

Variation in growth in Sandwich Tern chicks *Sterna sandvicensis* and the consequences for pre- and post-fledging mortality

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Fitness consequences of variation in body mass growth and body condition were studied in a Sandwich Tern *Sterna sandvicensis* colony on Griend, Dutch Wadden Sea, during 1990–2000. Body mass increment during the linear growth phase predicted nestling survival probabilities accurately. Chicks growing less than 8 g per day had low survival probabilities until fledging, but within a range of 8–11 g per day growth only small effects on chick survival were observed. Effects of slow growth on survival became obvious after about 10 days after hatching. Slow growing chicks reached a much lower fledging mass, whereas slow growth had only small effects on structural size at fledging. Body condition of the chicks was highly variable and had strong effects on survival until fledging. However, body condition during the nestling stage did not influence post-fledging survival. Body condition at fledging had no effects on post-fledging survival and did not affect final mass or body size. It is argued that low fledging mass can be overcome soon after fledging, as parents take their fledglings closer to the foraging areas, thereby avoiding high rates of kleptoparasitism by Black-headed Gulls *Larus ridibundus*.

Many birds show great flexibility in growth. When food availability is low, maturation of the chicks slows down and normal growth is resumed when the restrictions are lifted, without any consequences for final mass or morphology. However, in other species, poor feeding conditions result in reduced fledging weight and may even affect adult size (Schew & Ricklefs 1998). Moreover, slow growth can increase chick mortality and may have negative effects on post-fledging survival or recruitment, as has been reported in many species (Gebhardt-Henrich & Richner 1998). Most seabirds depend on highly unpredictable food resources that show large temporal and spatial variations. Superimposed environmental conditions, such as weather and tide, demand an even greater flexibility in seabirds. One would

therefore expect that adaptive features such as variable growth rate are well developed, especially in highly specialized seabirds, such as the Sandwich Tern *Sterna sandvicensis*, that undertake long feeding trips. For Sandwich Tern parents, reduced offspring growth means a considerable reduction in the costs for rearing their young (Klaassen *et al.* 1992). This might be an important mechanism for this species to cope with unpredictable food resources. However, the estimates of Klaassen *et al.* (1992) were based on laboratory-raised chicks. In the field, the limits of the parents are set by present and future costs for rearing the young. It may be argued that if parental effort has consequences for their own future survival, parents will probably lower feeding rates to the chicks when conditions are poor. By contrast, if reduced growth also has fitness consequences in terms of chick mortality or post-fledging survival, this could reduce the extent to which growth can be adjusted.

This paper focuses on the fitness consequences of poor development in Sandwich Terns. We hypothesize that the growth rate of Sandwich Tern chicks is highly flexible and that reduced growth has minimal

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consequences for nestling and post-fledging survival. Sandwich Terns depend on only a few fish species that show strong fluctuations in their horizontal and vertical distributions (Stienen *et al.* 2000). They have to cope with strong variations in the amount of food they can offer to their chicks owing to variable weather conditions (Stienen *et al.* 2000) and food losses to kleptoparasitizing gulls (Stienen *et al.* 2001, Stienen & Brenninkmeijer 2002). Here, we use data on growth and survival of Sandwich Tern chicks held in enclosures on Griend, the Dutch Wadden Sea, to examine the consequences of variation in growth rate and body condition for nestling survival. Next, we discuss the effects of poor growth during early development on the body weight at fledging. Using ring recoveries, we examine whether a poor body condition during the nestling phase or at fledging has repercussions for an individual's chance to recruit to the colony in later years. Because Sandwich Terns are not full-grown at fledging, we also investigate post-fledging growth patterns and the consequences of poor fledging condition for the final size of an individual.

METHODS

Study area

The study was conducted on the isle of Griend during 1990–2000. Griend (57 ha) is situated in the western part of the Dutch Wadden Sea (53°15'N, 5°15'E). The island supports large colonies of Black-headed Gulls *Larus ridibundus* (about 23 000 pairs in the 1990s), Common Terns *S. hirundo* (about 2100 pairs) and Sandwich Terns (about 7000 pairs) and smaller colonies of Mew Gulls *L. canus*, Herring Gulls *L. argentatus* and Arctic Terns *S. paradisaea*. During the study period, the population of Sandwich Terns fluctuated between 5600 (1996) and 8300 (1994) pairs, consisting of several subcolonies. In 1992–98, part of a subcolony, containing 50–100 nests, was fenced (by enclosures) to prevent the chicks from walking away from the nest-site (see also Stienen & Brenninkmeijer 1999). Accurate data on chick growth and survival were obtained from enclosed chicks. In addition, each year a number of free-living chicks, mainly of unknown age, were ringed and retrapped as often as possible. Statistical tests were performed using the SPSS/PC+ 4.0 (Norusis 1990) and the GENSTAT statistical package (Genstat 5 Committee 1993).

