BROOD SIZE AND FOOD PROVISIONING IN COMMON TERNS *STERNA HIRUNDO* AND ARCTIC TERNS *S. PARADISAEA*: CONSEQUENCES FOR CHICK GROWTH
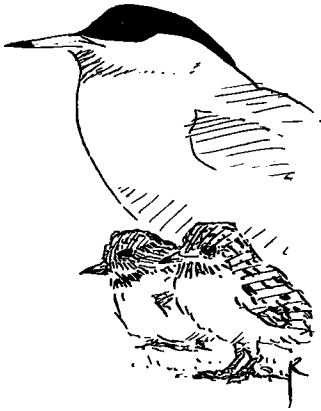
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Food provisioning rates and chick growth rates of Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea* were studied in Northeast England. Adult terns of both species fed large broods more frequently than those containing fewer chicks. Energy supply per nestling declined slightly as brood size increased and as a result, chicks in large broods developed body mass at a slightly lower rate than those in small broods. Although brood size had no effect on fledging mass in either species, Common Tern chicks from large broods reached fledging mass later than those in small broods. Despite significant effects of brood size, mass growth rate hierarchies did not occur *within* broods of either species and hatching position had no effect on the mass of fledglings. Brood size and hatching position had no effect on the rate at which chicks developed structurally or on final body size. These results suggest that flexibility of mass growth rates in Arctic and Common Terns may act as a fine-tuning mechanism, allowing parents to increase their annual reproductive output through slower mass growth rates of chicks.

Key words: *Sterna paradisaea* - *Sterna hirundo* - brood size - provisioning rates - chick growth rates

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INTRODUCTION

Among birds, interspecific differences in brood size partly reflect the amount of food that parents are capable of supplying to the nest during the chick-rearing period (Lack 1968). Differences in brood size also occur intraspecifically, and these reflect variation in sustainable provisioning rates by parents during chick-rearing, linked in turn to features such as foraging ability (Bryant & Westerterp 1980; Drent & Daan 1980; Green & Ydenberg 1994). However, rates of parental provisioning are not always directly proportional to brood size and so per chick, nestlings in larger broods are often fed less frequently than those in smaller broods (Laido *et al.* 1998; Lozano & Lemon 1998).

The low annual reproductive output of seabirds is assumed to reflect the sparse and unpredictable distribution of marine food resources (Ashmole 1971), which places a low limit on the maximum rate at which parents can provide food for offspring. Thus adults presumably limit clutch size to the number of offspring that they can feed. However as clutch size decreases, this becomes an increasingly imprecise way of regulating reproductive effort, because each unit decrease in clutch size is a progressively larger proportionate decrease. One way in which adults might be able to increase their annual reproductive output is by reducing the growth rate of the whole brood or of

particular members of the brood. For instance, in terns, a 50% reduction in chick growth entails about a 40% reduction in a nestling's daily energy requirement (Klaassen *et al.* 1992). However, slow nestling development has been associated with reduced chick and post-fledging survival (Perrins *et al.* 1973; Jarvis 1974; Coulson & Porter 1985; Boag 1987; Richner *et al.* 1989) and increased susceptibility to ground predators (Lack 1968).

Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* are closely related species that breed synoptically at a number of locations in Britain. Brood size in terns may be limited to some extent by costs of egg production (Heaney & Monaghan 1995). However, adult terns have little extra time in their activity budgets to increase foraging during chick-rearing (Pearson 1968; Monaghan *et al.* 1989) and so brood size may also be limited by parental provisioning effort. Very little attention has focused on the effects of brood size on parental provisioning or the potential trade-off between chick growth rates and productivity in these species.

The aims of this study were to investigate how brood size influences parental provisioning and energy supply rates to Arctic and Common Tern chicks, and to determine the consequences of variations in provisioning rates for the growth rates and fledging weights and sizes of individual chicks within and between broods of different sizes.

