

Importance of marine prey to growth of estuarine tern chicks: evidence from an energetic balance model

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We assessed the effects of quality and quantity of prey species on the growth of Little Tern *Sterna albifrons* chicks raised in salinas (salt-pans), Algarve, Portugal. An energetic balance model was developed, which estimated the total amount of energy ingested by all chicks in a nest and the energy expenditure by the chicks when either growing alone or in groups of two and three per nest. Energy intake per chick depended on the energy available per nest and a competition value for food between chicks. Energy expenditure was defined by the basal metabolic rate (BMR), which depends on chick's weight, plus a multiple of BMR, obtained by calibration and accounting for unspecified energetic losses. Prey species ingested by Little Tern chicks were mainly the fishes sand-smelt *Atherina* spp., Sardine *Sardina pilchardus*, Garfish *Belone belone* and mummichog *Fundulus* spp., but also two types of shrimp (*Palaemonetes* spp. and *Palaemon* spp.). Although prey species more abundant in salinas (shrimps and *Fundulus* spp.) were delivered at a higher rate, and *Fundulus* spp. had the greatest calorific content, chick growth was more sensitive to alterations in the ingestion of typically marine fish species, such as *Sardina pilchardus* and *Belone belone*. Model predictions were in agreement with data obtained in the field, as adults breeding in salinas foraged regularly at sea. Practical considerations from the present results are: (1) birds breeding in salinas rely on a sufficient amount of typically marine prey to ensure the growth of their chicks; (2) in some years foraging conditions in the salinas can be favourable, apparently because high food abundance (plus proximity to nests) may compensate for relatively poor quality of food types encountered.

Key words: Little Tern, chick growth, marine prey, estuarine terns, energetic balance model, salinas

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INTRODUCTION

Variation in food supply has a marked effect on breeding parameters and productivity of seabirds. In particular, smaller species such as terns (Monaghan *et al.* 1989, Ramos 2001, Taylor & Roe 2004) are strongly affected because they possess little leeway in their energy budgets and spend a greater proportion of their time foraging than larger species (Pearson 1968). As a consequence, declines in prey fish stocks has led to breeding failure of entire tern colonies (Monaghan *et al.* 1992). Prey species vary in calorific content (Hislop *et al.* 1991, Anthony *et al.* 2000, Pereira 2002, Paiva *et al.* 2006), and energy limitation to chick growth may occur if the abundance of high-energy species is low (Dahdul & Horn 2003). Relationships between seabird populations and their prey composition or abundance are also important to detect changes in marine ecosystems, particularly in specific prey stocks (Furness & Nettleship 1991, Monaghan *et al.* 1991, Montevecchi 1993, Le Corre & Jaquetmet 2005, Zuria & Mellink 2005).

Little Terns *Sterna albifrons* are the most estuarine of the temperate terns and forage closer to the breeding colonies than other tern species (usually within 5 km; Allcorn *et al.* 2003). Foraging areas are characterized by low depth and transparent marine, estuarine, freshwater and brackish water environments (Cramp 1985, Fasola & Bogliani 1990, Brenninkmeijer *et al.* 2002). Their prey – both for themselves and for the chicks – consists of small fish, crustaceans and insects (Cramp 1985, Bogliani *et al.* 1992, Bogliani *et al.* 1994, Paiva *et al.* 2006). During poor environmental conditions, such as strong winds, prolonged rainfall and decreased water visibility (Weimerskirch & Stahl 1988, Frank 1992, Stienen *et al.* 2000, Brenninkmeijer *et al.* 2002), tern parents have difficulties in finding sufficient food for their chicks.

Studies on Little Tern chick growth are scarce. Norman (1992) provided a few data on Little Tern chick growth in Gronant, Wales, and suggested that the type and size of available food are the main factors influencing their growth rate. However, little is known about the growth of Little Tern

chicks in southern Europe, where patterns of food abundance and feeding behaviour differ from those of northern Europe (Paiva *et al.* 2006). In the Algarve, southern Portugal, Little Terns feed in natural (estuarine lagoons and the adjacent sea) and man-made (salinas and artificial channels) habitats. There are significant differences between the diet composition of chicks from sandy beaches and salinas, and the early growth rate of chicks on beaches is higher than that of chicks in salinas (Paiva *et al.* 2006). This suggests that the proximity to marine foraging areas is important to raise chicks.