Enclosures

Within the enclosures, all chicks were ringed within 3 days of hatching and each chick's position in the hatching order was noted. The age of the chicks was estimated from the state of the egg during the previous control, feather characteristics, total head length, and from whether or not the chick was still wet or had eggshell remains on its back. The chick's body weight and total head length (i.e. head and bill) were measured within 3 days of hatching, whenever possible, and subsequently every third day. To minimize disturbance in the colony, stretched wing chord was measured less often than this. Due to weather conditions and to reduce disturbance, not all chicks were measured during each visit. Dead chicks were collected, and their body mass and total head length were measured. The day of death was estimated from biometrics, smell, features of the eyeball and state of putrefaction. Chicks younger than 25 days, that were missing from the enclosures, were categorized as lost to predators. If the age of a missing chick was more than 24 days, the chick was presumed to have fledged. Probably the best way to describe fledging in Sandwich Terns is by using wing length as a reference for the ability to fly (Stienen & Brenninkmeijer 1999). However, because wing length was not known for some enclosed chicks, we used their age instead. Although deviations were sometimes large, there was a strong relationship between age and wing length in enclosed chicks (Fig. 1).

Within the enclosures, parents on average laid 1.6 eggs per nest. Over all years, of all pairs that laid two eggs only 0.7% were able to fledge two chicks. Fledging success averaged 0.64 chicks per pair.

Growth and condition

For age 0–24 days, missing body masses of enclosed chicks were interpolated assuming linear growth between two measurements. To avoid unrealistic biases caused by incompletely digested meals, only measurements with an interval of more than two days were used. For each single or first-hatched chick for which at least three measurements of body mass were available and for which the first measurement was made when less than 6 days old, average growth rate was computed for the linear part of the growth curve (i.e. age 4–14). We used average growth rate instead of using regression analysis or parameters of logistic growth (e.g. Harris & Rothery 1985, Nisbet *et al.* 1998, 1999) because body mass development

