotzdem in Zweiergelege investieren, wird als Strategie gegen einen frühzeitigen Verlust eines der Eier oder Küken gedeutet. Elternpaare mit Zweiergelegen erreichten durchschnittlich einen geringfügig höheren Bruterfolg als Elternpaare mit nur einem Ei. Unterernährung war

die wichtigste Todesursache der Küken auf Griend und Hirsholm, entweder aufgrund Verhungerns oder indirekt durch selektive Prädation von Küken in schlechter Kondition. Diese Ergebnisse sowie frühere Publikationen weisen darauf hin, dass Brandsee-schwalben im Niederländischen Wattenmeer unter Nahrungsengpässen leiden.

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