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Effects of diet on growth-related patterns of energy and macronutrient assimilation efficiency in a semi-precocial bird, the Gull-billed Tern *Gelochelidon nilotica*

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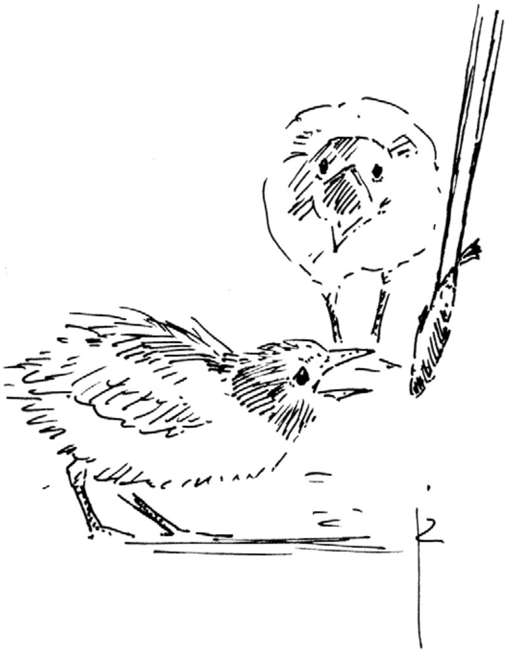

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Despite the extensive literature on energy assimilation efficiency in birds, only a few studies have dealt specifically with offspring, and to our knowledge there is no information on macronutrient assimilation efficiencies during the growth period of chicks. We studied growth-related energy and macronutrient assimilation efficiencies of semi-precocial chicks of Gull-billed Terns *Gelochelidon nilotica* as a function of their diet. We experimentally evaluated several digestive parameters in chicks fed different diets – fish vs. insects – when 10, 15 and 22 days old. Gross daily energy intake was similar in the two groups throughout the growth period, but fish-fed chicks showed consistently higher energy and macronutrient assimilation efficiencies than chicks fed insects. Energy and macronutrient assimilation efficiencies varied with age, peaking at 15 days old. The only digestive parameter that did not decrease during the last phase of growth was the lipid assimilation efficiency. Fish-fed chicks grew significantly faster than those fed on insects, which showed delayed growth. We suggest that semi-precocial chicks could modulate energy and macronutrient assimilation efficiency according to their growth requirements and that such digestive parameters can help us to understand differences in chick growth rates and breeding success in a natural environment.

Key words: assimilation efficiency, chicks, delayed growth, diet, Gull-billed Tern, logistic growth model, macronutrients, migratory birds

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The reproductive success of birds may be limited by the availability and quality of different food sources (Paillisson *et al.* 2007). To compensate for variation in food availability, parents show behavioural changes such as adjusting provisioning rates (Quillfeldt & Peter 2000, Eilertsen *et al.* 2008) or foraging time (Litzow & Piatt 2003, Gingras & Paszkowski 2006) and diet switching (Crawford & Dyer 1995, Le Corre *et al.* 2003). The food type that chicks receive from their parents has a marked effect on their growth and survival (Massias & Becker 1990, Dahdul & Horn 2003, Romano *et al.* 2006). It has been suggested that chicks have developed the ability to adapt morphologically, physiologically and behaviourally in response to qualitative and quantitative variation in energy intake (Lance & Roby 2000, Dawson 2008). These adjustments are not related solely to changes in growth patterns (Schew & Ricklefs 1998, Robinson & Hamer 2000), since the chick's digestive properties can also be affected (Karasov 1996, McWilliams & Karasov 2001, Brzek *et al.* 2009).

The energy assimilation efficiency (AE) depends on the composition of the food ingested, and the ability to transform absorbed nutrients into energy (Murphy 1996). There is an extensive literature dealing with adult birds' AE when feeding on different food types (e.g. see review by Castro *et al.* 1989, Brekke & Gabrielsen 1994), but information about macronutrient assimilation efficiency (AEm) of different types of food is scarce (Castro *et al.* 2008). In chicks, AE has been determined for several bird species with different diets (reviewed in Visser 2002, Niizuma & Yamamura 2004), but results concerning the dependence of AE on age have been contradictory (Heath & Randall 1985, Klaassen & Bech 1992). In the case of AEm, to our knowledge, there is no information. Data on both digestive parameters could be key to understanding developmental patterns in chicks.