METHODS

Study site and field procedures

Fieldwork took place from 1 May to 20 July 1996 at a mixed colony of Common and Arctic Terns on Coquet Island, Northumberland (55°20'N, 1°32'W). Sample plots were established early in the breeding season of 1996 in the central areas of the Common and Arctic Tern colonies. To minimise disturbance and facilitate location of chicks, shortly before hatching 18 nests of each species from within these plots, with laying dates ± 2 days

of the modal value for the colony, were surrounded by small wire-mesh enclosures *c*. 30 cm high, similar to those used in previous studies (Pearson 1968; Nisbet & Drury 1982; Monaghan *et al.* 1989). Of those that hatched, 90.3% of Arctic Tern chicks and 83% of Common Tern chicks in the study nests survived until fledging and all chick deaths/predation events occurred within the first two days of hatching. The sizes of individual broods in this study refer to those recorded three days after the last chick in the brood had been hatched.

Chick diets and provisioning rates

Prey delivery rates to broods within enclosures were recorded from hides positioned within each colony. For each species, nests were observed simultaneously for a total of 90 hours, divided over 30 three-hour periods spanning the first 20 days of the nestling period (until chicks attained asymptotic body mass; see below) and divided evenly across all hours of daylight (04:30-22:30h). Adult terns deliver single prey items in their bills and the rate at which food was brought to chicks was assessed by direct observation. Prey items were identified as sandeel (predominantly *Ammodytes marinus*), clupeids (Herring *Clupea harengus* and Sprat *Sprattus sprattus*), gadids (predominantly Whiting *Merlangius merlangus* and Saithe *Pollachius virens*), rocklings *Ciliata* sp. and crustaceans. Fish were divided into four size categories (< 3 cm, 3.1-6 cm, 6.1-9 cm and > 9 cm) and the energy content of each prey item was estimated using conversion factors for appropriate species and sizes-classes from Harris & Hislop (1978) and Massias & Becker (1990). These data were then used to estimate energy delivery rates to each brood. The accuracy with which observers placed fish in different size categories was assessed at the start of the breeding season in 1996 using a mount of a Common Tern, with small fish (2-15 cm) collected at the colony which had been dropped by male terns during the courtship period. After some practice, all observers placed fish into the correct size category on > 90% of occasions.

Data for individual chicks were collected repeatedly over many days. To account for these repeated measures, the linear period of growth period was divided into two five-day age-classes, 6-10 days and 11-15 days. Data for each age-class were aggregated into a single mean value for each chick, and test statistics were calculated from aggregated mean values, following Sokal & Rohlf (1981). Degrees of freedom were adjusted for analysis of age-specific effects to the number of nests studied rather than the number of observations across all age-classes (see Bolton 1995). For all data concerning food provisioning rates, degrees of freedom thus refer to the number of broods studied and not the number of individual chicks.

Chick Growth

Chicks from each enclosed nest were individually marked shortly after hatching and were then weighed daily (to the nearest 1 g using a Pesola balance) at midday until fledging. Wing length (minimum wing chord, including down, measured to the nearest 1 mm with a slotted metal ruler) and head plus bill length (from the tip of the upper mandible to the back of the head, measured to the nearest 0.1 mm using Vernier callipers) were also measured at around midday every three days until fledging. Regression equations were fitted to growth data collected during the periods of linear growth of each variable (5-14 days post-hatching for body mass and head plus bill length; after five days post-hatching for wing length in both species) for chicks from different brood sizes and hatching positions within broods (i.e. first hatched, second hatched and third hatched chick). The slopes (i.e. growth rates) of these regression lines were then compared using analysis of covariance. To determine whether growth data within individual broods were related, regression lines were also fitted to growth data for individual broods. The slopes of these regression lines were compared using analysis of covariance. None of these tests were significant at the 5% level and therefore data for all nests were used in the analyses of covariance testing for the effects of hatching position on growth rate. The growth data were

collected repeatedly from individual chicks and were not truly independent. Therefore the degrees of freedom used in the analyses were adjusted to the number of individual chicks measured during the study rather than the total number of individual measurements. Body masses and head plus bill lengths at fledging were estimated from mean values for individual Common Tern and Arctic Tern chicks recorded beyond 23 and 21 days post-hatching respectively (Cramp 1985). Wing length was not measured in this way because flight feathers continue to grow beyond fledging in both these species.