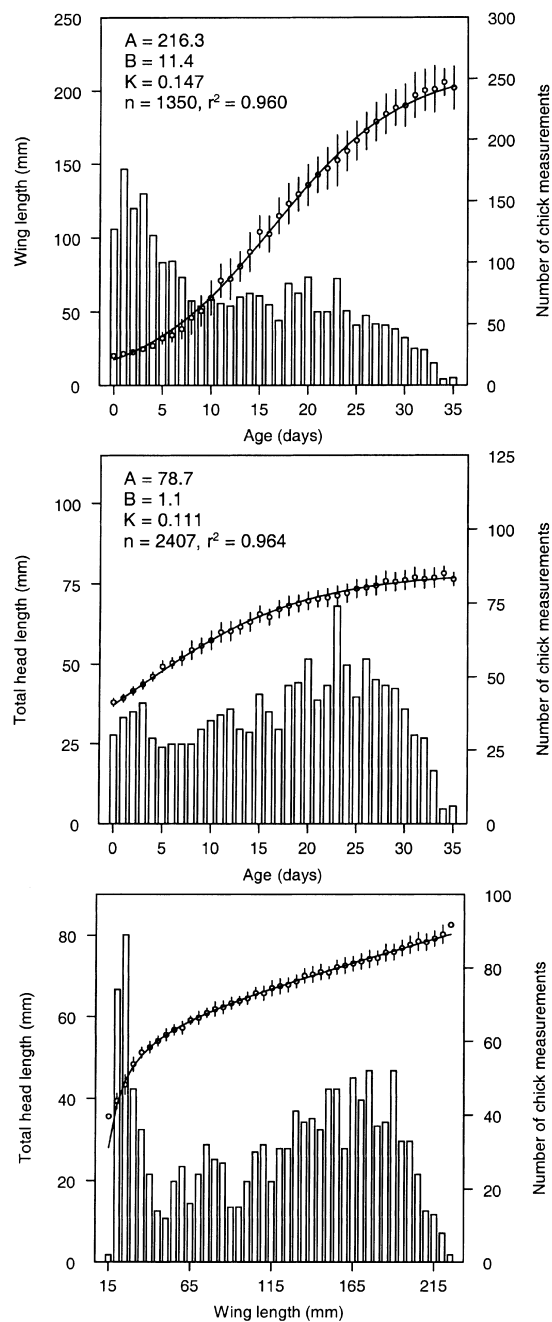


Figure 1. Development of wing and total head length (open symbols $\pm$ sd) with the age of enclosed Sandwich Terns on Griend in 1992–1998 (upper and middle graphs). Drawn lines are logistic growth curves ($\text{length} = A/(1 + B \cdot e^{-K \cdot \text{age}})$) for which the parameters are shown in the top of the graphs. The lower graph shows the relationship between wing length (15 = 12.5 – 17.4 mm, 20 = 17.5 – 22.4 mm, etc.) and total head length. The drawn line is a quadratic by linear curve: $\text{total head length} = 57.1 + 69.5/(1 - 0.22 \cdot \text{wing length}) + 0.11 \cdot \text{wing length}$, $n = 1350$, $r^2 = 0.978$. Bars denote the number of chick measurements (right axis).

of the chicks often was very irregular. Among other things, body mass growth showed large variations with weather conditions (Stienen & Brenninkmeijer 2002).

For enclosed chicks, an index of body condition (CI) was defined as the proportional deviation of measured body mass (M , g) from average body mass (M_{exp} , g) of surviving chicks (i.e. age at final measurement ≥ 25 days) with similar total head length (Eq. 1).

$$\text{CI} = (M - M_{\text{exp}})/M_{\text{exp}} \quad (1)$$

We used total head length as a reference for age because the age of most unenclosed chicks was missing, allowing us to use the same index of body condition for unenclosed chicks. For enclosed chicks there was a strong correlation between age and total head length on the one hand and between wing length and total head length on the other (Fig. 1).

Unenclosed chicks

In addition, a number of unenclosed chicks of varying age were ringed each year. Unenclosed chicks were only used to analyse the effect of fledging condition on the probability of recruitment to the colony in later years. Compared to enclosed chicks, most free-living chicks experience higher food intake rates and growth (Stienen & Brenninkmeijer 1999). By including unenclosed chicks, the sample size was enlarged and variation in fledging condition increased.

For enclosed and unenclosed chicks, fledging condition was defined as the average body condition of chicks with a total head length between 75 mm and 80 mm. Wing length of these chicks averaged 189.2 ± 14.4 mm. At this wing length about 43% of the chicks were able to fly (Stienen & Brenninkmeijer 1999). As the age of most unenclosed chicks was unknown, we applied an alternative definition of fledging. In all analyses referring to recruitment, enclosed and unenclosed chicks were presumed to have fledged when total head length exceeded 75 mm. The average age of 62 enclosed chicks with a head of 75 mm was 27.6 ± 3.9 days.

Recruitment

From 1994 to 2000, effort was put into reading metal rings of adult Sandwich Terns. The rings were read by telescope from a movable hide. Most

Table 1. Number of Sandwich Tern chicks ringed on Griend per annum and the number of first recoveries in later years.

Year of ringing	Number of chicks ringed	Year of recovery							Total
		1994	1995	1996	1997	1998	1999	2000	
1990	150	3	9	2	0	0	0	1	15
1991	879	5	17	6	3	1	0	1	33
1992	2195	1	56	70	17	10	19	20	193
1993	1024	0	1	52	22	9	18	12	114
1994	3412		0	5	33	76	82	87	283
1995	3168			0	3	72	180	181	436
1996	2749				0	2	61	89	152
1997	2489					0	15	137	152

rings were read during the birds' courtship display in the colony, at beaches near the colony where females fed on shell fragments just before egg laying (Brenninkmeijer *et al.* 1997), and at roosts near the colony. In addition, some ringed adults were caught on their nest. Although some birds, whose rings were read by telescope, were trapped on their nest later in the season, and most birds were engaged in courtship or nesting activities, there was no absolute certainty that all recovered birds actually started breeding on Griend, but for convenience we call them all recruits. Only a small proportion of the ringed birds present on the island was recovered, so the presented return probabilities cannot be used as estimates of survival or recruitment. We further assume that the resighted birds are representative of the entire population. The number of chicks ringed and the number seen on Griend in later years are listed in Table 1. In total 850 ringed birds were seen on Griend, corresponding with 4.9% of all chicks ringed. Birds were first seen when 2 years old, but most were first seen when 3–5 years old. As not all chicks that were born after 1997 might yet have returned to Griend they were omitted from the analyses.