Terns are typically piscivorous birds (Gochfeld & Burger 1996), but some species incorporate a significant portion of insects into their diet (e.g. Cramp 1985, Dunn & Agro 1995). The Gull-billed Tern *Gelochelidon nilotica* is a particularly opportunistic species which takes a wide spectrum of different sizes and types of prey, including insects, in its breeding habitats (Sánchez *et al.* 1991, Sánchez *et al.* 2004a, Dies *et al.* 2005).

In colonies of Gull-billed Terns located in SW Spain, chicks relying on fish grow faster than chicks from colonies where the main food provided by parents is insects (unpubl. data; Villegas 2007). We studied growth and several digestive traits of Gull-billed Tern chicks that were hand-fed until fledging with either a fish or an insect diet. We tested whether chicks with an insect-based diet showed a delayed development in body mass and/or size, as well as the potential role of AE and AEm on developmental patterns of both experimental groups. Given the wide variety of diets that has been documented for the species and the diversity of foraging habitats that it uses (Sánchez *et al.* 1991, Sánchez & Fasola 2002), the Gull-billed Tern is an ideal model species to test variation in growth, development and digestive traits in semi-precocial birds depending on the diet. We hypothesized that both AE and AEm are affected by food type, and that chicks will show differences in these digestive traits in relation to the variation in energy and nutrient needs imposed by growth.

METHODS

Chick collection and care

Eggs of Gull-billed Terns were collected in May 2008 under a permit of the 'Junta de Extremadura'. The colony was located on an island in the Alange reservoir (see map in Sánchez *et al.* 2004b), SW Spain (38°47' N, 6°16' W), where about 1000 pairs nested. A total of 17 fresh laid eggs (one egg per nest) of nests at risk to be flooded due to a waterlevel increase were collected and transported to the laboratory for incubation. After hatching (n = 13), chicks were marked for individual identification and housed in cardboard boxes (90×45×40 cm). They were kept under constant temperature conditions of 35°C using infra-red lights and a light–dark cycle similar to the natural one (15:9 L:D) for the first 10 days. They were then kept in outdoor aviaries (mean temperature: 23.1 ± 0.8°C; 15:9 L:D). All birds were weighed daily to the nearest 0.1 g in the early morning, just before feeding. Each day we measured tarsus, head plus bill (henceforth, head) and wing length. All measurements were taken by the same person using an electronic calliper (± 0.01 mm), except wing length which was measured with a ruler (± 1 mm). At the end of the experiment, the fledglings were released into the nursery area of the breeding colony.

Feeding protocol

Chicks were randomly assigned to two experimental groups: (1) insect diet (n = 6), and (2) fish diet (n = 7). All individuals of a given treatment were kept together as a group. They were hand-fed *ad libitum* 8–9 times per day at regular time intervals from sunrise to sunset. At each feeding, they were fed until they refused to eat more. Water was provided with a syringe until satiation. The insect diet consisted mainly of Common Crickets (*Acheta domestica*; 46% of wet mass) and was completed with field crickets (*Gryllus campestris*), grasshoppers (*Chorthippus parallelus*), and mealworms (*Tenebrio molitor*). The fish diet consisted primarily (64%) of Bleak *Alburnus alburnus*, completed with Sand Smelt *Atherina boyeri*, European Carp *Cyprinus carpio*, Black Bass *Micropterus salmoides* and Sunfish *Lepomis gibbosus*. At the times of estimating the assimilation efficiency (see below) chicks were fed exclusively with fresh Common Crickets or fresh Bleak depending on the experimental group.

Energy and macronutrient assimilation efficiency

For each individual we estimated energy and macronutrient assimilation efficiency when 10, 15 and 22 days old. Each trial began at 7:00 h (GMT + 2 h). Chicks did not feed overnight, so that they were in a post-absorptive state in early morning. Each chick was placed individually in a cardboard box (30×22×23 cm) with a metal mesh floor over an aluminium tray to collect faeces. Individuals were fed in the above mentioned way, recording total food intake. Total daily excreta of each individual were collected the next morning just before feeding. Faecal samples were homogenized and stored frozen at –80°C until analysis.