To understand the influence of quantity and quality of prey fish on chick growth, energetic balance models can be used (Martins *et al.* 2004). Martins *et al.* (2004) modelled the variation in chick growth in relation to the ingestion of different quality prey by Roseate Terns *Sterna dougalli*. However, they did not distinguish between different chicks within the same brood. Furthermore, they did neither account for competition among siblings nor for hatching delay of chicks within the same brood. These aspects seem to be very important for the allocation of food brought to the brood, as first-hatched, larger chicks (A-chicks) have better chances to obtain food (Schew & Ricklefs 1998, pers. obs.). Asynchronous hatching has therefore been viewed as a mechanism that facilitates brood reduction during food shortages by selective starvation of smaller, less competitive individuals (Lack 1947, 1954, Schew & Ricklefs 1998).

In the Algarve, Little Terns prefer sandy beaches to breed (Cтры *et al.* 2004). Reasons for this are unknown but preference for marine prey, which could be more profitable to chicks (Paiva *et al.* 2006), may be a reason. In this study, we developed an energetic chick growth balance model, using data on delivery rates of food to chicks, prey calorific content and biomass, to answer the following questions: (1) Can the model describe and predict the growth of Little Tern chicks in several years, based on competition for food among chicks and hatching delay? (2) What are the effects on chick growth of changes in the main prey delivered (especially different prey types such as shrimps vs.

fish and lagoon vs. marine fish species)? (3) How does chick growth respond to scarcity of food? To further understand why terns prefer beaches as breeding site, we described the foraging habitats (salinas, lagoon and sea) used by adults breeding in salinas and sandy beaches.

METHODS

Data collection

We used data from a study of Paiva *et al.* (2006) on Little Tern chick growth and diet in 2003 and collected similar data in 2005. Data from both years were collected on the salinas (man-made salt-pans) of Santa Luzia, Ria Formosa, Algarve, Portugal (37°06'N 7°38'W), an area of salt-pans about 245 m distance from the lagoon, 1350 m from Gilão river and 835 m from the sea (Fig. 1).

FORAGING HABITATS OF ADULTS

Between 31 May – 2 June 2005, adults were trapped on the nest and colour marked with non-toxic paint. Ten individuals were captured on each breeding habitat: salinas (Santa Luzia) and sandy beach (Tavira barrier-island; Fig. 1), marked blue and green, respectively. This allowed us to compare foraging habitat use between individuals breeding on sandy beaches and on salinas. From 2 June – 9 July 2005, we searched for mark-ed individuals around the Santa Luzia colony and in the nearby Tavira and Armona barrier-islands, covering the different types of foraging habitats (lagoon, sea, lagoon channel entrance and salt-tanks) by walking transects. Only irregular searches were made in the gullies in the eastern part of the salinas, since virtually no foraging birds were observed there, presumably because of salinas abandonment and human disturbance. When marked terns were observed, the position (Global Positioning System) was recorded and the approximate distance from the coast was visually estimated (Fig. 1).

CHICK GROWTH

In 2003 and 2005, twelve nests were selected within an area of approximately 1500 m² and

fenced with 0.3 m high, 1 cm square mesh hexagonal wire to keep chicks near the nest site. Fences were about 1.5 m in diameter. Inside the fences, we added some rocks to be used as perches by the parents, as well as a wooden shelter and some vegetation to provide chick protection against the sun and possible avian predators. Chicks were designated as A, B and C according to hatching order (when two chicks hatched on the same day, we considered the A-chick as the heavier and larger individual). Each chick of a nest was marked, using a non-toxic paint, with a different colour on the head and breast. All chicks were weighed daily between 8:00 and 11:00; 32 chicks in 2003 until 19–22 days and 28 chicks in 2005 until 16–18 days of age. Two parameters were calculated to characterize growth of chicks after the age of four days: linear growth rate (LGR) and asymptotic mass (AM). LGR was defined as the slope of a regression line of chick mass, wing-length and tarsus-length against date (Nisbet *et al.* 1995) during the linear growth period (5–14 days). AM was defined as the mean of all masses measured during the period of near-constant mass (15–22 days; Nisbet *et al.* 1998).

FOOD DELIVERY

Food delivery to fenced chicks was observed in the periods 11 June – 5 July in 2003 and 10 June – 3 July in 2005. From the fenced nests, ten were selected according to their location. Two portable hides, placed 2–7 m from these nests were used to observe and identify prey delivered to chicks, using 10x40 binoculars. A total mean value of 90 h of observation was made each year, divided into periods of one to ten hours (median = two hours). The observations were randomly spread across the 3-week period, the daylight hours and tidal phases. Each nest was sampled equally (same number of hours per nest; Paiva *et al.* 2006 for further details on food delivery procedures).