RESULTS

Chick diets and provisioning rates

Provisioning and growth data were collected for five one-chick and thirteen two-chick Arctic Tern broods and three one-chick, five two-chick and ten three-chick Common Tern broods. Over 99% of the diets of both species comprised sandeels and clupeids (Arctic Tern: 99.7%, $n = 2,498$; Common Tern: 99.2%, $n = 2,699$). There was no significant difference between brood sizes in the sizes of fish fed to chicks of either species (Common Terns; $\chi^2_4 = 1.91$, n.s.; Arctic Terns; $\chi^2_3 = 4.2$, n.s.), > 98% of fish delivered to all broods being between 3 and 9 cm long. There was also no significant difference between brood sizes in the energy content of individual feeds delivered to nestlings (Table 1; one-way ANOVA; Common

Table 1. Energy content of individual meals delivered to Arctic and Common Tern nests in relation to brood size on Coquet Island in 1996 (mean ± SD).

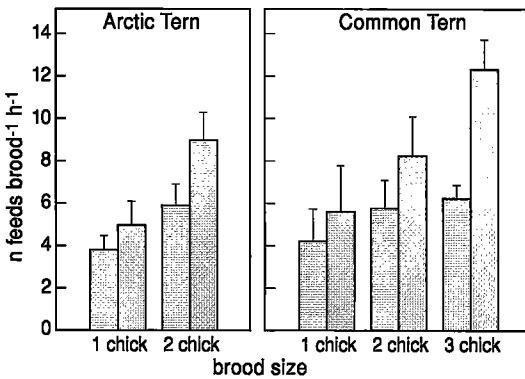|	Brood size	n	kJ feed^{-1}
Arctic Tern	1-chick	196	2.7 ± 5.1
	2-chick	2300	2.5 ± 3.1
Common Tern	1-chick	93	3.6 ± 5.0
	2-chick	864	4.2 ± 6.6
	3-chick	1718	4.4 ± 8.4

Fig. 1. Fish delivery rates ± SE for Arctic and Common Terns in relation to brood size on Coquet Island, 1996 (open bars = broods 6-10 days old; shaded bars = broods 11-15 days). Sample sizes: Arctic Tern 1-chick = 5, 2-chick = 13; Common Tern 1-chick = 3, 2-chick = 5, 3-chick = 10.

Fig. 2. Energy delivery rates ± SE for Arctic and Common Terns in relation to brood size on Coquet Island, 1996 (open bars = broods 6-10 days old; shaded bars = broods 11-15 days). Sample sizes: Arctic Tern 1-chick = 5, 2-chick = 13; Common Tern 1-chick = 3, 2-chick = 5, 3-chick = 10.

Terns; $F_{2,2673} = 1.5$, n.s.; Arctic Terns; $F_{1,2494} = 0.8$, n.s.).

During the period of linear mass growth (6-15 days post-hatching in both species), the frequency of food delivery increased with both brood size and brood age in both Common Terns (Fig. 1.; two-way ANOVA; brood size; $F_{2,15} = 19.1$, $P < 0.01$: age; $F_{1,16} = 40.5$, $P < 0.01$) and Arctic Terns (Fig. 1.; brood size; $F_{1,16} = 28.8$, $P < 0.01$: age; $F_{1,16} = 21.7$, $P < 0.01$). Per nestling, feeding frequency declined with increasing brood size but increased with brood age in Common Terns (two-way ANOVA: brood size; $F_{2,15} = 7.0$, $P < 0.01$: age; $F_{1,16} = 40.2$, $P < 0.01$) and Arctic Terns (brood size; $F_{1,16} = 7.7$, $P < 0.05$: age; $F_{1,16} = $
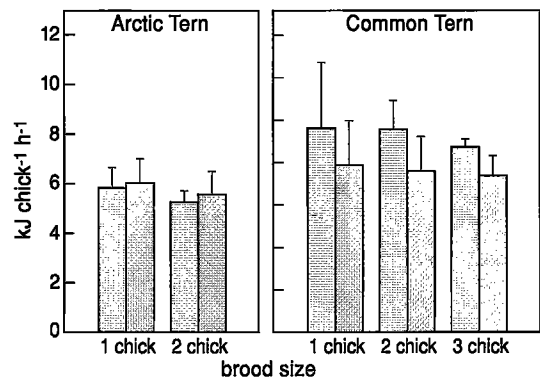
23.7, $P < 0.01$). Combining data for feeding frequency and meal size, rates of energy supply per nestling were slightly lower for larger broods in Common Terns (especially between 1-chick or 2-chick and 3-chick broods) (Fig. 2.; two-way ANOVA; brood size; $F_{2,15} = 4.8$, $P < 0.05$: age; $F_{1,16} = 4.7$, $P < 0.05$) and Arctic Terns (Fig. 2.; brood size; $F_{1,16} = 13.9$, $P < 0.01$: age; $F_{1,16} = 21.7$, $P < 0.01$).