Gross energy intake (GEI; kJ/d) was estimated per chick as the amount (g dry mass) of total protein, lipids and carbohydrates ingested, multiplied by the energy density of these macronutrients (23.65, 39.55, 17.16 kJ/g of dry protein, dry lipid, and carbohydrate, respectively; Crisp 1984). Gross energy output (GEO) per chick was estimated as the amount (g dry mass) of total protein, lipids and carbohydrates excreted, multiplied by the energy density of these macronutrients plus the amount (g dry mass) of excreta in the form of uric acid and urea multiplied by their energy density (11.5 kJ/g for dry uric acid and 10.5 kJ/g for dry urea; Bell 1990).

The energy assimilation efficiency (AE) was calculated following Castro *et al.* (1989):

$$\text{AE (\%)} = 100 \times (\text{GEI} - \text{GEO}) / \text{GEI}$$

The daily assimilation efficiency for each macronutrient was calculated in the same way as the energy assimilation efficiency. The apparent metabolizable energy intake (AME; kJ/d) was the difference between the total energy ingested and the energy excreted per day (Miller & Reinecke 1984).

Faecal and prey sample assays

Faecal and prey samples were dried at 60°C to constant mass. Water content was calculated as the difference between wet and dry mass of each sample. Nitrogen content was determined by the Kjeldahl method (Lynch & Barbano 1999). Protein content was determined according to Lowry *et al.* (1951). It was assumed that N makes up 16% of protein, so protein content equals 6.25 times N (McDonald *et al.* 1995). Total lipid content was determined gravimetrically after extraction of a homogenized sample in diethyl ether (AOAC 1995). Carbohydrate content was determined by colorimetry using the phenol-sulphuric acid reagent (Dubois *et al.* 1956). The amounts of water, nitrogen, fat and carbohydrates in the prey supplied to each group (crickets and Bleak) were determined as in the faeces. Lastly, we assumed that 75% of excreted N originated from uric acid and 25% from urea (Karasov 1990).

Chick growth

We determined the relationship between body mass (M, in g) and age (t, in days post-hatch) for each individual by nonlinear regression using the logistic growth equation:

$$M = A / 1 + \exp[-k \times (t - t_i)]$$

where A is asymptotic body mass (g), k is the growth constant (1/d), and t_i is the inflection point of the curve (days; Starck & Ricklefs 1998). The growth parameters of tarsus, head and wing length were determined similarly to body mass. Lastly, we estimated a body condition index for full-grown birds by calculating residuals from a regression line of body mass on tarsus length (e.g. Lislevand *et al.* 2009).

Data analysis

Since AE, AEm, AME and GEI were repeatedly measured for each chick at three different ages, we used a repeated-measures analysis of variance to test the effects of age (three levels) and diet (two levels) on these variables. Post-hoc Tukey tests were carried out when the results were significant. The parameters of the logistic growth models for the various size measurements were compared between diets using a *t*-test. Results were considered significant when $P < 0.05$. Data were tested for normality and homogeneity of variance and no transformations were necessary. Mean values are presented ± SE. Data were analyzed using Statistica (StatSoft, version 7.0).

RESULTS

The content of protein, lipid and carbohydrate (in % dry weight) for insects and fishes was 67.8 ± 0.9, 12.3 ± 0.1, 12.5 ± 0.1% and 69.1 ± 1.3, 20.4 ± 0.4, 0.9 ± 0.0%, respectively. Accordingly, energy density of insects and fishes was 23.0 kJ/g dry mass and 24.4 kJ/g dry mass, respectively. The initial body mass of chicks prior to the experiment averaged 24.2 ± 1.0 g, and was similar in the two groups (fish diet: 23.1 ± 0.9 g; insect diet: 25.6 ± 1.7 g; $t_{11} = 1.3$, $P = 0.22$). GEI was also similar for both groups (Fig. 1A, Table 1). Fish-fed chicks showed consistently higher values of AE, AEm and AME than those fed with insects (Fig. 1, Table 1). This difference between both groups in macronutrient assimilation efficiency was much more evident for protein than for lipid (Fig. 1D,E). All the digestive parameters varied with age and peaked when 15 days old (Fig. 1, Table 1) except lipid assimilation efficiency which remained high after day 15 in both groups (Fig. 1E). In the case of lipids the interaction between age and diet was also significant (Table 1). Because the carbohydrate content in the faeces of fish-fed chicks was negligible it is not shown in Fig. 1.