RESULTS

During the linear growth phase of 143 first-hatched and single Sandwich Tern chicks, body mass growth averaged 8.7 ± 2.1 g per day. Survival probabilities of the chicks were closely linked to growth rate between 4 and 14 days (Fig. 2). Nestling survival sharply increased from 0.3 for chicks growing 1 g per day to more than 0.8 when growth exceeded 8 g per day. Presumably, the effect of growth rate on survival probabilities is even more dramatic than presented in Fig. 2, because most slow-growing chicks are not

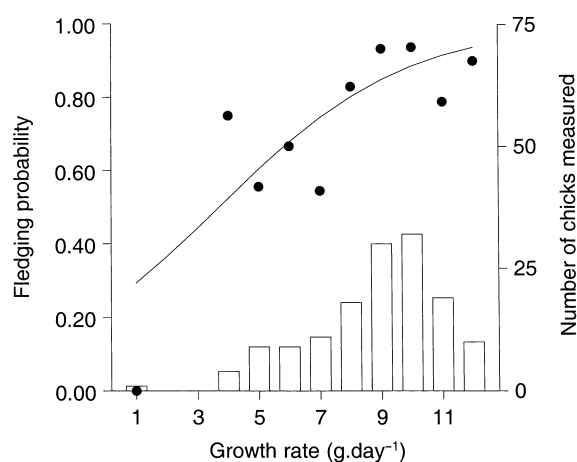


Figure 2. Relationship between body mass increase during the linear part of growth and survival probabilities until fledging (dots) of first-hatched and single Sandwich Tern chicks on Griend in 1992–1998. Drawn line represents the logistic curve (logistic regression, survival probability = $1 - \{\exp(1.207 - 0.326 \cdot \text{growth}) / [1 + \exp(1.207 - 0.326 \cdot \text{growth})]\}$, deviance = 10.4, $P < 0.01$). Bars denote the number of chicks measured (right axis).

represented in the graph, as they had already died before they could be measured three times.

Growth and fledging condition

Body mass growth during the linear growth phase had no consequences for the condition of a chick at fledging (Pearson regression: $n = 92$, $r^2 = 0.02$, $P > 0.05$). On average, enclosed chicks that fledged in poor condition (i.e. fledging condition ≤ -0.10) experienced normal growth of body mass during the first 10 days of their lives, but deviated from the growth pattern of chicks in good fledging condition (i.e. fledging condition ≥ 0.10) after that age (Fig. 3).

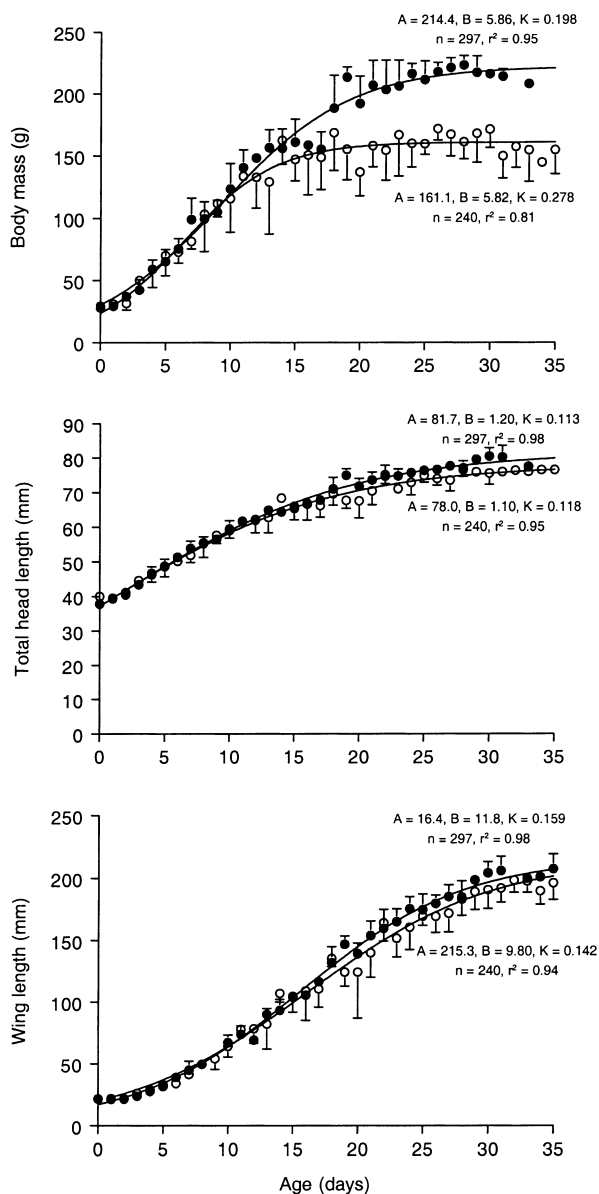


Figure 3. Pre-fledging development (means $\pm$ sd) of body mass (upper graph), total head length (middle graph) and wing length (lower graph) in Sandwich Tern chicks fledging in poor (fledging condition ≤ -0.10 , open circles) and good condition (fledging condition ≥ 0.10 , dots). Only chicks that reached an age of 25 days were included in the analysis. Drawn lines represent logistic growth curves for which the parameters are shown in the top of the graph.