Chick growth

Chick mass growth rates declined slightly with increasing brood size in both species (Table 2; ANCOVA for differences in the slopes of regression lines fitted to linear growth data; Com-

Table 2. Growth rates of Arctic and Common Tern nestlings which survived until fledging in relation to brood size on Coquet Island in 1996 (mean ± SD).

	Brood size	n	Body mass (g day^{-1})	Head plus bill length (mm day^{-1})	Wing length (mm day^{-1})
Arctic Tern	1-chick	5	6.9 ± 0.3	1.6 ± 0.8	8.1 ± 3.6
	2-chick	13	6.8 ± 0.1	1.6 ± 0.3	8.4 ± 1.4
Common Tern	1-chick	3	8.4 ± 0.3	1.8 ± 0.5	8.7 ± 2.0
	2-chick	5	7.6 ± 0.1	1.7 ± 0.2	7.6 ± 0.8
	3-chick	10	7.1 ± 0.1	1.8 ± 5.9	7.1 ± 2.4

Table 3. Growth rates of Arctic and Common Tern nestlings from 2-chick and 3-chick broods which survived until fledging in relation to hatching position (first, second and third hatched) on Coquet Island in 1996 (mean ± SD).

	Position within brood	n	Body mass (g day^{-1})	Head plus bill length (mm day^{-1})	Wing length (mm day^{-1})
Arctic Tern	first	13	7.0 ± 0.1	1.6 ± 0.5	8.6 ± 1.9
	second	13	6.7 ± 0.1	1.5 ± 0.5	8.4 ± 2.1
Common Tern	first	15	7.8 ± 0.1	1.9 ± 0.4	7.1 ± 1.2
	second	15	7.6 ± 0.1	1.6 ± 0.5	7.6 ± 1.6
	third	10	7.0 ± 1.8	1.6 ± 1.2	7.2 ± 3.1

Table 4. Body masses and head plus bill lengths of Arctic and Common Tern fledglings in relation to brood size on Coquet Island in 1996 (mean ± SD).

	Brood size	n	Body mass (g)	Head plus bill length (mm)
Arctic Tern	1-chick	5	106.2 ± 5.8	60.7 ± 1.5
	2-chick	13	107.4 ± 10.4	60.6 ± 2.4
Common Tern	1-chick	3	120.2 ± 14.8	67.5 ± 1.2
	2-chick	5	120.4 ± 12.2	65.8 ± 1.7
	3-chick	10	121.7 ± 10.1	65.7 ± 2.7

Table 5. Mean body masses and head plus bill lengths of Arctic and Common Tern fledglings from 2-chick and 3-chick broods in relation to hatching position (first, second and third hatched) on Coquet Island in 1996 (mean ± SD).

	Position within brood	n	Body mass (g)	Head plus bill length (mm)
Arctic Tern	first	13	104.8 ± 10.4	61.3 ± 2.3
	second	13	107.4 ± 10.8	59.5 ± 2.2
Common Tern	first	15	119.2 ± 28.1	66.2 ± 1.4
	second	15	124.6 ± 8.5	65.6 ± 2.0
	third	10	124.5 ± 3.4	61.8 ± 1.8

Table 6. Mean age at which Arctic and Common Tern nestlings first reached fledging mass, 107g and 123 g respectively, in relation to brood size on Coquet Island in 1996.