During the breeding season of 2003, the five most abundant prey types consumed by Little Tern chicks were: Mummichog *Fundulus* spp., Sand-smelt *Atherina* spp., shrimps (*Paleomon* spp. and *Paleomonetes* spp.), Sardine *Sardina pilchardus* and

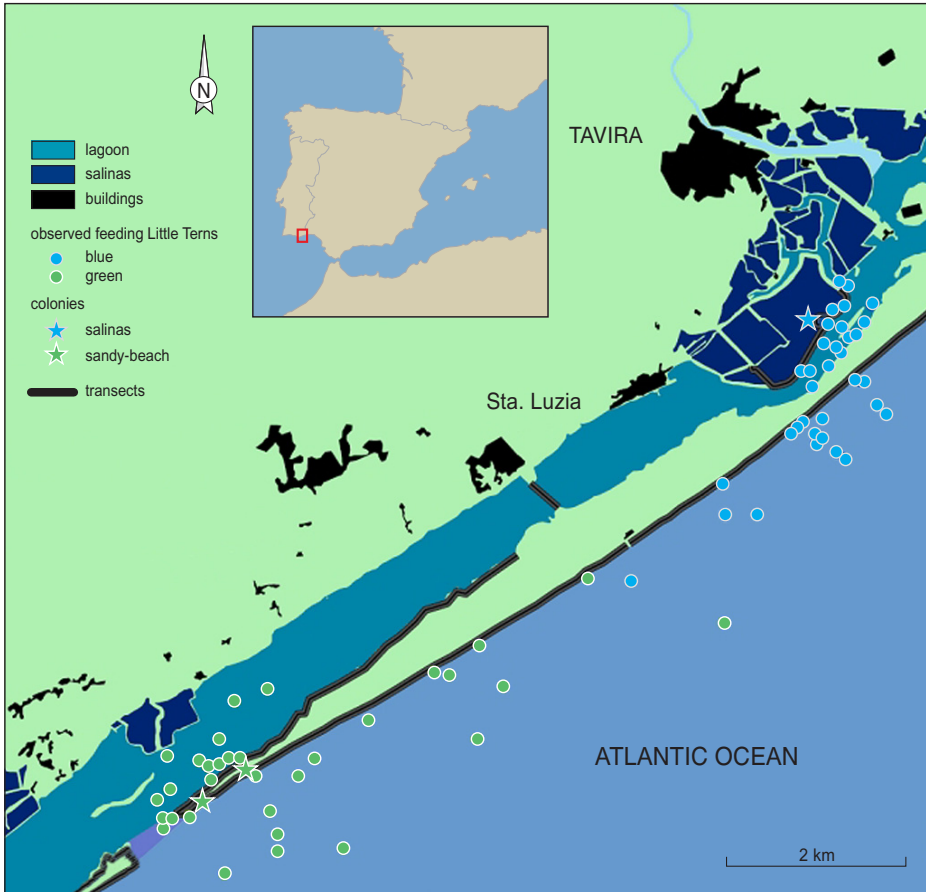


Figure 1. Representation of the study area with the two colonies where adult Little Terns were marked (salinas, Sta. Luzia and sandy beach, Tavira barrier-island) and the sightings of foraging birds from the two colonies. Transects to locate foraging birds are shown.

Garfish *Belone belone*. Other prey were Atlantic Sauri *Scomberesox saurus*, Mugilidae (the most common species of the family is Mullet *Liza* spp. (Erzini *et al.* 2002), and bottom fishes (Soleidae, Common Goby *Pomatoschistus* spp. and Gobiidae/Blenniidae; Paiva *et al.* 2006, Catry *et al.* 2006). In 2005, the main prey items were *Atherina*, shrimps (*Paleomon* and *Paleomonetes*) and *Sardina pilchardus*. Less important prey types (< 6 times delivered to the chicks) were *Trachinus vipera*, *Dicentrarchus* spp., *Loligo* sp., *Raja clavata*, *Microchirus boscanion*, *Nerophis ophidion*, *Engraulis encrasicolus*,

Symphodus melops, *Spondylisoma cantharus*, *Symphodus bailloni*, *Ammodytes* spp., *Trachurus trachurus*, Sygnathidae, Sparidae, and Soleidae. The length of each prey delivered was determined in relation to the mean Little Tern adult bill-length (Paiva *et al.* 2006) and transformed into mass using regression equations (Table 1).