The deviation of structural growth (total head length and wing length) occurred somewhat later and was much smaller than the deviation of body mass growth. Asymptotic body mass of fledglings in poor condition amounted to 161.1 g; a difference of -27.4% compared with chicks fledging in good condition

(asymptotic mass 222.0 g). This was accompanied by an average decrease in asymptotic total head and wing lengths of only 4.6 and 0.5%, respectively.

Pre-fledging mortality

To analyse whether the body condition of a chick at any moment during the nestling period had consequences for its chance to survive until fledging, we divided the chick period into five categories of total head length, so that each category coincided with a difference in average age of 2–5 days (Table 2). In a logistic regression approach, we first controlled for hatching position (two groups: first-hatched or single chicks and second-hatched chicks). For enclosed chicks with a total head length < 65 mm, hatching position had a strong effect on nestling survival (Table 2), with second-hatched chicks having a much lower survival probability. If second hatchlings survived until their total head length was 65 mm or more, their survival probability no longer differed from first-hatched or single chicks.

The body condition of very young chicks (total head length < 50 mm) did not influence their survival until fledging (Table 2). In the later periods until total head length was at least 70 mm, chicks in poor condition experienced lower survival chances, whereas near fledging ($70 \text{ mm} \leq \text{total head length} < 75 \text{ mm}$) body condition no longer influenced survival. Although some even older chicks (total head length ≥ 75 mm) were found inside the enclosures, their survival could not be estimated because some of these chicks had already fledged. Nevertheless, their survival probability seems very high. Of 2009 chicks (both enclosed and unenclosed) with a total head length ≥ 75 mm only 27 were found dead on Griend, indicating that most left the island successfully. The interaction term 'body condition $\times$ hatching position' was significant only for chicks with a total head length of 65–70 mm (Table 2), showing a slower increase in survival probability with body condition for second-hatched chicks.

Post-fledging mortality

Next, the effect of body condition on the probability of being resighted in the colony some years later was analysed (further referred to as recruitment). For this analysis, we selected only those chicks that survived until fledging. To increase the sample size, unenclosed chicks were also included in the analysis.

Table 2. Logistic regression analysis examining the effect of hatching position (two categories: first-hatched or single chicks vs. second-hatched chicks) and body condition on the probability of being found dead before fledging for different categories of total length size of enclosed Sandwich Tern chicks on Griend in 1992–1998. In all cases hatching position was entered into the logistic regression model first, following body condition and the interaction term 'hatching $\times$ body condition'. N chicks: the number of chicks measured; the number of chicks found dead is shown in parentheses. Age, wing length and body condition are means $\pm$ se. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Total head (mm)	Age (days)	Wing (mm)	N chicks	Range in body condition	Change in deviance		
					Body condition	Hatching position	Hatching position $\times$ body condition
< 40	0.8 $\pm$ 0.06	20.6 $\pm$ 0.24	170 (101)	–0.42 to 0.70	78.3***	0.0	1.3
40–49	3.1 $\pm$ 0.08	24.5 $\pm$ 0.24	288 (140)	–0.48 to 0.38	104.6***	1.5	0.1
50–59	8.0 $\pm$ 0.12	47.1 $\pm$ 1.03	218 (77)	–0.47 to 0.31	66.1***	10.2**	0.4
60–64	13.2 $\pm$ 0.15	84.2 $\pm$ 1.12	154 (25)	–0.38 to 0.28	5.3*	12.3**	0.8
65–69	17.9 $\pm$ 0.20	121.9 $\pm$ 1.16	170 (21)	–0.50 to 0.69	1.4	46.3***	4.3*
70–74	23.8 $\pm$ 0.21	159.0 $\pm$ 0.94	179 (2)	–0.23 to 0.49	0.0	0.1	0.0