The high pseudo-R^2 values (> 98%) indicated that the logistic model fitted the growth patterns well. The growth constant (k) was consistently higher for fish-fed chicks (Fig. 2, Table 2) and the time to reach the maximum growth rate of body mass, head length and wing length was significantly shorter for this group (Table 2). Only the inflection point (t_i) of the tarsus length growth curve did not differ between diets (Table 2). The insect-fed chicks had higher asymptotic values (A) for all variables other than tarsus length (Fig. 2, Table 2) and reached a higher body condition at the end of development (0.8 ± 0.2 and –0.7 ± 0.3 for insect and fish-fed chicks, respectively; $t_{11} = 4.2, P < 0.01$).

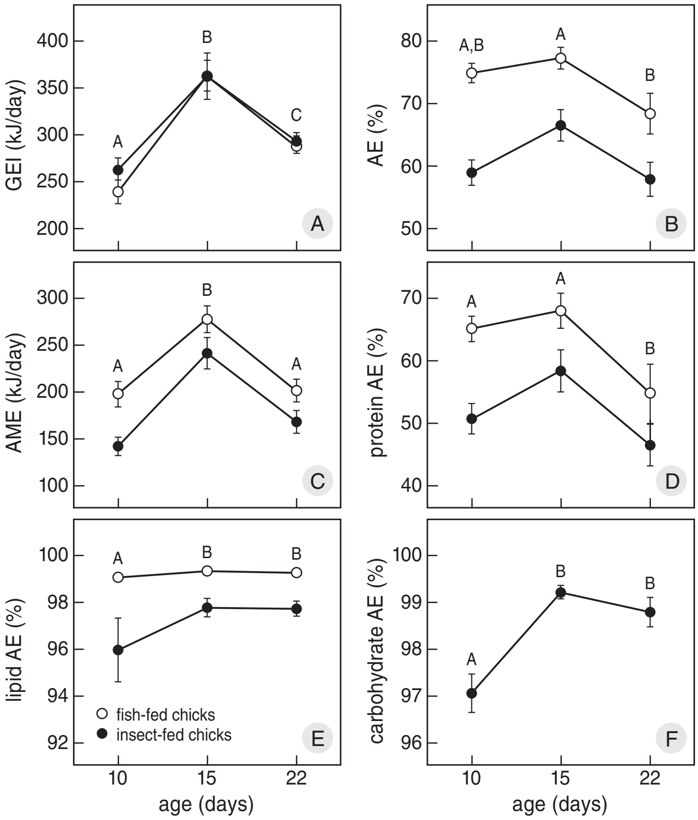

Figure 1. Gross energy intake (A), energy assimilation efficiency (B), apparent metabolizable energy (C), protein assimilation efficiency (D), lipid assimilation efficiency (E) and carbohydrate assimilation efficiency (F) of hand-fed Gull-billed Tern chicks. Data are presented as means ± SE. Fish-fed chicks (n = 7), insect-fed chicks (n = 6). Significant differences throughout the experimental period are identified with different letters.

Table 1. Results of repeated-measures ANOVA testing the effects of diet (fish or insects) and age on energy assimilation efficiency (AE), apparent metabolizable energy (AME), protein assimilation efficiency (PAE), lipid assimilation efficiency (LAE) and gross energy intake (GEI). Lipid assimilation efficiency was lower in insectivorous chicks of age 10 days (significant interaction Age × Diet; Tukey test).