	Brood size	n	Age at which chicks first reached fledging mass (mean no. days post-hatching ± SD)
Arctic Tern	1-chick	5	17.7 ± 2.5
	2-chick	13	17.7 ± 3.0
Common Tern	1-chick	3	16.5 ± 2.1
	2-chick	5	20.1 ± 2.6
	3-chick	10	21.2 ± 2.9

mon Terns: $F_{2,15} = 5.3$, $P < 0.05$; Arctic Tern; $F_{1,16} = 9.7$, $P < 0.01$. Paired tests indicated significant differences between rates of all brood sizes) but there was no significant difference between the mass growth rates of chicks of different hatching positions within broods containing more than one nestling (Table 3; ANCOVA; Arctic Tern; $F_{1,16} = 0.4$, n.s.; Common Tern; $F_{2,15} = 1.5$, n.s.).

In neither species did brood size have an effect on the rate of head plus bill growth (Table 2; ANCOVA; Common Tern: $F_{2,15} = 0.2$, n.s.; Arctic Tern; $F_{1,16} = 0.01$, n.s.) or wing growth (Table 2; ANCOVA; Common Tern: $F_{2,15} = 1.0$, n.s.; Arctic Tern; $F_{1,16} = 0.1$, n.s.). Hatching position also had no effect on the growth of head plus bill length (Table 3; ANCOVA; Common Tern; $F_{2,15} = 1.9$, n.s.; Arctic Tern; $F_{1,16} = 0.3$, n.s.) or wing length (Table 3; ANCOVA; Common Tern; $F_{2,15} = 0.6$, n.s.; Arctic Tern; $F_{1,16} = 0.1$, n.s.).

There were no significant effects of brood size or hatching position on the body masses of fledglings (Tables 4 and 5; two-way ANOVA; Common Tern: brood size; $F_{2,15} = 0.2$, n.s.; hatch position; $F_{2,15} = 0.6$, n.s.; Arctic Tern: brood size; $F_{1,16} = 0.2$, n.s.; hatch position; $F_{1,16} = 1.0$, n.s.) or head plus bill length of fledglings (Tables 4 and 5; two-way ANOVA; Common Tern: brood size; $F_{2,15} = 0.4$, n.s.: hatch position; $F_{2,15} = 4.1$, n.s.; Arctic Tern: brood size; $F_{1,16} = 0.0$, n.s.: hatch position; $F_{1,16} = 3.4$, n.s.). Common Tern chicks from larger broods reached fledging mass significantly later than those from smaller broods (Table 6; one-way ANOVA; $F_{2,15} = 4.1$, $P < 0.05$), but brood size did not have any effect on the time it took Arctic Tern nestlings to reach fledging mass (Table 6; $t_{16} = 0.0$, n.s.).

DISCUSSION

Brood size had a major influence on the feeding frequency of both Common and Arctic Terns (Fig. 1). In both species, the number of feeds delivered to the nest increased with the number of chicks in the brood. This relationship between food delivery and brood size has also been documented in many other species (Von Haartman 1954; Henderson 1975; Bryant & Gardner 1979; Nur 1984; Filliater & Breitsisch 1997; Olsen *et al.* 1998), although not all (Emms & Verbeek 1991; Nishimismi *et al.* 1996; Schadd & Ritchison 1998).

Feeding frequency is often higher per nestling for small broods than for large broods (Johnson & Best 1982; Laido *et al.* 1998; Lozano & Lemon 1998). However, adults can compensate for this constraint by delivering larger food items per trip to larger broods (Eybert & Constant 1998; Siikamaki *et al.* 1998; Meyer *et al.* 1997; Wright *et al.* 1998), so that parents rearing large broods deliver food per nestling at the same rate as those with fewer young (Rytkonen *et al.* 1996). In contrast, in the present study, brood size had very little effect on the species, sizes, and most importantly, energy content of meals delivered to Arctic and Common Tern nestlings; adult Arctic and Common Terns with large broods thus supplied energy at a slightly lower rate per nestling than those rearing small broods (Fig. 2.). In contrast, Wiggins (1989) showed that adult Common Terns in the USA provided equal amounts of food per nestling to all brood sizes suggesting adults with larger broods were able to increase foraging effort in proportion to brood size. The underlying reasons behind these contrasting results are unclear but evidence from many previous studies on terns suggest that between-year and between-colony variations in foraging conditions, especially food availability (Monaghan *et al.* 1989; Safina *et al.* 1988), environmental conditions (Dunn 1975; Frank 1992) and foraging range, can be extremely important in determining provisioning rates and growth strategies of terns. Therefore the conclusions drawn from any one study should not be applied generally.