Table 3. Logistic regression analysing the effect of year of birth and body condition on the probability to be seen on Griend in later years for different categories of total head length of Sandwich Tern chicks in 1990–1997. In all cases year was entered into the logistic model first, following body condition and the interaction term 'year $\times$ body condition'. N chicks: number of chicks measured; the numbers of chicks that were seen in the colony in later seasons are shown in parentheses. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Total head (mm)	N chicks	Range in body condition	Change in deviance		
			Year	Body condition	Year $\times$ Body condition
< 40	82 (13)	–0.24 to 0.37	7.2	1.5	6.7
40–49	254 (34)	–0.28 to 0.60	1.9	1.8	2.0
50–59	283 (34)	–0.30 to 0.34	4.4	0.2	5.7
60–64	204 (30)	–0.31 to 0.33	1.9	2.8	2.9
65–69	259 (29)	–0.25 to 0.28	10.2	0.7	2.0
70–74	273 (35)	–0.26 to 0.30	7.6	0.3	8.9
75–80	1620 (195)	–0.45 to 0.31	19.6**	2.5	6.3
≥ 80	390 (43)	–0.33 to 0.23	11.3	0.0	5.6

As the age of most unenclosed chicks was unknown, an alternative definition of fledging is used (see Methods). In a logistic regression analysis examining the probability of recruitment to the colony, we first controlled for possible effects of birth-year (Table 3). For chicks measured around fledging (total head length: 75–80 mm), year of birth had a significant effect on the probability of recruitment to the colony (Table 3). Chicks hatched in 1990 had a relatively low local recruitment probability, whereas chicks hatched in 1995 had the highest chance to be seen in the colony several years later. For all other groups of total head length, year of birth had no significant effect. Adding body condition and the interaction term 'year $\times$ body condition' to a model already containing birth-year produced no significant change in deviance in any of the 'age-groups' (Table 3).

The results suggest that in Sandwich Terns, poor development of a chick influences survival until

fledging, and this has large effects on the body mass at fledging, but less effect on the size at fledging. However, it also shows that fledging condition has no consequences for post-fledging survival. In agreement with this, fledging condition of 24 juveniles, which were found dead within 3 years of fledging, did not differ significantly from that of 249 recruited terns (0.040 ± 0.086 and 0.008 ± 0.009 , respectively, Student's t -test, $t_{271} = 1.75$, $P = 0.08$).

Post-fledging growth

Body mass, total head and wing length of 30-day-old young, that were still in the colony, amounted to approximately 75, 73 and 62%, respectively, of that of incubating adults on Griend (Fig. 4). In total, 13 juveniles of known age were mist-netted shortly after the breeding season in 1997 and 1998 at the isle of the Richel, situated 9 km north-west of Griend.

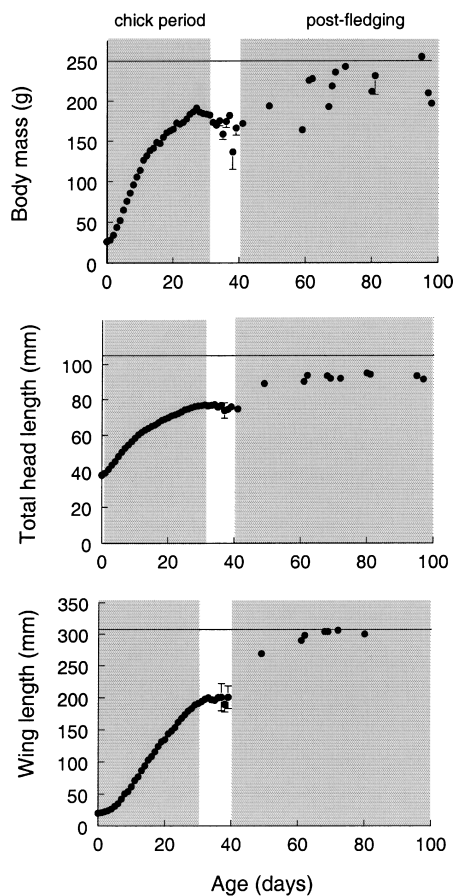


Figure 4. Pre- and post-fledging development of body mass, total head length and wing length in Sandwich Terns. Data on post-fledging development were derived from juveniles caught in mist nets at the isle of the Richel, 9 km north-west of Griend. Drawn lines indicate average body mass, total head length and wing length of 766 incubating adults of Griend in 1992–1999.

Biometric measurements of these individuals indicate that the growth of body mass and wing length are almost completed within 100 days from hatching, although the total head length reached only 89% of adult total head length (Fig. 4).

A total of eight adults with known fledging condition were trapped on the nest on Griend some years later. Additionally, shortly after the end of the breeding seasons of 1997 and 1998, four adults with known fledging condition were mist-netted at the isle of the Richel. These adults represent a range in fledging condition between -0.02 and 0.16 . There were no significant effects of capture location (Griend or Richel) or fledging condition on any biometric measurement of adult Sandwich Terns (ANCOVA, ns in all cases) (Fig. 5).