	Diet				Age (days)					Age × Diet	
	Fish	Insects	$F_{1,11}$	P	10	15	22	$F_{2,22}$	P	$F_{2,22}$	P
AE (%)	73.5 ± 1.5	61.2 ± 1.5	25.04	<0.001	67.6 ± 2.5	72.3 ± 2.1	63.5 ± 2.5	10.12	<0.001	1.08	ns
AME (kJ/d)	225.8 ± 10.7	184.1 ± 12.2	8.82	<0.05	172.2 ± 11.1	261.4 ± 10.9	186.1 ± 9.13	54.92	<0.001	0.96	ns
PAE (%)	62.5 ± 2.2	51.8 ± 2.0	9.91	<0.01	58.3 ± 2.5	63.4 ± 2.4	50.9 ± 3.1	11.50	<0.001	0.78	ns
LAE (%)	99.1 ± 0.1	97.1 ± 0.3	108.20	<0.001	97.6 ± 0.5	98.6 ± 0.2	98.5 ± 0.2	12.20	<0.001	6.20	<0.01
GEI (kJ/d)	306.9 ± 12.8	297.3 ± 14.1	0.36	ns	252.4 ± 8.7	362.8 ± 14.6	292.3 ± 5.7	43.84	<0.001	0.58	ns

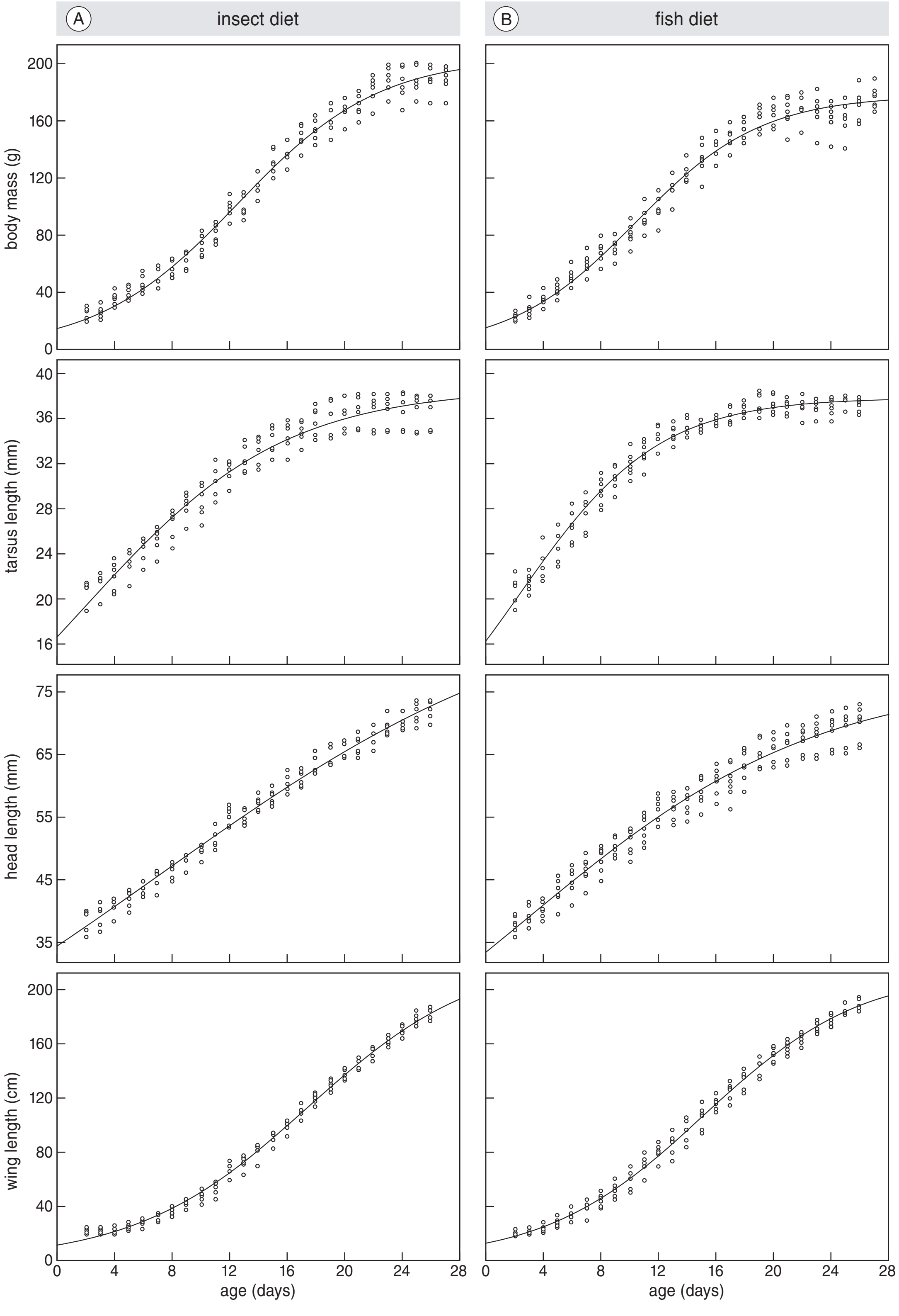

Figure 2. Changes in body mass, tarsus, head+bill and wing length of Gull-billed Tern chicks hand-reared on insects (A) or fishes (B) fitted with a logistic growth model (see also Table 2).

Table 2. Results of the Student *t*-test for the effect of diet (fish vs. insects) on growth parameters of body mass (g), tarsus, head+bill and wing length (mm) of Gull-billed Tern chicks from 2 to 26 days of age. A is the asymptote (in g or mm), k the growth constant (per day), and t_i the inflection time (in days).

Growth	A				k				t_i			
parameter	Insects	Fish	*t*	*P*	Insects	Fish	*t*	*P*	Insects	Fish	*t*	*P*
Body mass	204.65 ± 3.64	177.97 ± 4.27	4.66	<0.001	0.20 ± 0.01	0.23 ± 0.00	−2.94	<0.05	12.60 ± 0.10	10.43 ± 0.42	4.65	<0.001
Tarsus length	38.62 ± 0.72	37.68 ± 0.36	1.22	ns	0.15 ± 0.00	0.21 ± 0.01	−7.00	<0.001	1.90 ± 0.61	2.43 ± 0.31	0.81	ns
Head lenght	92.74 ± 2.34	77.78 ± 1.24	5.90	<0.001	0.07 ± 0.00	0.10 ± 0.00	−7.16	<0.001	7.55 ± 0.76	2.91 ± 0.40	5.60	<0.001
Wing lenght	225.90 ± 0.98	214.26 ± 3.18	3.26	<0.01	0.17 ± 0.00	0.18 ± 0.00	−2.97	<0.05	17.39 ± 0.19	15.14 ± 0.36	5.23	<0.001

DISCUSSION

Energy and macronutrient assimilation efficiencies varied consistently with food type and chick age. It is known that energy assimilation efficiency is strongly determined by food composition (Castro *et al.