In most bird species, increased brood size has a negative effect on nestling growth (see Klomp 1970 for a review). However, there are some exceptions in which brood size has no effect (Platteeuw *et al.* 1995; Scolaro *et al.* 1996), or even a positive effect (Markman *et al.* 1995) on the pace of chick development. At Coquet Island, Arctic and Common Tern chicks from large broods

increased mass more slowly than those from small broods although these differences were small (Table 2). This presumably reflected, in part, the lower per capita rate of energy supply to chicks in larger broods. However, components of the nestling energy budget other than growth may also have been affected by brood size. For example, nestlings in large broods may have required more energy for activity when competing for food with siblings or less energy for thermoregulation due to savings made through huddling. This may explain why many of the brood size related differences in energy supply and mass growth rates were not proportional. Brood size had no effect on structural growth rates, final body size, or final body mass in either species (Tables 2 and 4). We suggest that in Arctic and Common Terns on Coquet Island, resources were preferentially allocated to the growth of structural features at the expense of mass retardation, however small, so that normal final body size was successfully reached irrespective of brood size.

In many birds, including Larids, chicks reared in broods containing more than one nestling grow at different rates (Furness 1983; Nisbet et al. 1995) due to unequal distribution of food caused by asymmetrical sibling competition (Magrath 1990; Ricklefs 1993). In the present study, the hatching position of a tern chick within a brood had no effect on the rate at which it developed (Table 3) or its final fledging mass or size (Table 5). Although it was not possible to measure the amount of food that individual chicks within a brood received in this study, the growth data indicated that within large broods energy was distributed equally to nestlings of these two species. In contrast to these results, other studies have shown that the last hatched chick within Common and Arctic Tern broods grows more slowly than it's older siblings (e.g. Langham 1972; Lemmetyinen 1972). Fledging success of both species was particularly high on Coquet Island in 1996 and none of the c-chicks in study nests which survived the first two days of hatching died subsequently, indicating food availability was high. Fledging success was comparatively much lower in the studies of Langham (1972) and Lemmetyinen (1972) and most c-chicks died, presumably from starvation, prior to fledging. These contrasting results suggest that adult terns which are able to distribute food evenly among chicks, e.g. during years when food availability is high, are able to fledge large broods whereas those which cannot suffer higher levels of chick mortality.

Although mass growth rates were lower, chicks from larger broods fledged at similar weights and sizes to those from small, faster growing broods (Table 4). Langham (1972) showed that fledging mass declined with brood size in Common Terns on Coquet Island in the 1960s indicating again that food availability may have been particularly good in the vicinity of Coquet Island in 1996 and that parents were able to distribute food evenly to all chicks within a brood up until the period of fledging. However, Common Tern nestlings from larger broods took longer on average to reach fledging mass than those from smaller broods (Table 6). This protracted nestling period potentially increased the period during which Common Tern nestlings were susceptible to ground based predators. However, tern chick predation events in northern Britain usually occur very early in the nestling period (Uttley et al. 1989; Robinson & Hamer 1998) so a longer fledging period may not lead to increased predation in these species. In 1996, only one Arctic Tern chick and one Common Tern chick were taken by predators and both chicks were less than three days old. Several chicks of both species climbed out of the wire enclosures before they could fly and therefore it was impossible to determine the actual time it took individual nestlings to fledge.