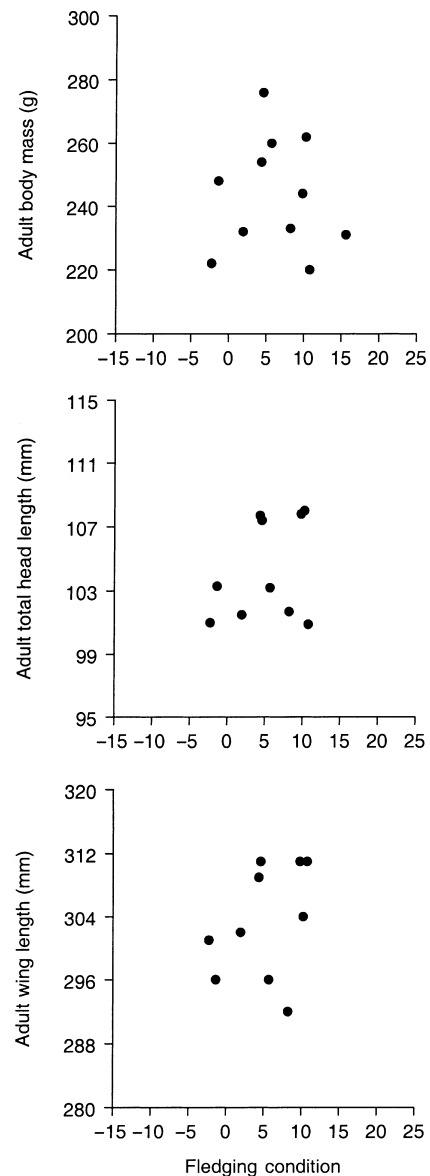


Figure 5. Relationship between adult biometrics and fledging condition in Sandwich Terns.

DISCUSSION

Nestling survival

The body condition of a chick reflects the amount of body tissue reserves that can be used during periods of food shortage. Therefore, a chick in poor condition might experience a decreased chance of survival in the short term. Indeed, in Sandwich Terns, body mass increment during the linear phase of growth, as

Table 4. Relationship between body mass at fledging and post-fledging survival or local recruitment, and the age at which chicks become independent of their parents in several species of seabirds.

Species	Relationship between fledging weight and post-fledging survival/ local recruitment	Age of independence	Authors
Sooty Shearwater	Yes	Around fledging	Sagar and Horning (1998)
<i>Puffinus griseus</i>			
Manx Shearwater	Yes	Just before fledging	Perrins <i>et al.</i> (1973)
<i>P. puffinus</i>			
Cape Gannet	Yes	Soon after fledging	Jarvis (1974)
<i>Sula capensis</i>			
Sandwich Tern	No	> 4 months after fledging	This study
<i>Sterna sandvicensis</i>			
Guillemot	No	At least a few weeks after fledging	Hedgren (1981)
<i>Uria aalge</i>			
Razorbill	No	Cared for after fledging, but period unknown	Lloyd (1979)
<i>Alca torda</i>			
Puffin	No	Just before fledging	Harris and Rothery (1985)
<i>Fratercula arctica</i>			

well as body condition, showed a strong relationship with chick survival. Nisbet *et al.* (1998, 1999) also found that growth predicted chick survival accurately in Roseate Terns *S. dougallii*. In that species, survival could be predicted from body mass growth in the first few days after hatching. In contrast, our results suggest that in Sandwich Terns, body mass in the first few days after hatching is not important for survival, suggesting that poor nourishment during an early stage of life could be overcome. Nisbet *et al.* (1998) suggest that chick growth and survival, which are already manifested during the first days after hatching in Roseate Terns, are primarily determined by parental performance. In Sandwich Terns, it seems relatively easy for most parents to meet the food requirements of their newly hatched chicks. Only when the chicks grow and energy demands, as well as the proportion of food parents lose to kleptoparasitizing gulls, sharply increase (Stienen *et al.* 2001), differences in parental quality might be manifested. Especially in years when the chicks' diet is dominated by sandeels, resulting in high rates of kleptoparasitism (Stienen & Brenninkmeijer *in press*), aspects of parental performance might determine the chick's body condition and survival.