CALORIFIC CONTENT

In 2003 fresh prey found in the colonies were measured (standard length, total length, maximum width), weighed, washed with fresh water and

frozen. The energetic content of each prey species was determined in a PARR 1425 bomb calorimeter, using the mean value of three measurements per prey item. The conversion from $J\ g^{-1}$ of dry weight to $J\ g^{-1}$ of wet weight was made using the theoretical relationship of 1:5 (Jørgensen et al. 1991). All measurements were taken by one of us (VHP).

Model building

The model takes into account the specific energy of the principal prey items, derived from their biomass and calorific content, and meal delivery rate to chicks, contributing to the pool of energy available for chicks to be divided among A-, B- and C-chicks based on a competition factor and a hatching delay factor. Energy assimilated in surplus of the energy needed for metabolism and activities will be used for a chick's growth until an asymptotic weight is attained (Fig. 2). The growth model was calibrated with data obtained in 2003 and validated with data obtained in 2005 (in both approaches we compared growth curves created by the model with those obtained during field work). The model was constructed using STELLA 7.03 software (STELLA 1997).

We followed the procedure applied by Martins et al. (2004) on a Roseate Tern chick growth model, with the following changes and additions: (1) we made a distinction between the growth of chicks within the same brood (growth of A-, B- and C-chicks). (2) We multiplied the delivery rate of each species by 13 h, the number of daylight hours at this time of the year, since parents do not deliver food at night (Davies 1981). (3) The total energy available per chick was multiplied by the number of chicks in the model (we were interested in 3 chicks per brood, but the model can also predict growth of 2 or 1 chick per brood). (4) On the basis of our model we estimated that a brood needed 118 kJ per day for each chick to achieve normal growth. We calculated which percentage was obtained from each of the main delivered prey types and the total amount of energy brought to the nest was allocated among the chicks based on a competition factor (CF). This factor assumes that

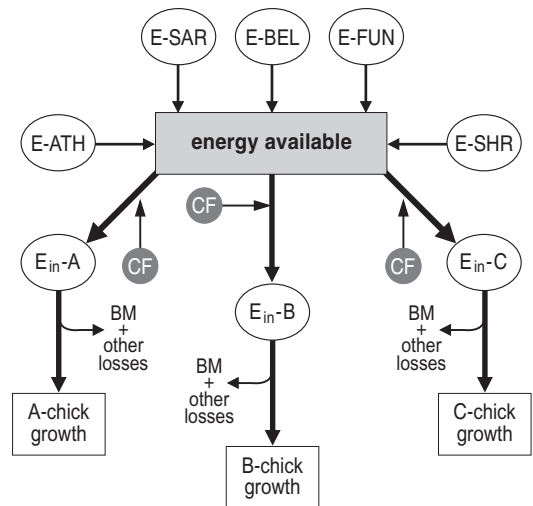


Figure 2. Schematic simplified representation of the growth model defined with data from 2003. The energy of the different prey species delivered (eg. E-ATH) is assembled in a pool of energy available to all chicks. This energy is divided by the three chicks in a nest (energy intake E_{in-A} , E_{in-B} , E_{in-C}) depending on a competition factor (CF). Part of the energy intake will be used in basal metabolism and other energetic losses (BM + other losses), and the surplus channels into chick growth. The most important prey delivered in 2003 were: *Atherina* (ATH), *Sardina pilchardus* (SAR), *Belone belone* (BEL), *Fundulus* (FUN) and shrimp (SHR).

Table 1. Equations regressing weight (W, g wet weight) on total length (TL, cm) for the species used in the model.

Species	Equation	Reference
<i>Atherina</i> spp.	$W=0.0069*TL^3$	Fishbase 2005
<i>Sardina pilchardus</i>	$W=0.0060*TL^3$	Fishbase 2005
<i>Belone belone</i>	$W=0.0020*TL^{2.87}$	Fishbase 2005
<i>Fundulus</i> spp.	$W=0.0142*TL^3$	Fishbase 2005
Shrimps	$W=0.0042*TL^{2.4}$	Unpubl. obs.