* 1989), and that high-lipid prey generally results in higher assimilation efficiencies than low-lipid prey (Brekke & Gabrielsen 1994, Niizuma & Yamamura 2004). Independently of diet, the chicks were far more efficient at assimilating energy from lipids (93%) than from proteins (58%), which led to higher energy assimilation efficiencies in chicks fed on high-lipid fish. Because the difference between insect and fish-fed chicks was bigger in protein assimilation than in lipid assimilation efficiency, it seems likely that the low digestibility of cuticle accounts for at least part of this difference (Weiser *et al.* 1997). Insect-fed chicks did not compensate for their lower assimilation efficiencies by eating more, since GEI was similar for both diets throughout the growth period. Probably this reflects low digestibility of prey items with an exoskeleton, constraining energy intake rate through a digestive bottleneck (Kenward & Sibly 1977).

Assimilation efficiencies at first increased with age due to time required for the functional development of the gut (Brzek *et al.* 2009). When body mass and wing feathers grew fastest, energy and macronutrient assimilation efficiency were maximized. Both assimilation efficiencies decreased as the chicks approached adult size and their flight feathers were nearly full grown, probably due to the high metabolic costs accompanying high digestion rates (Karasov & Hume 1997). Lipid assimilation efficiency in fish-fed chicks remained high throughout the whole growth period, while in insect-fed chicks it initially increased and then levelled off (Fig. 1). The lower value of lipid assimilation efficiency during the early phase of growth of insect-fed chicks could be associated with the time required for digestive adjustments in response to low-lipid prey (Hilton *et al.* 2000) as well as with high metabolic costs of absorbing a scarce nutrient (Karasov 1996). In both groups lipid assimilation efficiency stayed at a constant level after reaching the maximum, probably because the chicks' energy demand relative to nutrients demand increased during the final growth period when relative growth rates had slowed (Ricklefs *et al.* 1998). Additionally, chicks can increase their energy reserves by storing more fat during the later part of the developmental period, thus enhancing the chances of successful fledging (Reid *et al.* 2000).