Post-fledging survival

In the long term, slow growth during the chick stage might affect survival at a later stage. The few studies on this subject have given different results. In Black-legged Kittiwakes *Rissa tridactyla*, slow growing chicks

had a lower probability of returning to the natal area (Coulson & Porter 1985), whereas Harris *et al.* (1992) found no difference in growth between Common Guillemots *Uria aalge* that survived to breed, and juveniles that were reported dead. Similarly, in Sandwich Terns, there seems to be no relationship between nestling development and post-fledging survival.

Several studies on seabirds have reported that a low body weight at fledging has a negative effect on post-fledging survival or local recruitment, whereas other studies found no effect (Table 4). All species, for which a relationship between fledging weight and post-fledging or local survival has been found, become independent of their parents just before or directly after fledging. Juvenile Common Guillemots, Razorbills *Alca torda* and Sandwich Terns, but not Atlantic Puffins *Fratercula arctica*, are fed by their parents for some time after fledging (Cramp 1998). Dependency on parents might therefore be a crucial factor that determines whether fledging weight affects post-fledging survival in seabirds. For juvenile Sandwich Terns, feeding conditions probably improve considerably after leaving Griend (*i.e.* a few days after fledging). In the first place, juveniles can be taken much closer to the feeding areas. Before the chicks fledge, parents have to travel, on average, about 12 km to the feeding grounds and feeding trips may last up to 3 h (Stienen & Brenninkmeijer *in press*). In addition, juveniles can be brought to sites that are free from Black-headed Gulls and other pirates that would otherwise reduce much of the prey brought to the ternery (Stienen & Brenninkmeijer

1999, Stienen *et al.* 2001). For these reasons, food intake rates probably improve greatly after fledging, making it possible for fledglings in poor condition to catch up on their shortfall in growth relatively easy. This would remove any effect of fledging condition on post-fledging survival.

In some species, birds attain a smaller adult size when confronted with poor food conditions during early development, whereas in other birds no effect on final size has been found (Schew & Ricklefs 1998). In turn, smaller size may affect the dominance status of the birds (e.g. Garnett 1981, Drent 1983), and growing large therefore might be of importance to occupy good nesting sites. In Sandwich Terns, poor body condition at fledging had no effect on adult body mass or size. Although the sample sizes were small, this suggests that early development is not important for the final size or dominance status.

Fluctuating food resources

Sandwich Terns on Griend depend on only a few species of prey fish for the rearing of their chicks. These prey species show large variation in numbers both between and within seasons (Fonds 1978, Corten 1990), and are patchily distributed (Stienen *et al.* 2000). Moreover, their availability for the terns depends on environmental conditions that affect vertical distribution of the prey and fishing success of the parents (Stienen *et al.* 2000). Such variation demands a great flexibility in features that are linked to food availability, such as growth, in order to minimize the effects on chick survival. Indeed, Sandwich Terns seem to be well adapted to unpredictable food resources. Growth rate of the chicks proved to be highly flexible, which might help to overcome short periods of food shortage. In periods of food stress, chicks allocated resources to growth of structural components (total head and wing) adequately, whereas body mass growth was reduced. Body mass growth of chicks that survived the chick stage varied between 1 and 11 g per day, which is comparable with other studies on Sandwich Terns (Pearson 1968, Klaassen *et al.* 1992). Growth can be reduced to about 8 g per day without serious consequences for chick survival. Slowing growth from 12 to 8 g per day would mean a reduction in energy needs of the offspring of 13% (Klaassen *et al.* 1992). Within this window parents can fine-tune chick growth to prevailing food conditions, with almost no consequences for the survival of their chicks and without consequences for their post-fledging survival or final size.

Despite the strong link between growth and nestling survival, 76.2% of all chicks of known growth-rate grew 8 g per day or more. Although this percentage might be biased upwards because very poorly growing chicks had already died before they could be measured three times, it suggests that during the first two weeks post-hatching most parents experienced no difficulties in providing sufficient food to their chicks. The same is suggested by the fact that body condition in the first 5 days did not significantly contribute to the birds' survival prospects. However, this might also be biased as the regression analysis of very young chicks is weakened by the inclusion of chicks that were initially in good condition but starved to death at a later stage. Nevertheless, the last two weeks before fledging, when the condition of a chick has strong effects on its survival, are probably the most strenuous period for Sandwich Tern parents. At this stage both the energy requirements of the chicks (Drent *et al.* 1992), and the rate of kleptoparasitism, are at their maximum levels (Stienen *et al.* 2001). Apparently some parents were unable to increase further the amount of food transported to their offspring and consequently growth was retarded. By contrast, the margins within which a chick can survive are very large. In this study, body mass of surviving chicks varied from 49% below to 77% above the mean body mass, showing that Sandwich Terns are well adapted to fluctuating food resources.

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