The results of this and previous studies have demonstrated that avian nestling growth rates declined with increasing brood size (see above). This trend suggests that parental provisioning rates to broods of different size are a compromise between the energy requirements of the nestlings and the effort that parents make whilst collecting food. 'Optimal Working Capacity' (proposed by Royama 1966) sets to explain this compromise in

terms of life-history theory and predicts that parents normally work at a capacity beyond which they would suffer risks to future survival and reproductive output. In the present study, the slightly higher rate of food delivery to larger broods suggest that this capacity may be higher in those parents raising such large broods (see also Wiggins 1978). A balance between the nestlings' and parents' energy requirements is particularly important in terns because they have little leeway in their activity budgets to increase the proportion of time they spend foraging during the chick-rearing period (Pearson 1968; Monaghan *et al.* 1989). Flexible mass growth rates of chicks may allow parents of these two species to increase reproductive output without having to increase daily foraging effort to their detriment. There is some evidence that experienced adult Common Terns are more efficient at delivering food than younger birds i.e. they can increase provisioning rate to some extent without increasing their daily energy expenditure (Galbraith *et al.* 1999). It is thus possible that terns rearing large broods delivered food more efficiently than those with small broods, and this requires further investigation.

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SAMENVATTING

Inter- en intraspecifieke verschillen in de aantallen jon-
gen die door vogels worden grootgebracht, zijn gedeel-
telijk een afspiegeling van de hoeveelheid voedsel die
de oudervogels kunnen aanbrengen. Toch zijn voedse-
laanvoer en het aantal kuikens in een nest niet propor-
tioneel aan elkaar gerelateerd en worden individuele
jongen in nesten met veel kuikens vaak minder frequent
gevoerd dan jongen met minder nestgenootjes. De klei-
ne legsels en de daarmee samenhangende geringe jaar-
lijkse productiviteit bij zeevogels wordt dikwijls in ver-
band gebracht met de spaarzame en onvoorspelbare
voedselbeschikbaarheid op zee. Het beperken van de
legselgrootte (omdat voor een groter aantal jongen niet
voldoende voedsel zou kunnen worden aangebracht) is
echter een tamelijk grove maatregel, zeker bij legsels
die toch al uit weinig eieren bestaan. Een aanmerkelijk
subtielere manier om de productie te verhogen, is na het
bebroeden van een groter aantal eierenen de groeisnel-
heid van enkele of alle jongen lager te houden, zodat
toch in de dagelijkse voedselbehoefte kan worden
voorzien. Zo zou een met 50% gereduceerde kuiken-
groei leiden tot een reductie van de dagelijkse voedsel-
behoefte met 40%. Er zijn echter ook nadelen aan een
vertraagde groei, zoals een verminderde overleving na
het uitvliegen en een toegenomen kwetsbaarheid van
jongen voor grondpredatoren.

Visdieven *Sterna hirundo* en Noordse Sterns *S.
paradisaea* zijn verwante, kustbewonende soorten
waarvan de legselgrootte mogelijk mede bepaald wordt
door de vermogens van de ouders om voldoende prooi-
en voor de jongen aan te dragen. In het hier beschreven
onderzoek, uitgevoerd op Coquet Island (Northumber-
land, U.K.), werd bekeken in hoeverre de legselgrootte
van invloed was op de aanvoer van vis door de ouder-
vogels en wat de gevolgen van verschillen in voedse-
laanvoer waren voor de groeisnelheid en het uitvliegge-
wicht van de individuele kuikens in legsels van vers-
chillende grootte. Bij beide soorten werden jongen in
grote legsels frequenter gevoerd dan jongen in kleinere
legsels. De jongen in de grotere legsels kregen individ-
ueel echter iets minder voedsel dan jongen in kleinere
legsels en de groei bleef navenant achter. Het uitvlieg-
gewicht was echter in alle gevallen gelijk. Dit werd bij
grotere legsels bewerkstelligd door een latere datum
van uitvliegen. Binnen de grotere legsels waren geen
verschillen in groei aantoonbaar tussen de individuele
jongen en eerder uitgekomen jongen, werden bijvoor-
beeld niet bevoordeeld ten koste van later uitgekomen
nestgenootjes. De resultaten ondersteunen het idee dat
fluctuaties in groeisnelheid van de jongen, als gevolg
van verschillen in voedselaanvoer (een afspiegeling
van voedselbeschikbaarheid) door deze sterns gebruikt
worden om de jaarlijkse productie te maximaliseren.
(CJC)