It has been proposed that chicks are able to modulate energy allocation and postnatal growth depending on the available resources (Schew & Ricklefs 1998, Dahdul & Horn 2003, Benowitz-Fredericks *et al.* 2006), and that this developmental plasticity allows offspring to manage their resources in response to variation in nutritional and energetic value of prey (Schew & Ricklefs 1998), leading to an increase in reproductive output (Robinson & Hamer 2000). Our results suggest that semi-precocial chicks could modulate both energy and macronutrient assimilation efficiencies depending on diet quality and growth requirements. Nevertheless, we cannot exclude that observed differences in total absorption efficiency were 'passive' changes due to the lower digestibility of insects and longer time required for efficient digestion by chicks. Further studies on retention time, activity of digestive enzymes or absorption efficiency in intestines are required to provide evidence for the existence of modulation of digestive physiology.

Delayed maturation in response to food restriction or reduction in food quality has been reported in many bird species, including terns (Schew & Ricklefs 1998, Robinson *et al.* 2002, Hegyi & Török 2007). Prolonging the growth period would permit individuals to reach a similar final body size as individuals that have been reared under optimal conditions (Dijkstra *et al.* 1990, Bize *et al.* 2003). Here, we showed that insect-fed chicks exhibited delayed growth in body mass and size, though finally reaching higher final size and body condition than fish-fed chicks. Previous studies also showed that chicks fed on low-energy prey (insects) grow slower than those fed on high-energy prey (fish) (Harris & Hislop 1978, Massias & Becker 1990). In combination with a longer growth trajectory, this may indicate an adaptive capacity associated with a reduction in daily energy requirements (Emlen *et al.* 1991, Moe *et al.* 2004). However, if conditions improve (e.g. when assimilation efficiencies increase) insect-fed chicks could show compensatory growth to catch up in size (Birkhead *et al.* 1999, Metcalfe & Monaghan 2001). Note that insect-fed chicks were fed until satiation several times per day throughout the growth period, which must be very rare in wild colonies and, therefore, the higher final values in size, body mass and body condition of insect-fed chicks could be viewed also as an artefact of the experiment in captivity.

Such a developmental strategy could be related not only to an energy shortage but also to a nutrient shortage: the protein fraction was much less efficiently assimilated by insect-fed chicks, while this macronutrient is essential for growth. Our results suggest that energy and macronutrient assimilation efficiencies are important factors for developmental strategies in birds. Differences in these parameters would help in explaining the reported differences in growth rate among colonies that differ in the relative availability of prey types (Sánchez *et al.* 2004b, Albano 2011). However, additional studies are required to establish the long-term effects of diet on the survival of Gull-billed Tern chicks and other opportunistic species.

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SAMENVATTING

Er is amper onderzoek gedaan naar de voedselvertering door jonge vogels, en er is daarom weinig bekend over de vertering van macronutriënten tijdens de groei van kuikens. We onderzochten de assimilatie van energie en macronutriënten door kuikens van de Lachstern *Gelochelidon nilotica* in afhankelijkheid van hun dieet. In het lab maten we de verteringsparameters bij kuikens van 10, 15 en 22 dagen oud die vis of insecten te eten kregen. De bruto energie-opname verschilde niet tussen de twee voedselgroepen maar de viseters assimileerden energie en macronutriënten beter dan de insecteneters. De assimilatie-efficiënties waren het hoogst op een leeftijd van 15 dagen. De enige parameter die niet afnam na dag 15 was de assimilatie-efficiëntie van vet. Kuikens op een visdieet groeiden sneller dan kuikens op een insectendieet, maar de insecteneters bleven een langere tijd groeien. Mogelijk passen kuikens de assimilatie van energie en macronutriënten aan hun behoeftes voor een optimale groei aan. Kennis over de verteringsparameters kunnen ons inzicht geven in het hoe en waarom van de groeisnelheden en het broedsucces in de natuurlijke omgeving. (PW)

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