larger chicks have a higher chance of getting food (i.e. have a higher fitness than smaller chicks (Shew & Ricklefs 1998, which was also confirmed during our observations) and was estimated as: $CF = x\text{-Chick weight} / \text{Total chicks weight}$. (5) The

competition factor was interrelated with the hatching delay: when compared to A-, B- and C-chicks hatched 0.29 ± 0.03 and 0.87 ± 0.05 days later, respectively (mean values \pm SE obtained from the fenced nests in 2003). Those values were set in the model, creating a delay in the available energy flow to B- and C-chicks. (6) Estimated assimilation efficiency coefficients for several species of terns range between 0.80 and 0.83 (Visser 2002, Klaassen *et al.* 1992, Drent *et al.* 1992). From these a value of 0.80 was obtained by calibration in the present work. (7) A conversion factor of 7.995 was used to convert energy assimilated to mass gained by birds (wet weight; Jørgensen *et al.* 1991). (8) The logistic growth curve, which has a sigmoid shape, enables the description of the development of body masses of chicks as a function of age (t , in days). The logistic growth rate constant ($K = 0.0249 \pm 0.01$) of Little Tern chicks was calculated by calibration using data from 2003 (i.e. the data set used to create and calibrate the model). (9)

The asymptotic mass (g) attained by A-, B- and C-chicks, on days 20, 19 and 22, was 43.0 ± 1.34 , 42.4 ± 1.32 and 43.0 ± 0.50 g, respectively. Most chicks began the asymptotic part of their growth at 15 days of age (Konarzewski *et al.* 1998, Starck & Ricklefs 1998). (10) Hatching weights corresponded to measured mean values and were 6.50 ± 0.17 , 6.40 ± 0.26 and 6.16 ± 0.31 g for A-, B- and C-chicks, respectively.

SENSITIVITY ANALYSIS

To check for which parameters growth was most sensitive, we followed the procedure described by STELLA's manual (STELLA 1997) also called 'individual parameter perturbation' (Madenjian & Gabrey 1995), which allows to examine the sensitivity of model performance to a variation in model parameters values. Changes of $\pm 10\%$ were imposed to the model parameters and the consequent variations on A-, B- and C-chicks growth were analysed.

Table 2. Energy content, mean foraging trip duration, mean body length and meal delivery rate (mean \pm SE, with n in parenthesis) of prey items used in the model and ingested by Little Tern chicks in the salinas of Santa Luzia, Algarve. Only prey that comprised $> 6\%$ in the diet are considered (data for 2003 after Paiva *et al.* 2006). Years are compared by t -tests.

Species	Energy (KJ g ⁻¹ wet weight)	Mean foraging trip duration (h)	Total length (cm)				Meal delivery rate (prey chick ⁻¹ hour ⁻¹)			
			2003	2005	t -stat.	P	2003	2005	t -stat.	P
Pelagic fishes										
<i>Atherina</i> spp.	3.7 \pm 0.6 (22)	0.40 \pm 0.03 (101)	5.0 \pm 1.0 (164)	5.1 \pm 1.0 (365)	0.2	0.86	0.5 \pm 0.04 (75)	0.6 \pm 0.04 (68)	2.6	0.01
<i>Sardina pilchardus</i>	4.1 \pm 0.5 (8)	0.38 \pm 0.03 (52)	3.6 \pm 1.3 (63)	4.0 \pm 0.8 (161)	2.6	0.01	0.3 \pm 0.05 (29)	0.3 \pm 0.04 (49)	0.2	0.87
<i>Belone belone</i>	4.0 \pm 0.2 (11)	0.37 \pm 0.07 (38)	8.4 \pm 2.0 (52)	7.6 \pm 2.8 (54)	2.3	0.02	0.3 \pm 0.04 (34)	0.2 \pm 0.04 (26)	1.7	0.09
Euryhaline fish										
<i>Fundulus</i> spp.	4.4 \pm 0.6 (8)	0.35 \pm 0.02 (201)	3.1 \pm 0.5 (261)	3.0 \pm 0.3 (57)	0.6	0.52	0.7 \pm 0.08 (72)	0.24 \pm 0.04 (25)	3.0	<0.005
Shrimps	3.6 ¹	0.27 \pm 0.02 (130)	2.6 \pm 0.3 (150)	2.6 \pm 0.3 (248)	0.3	0.73	0.7 \pm 0.13 (34)	0.7 \pm 0.07 (50)	1.0	0.34

¹ Mean caloric value obtained from *Paleomonetes* spp. and *Paleomon* spp.

THEORETICAL SCENARIOS

In order to understand the importance of the energetic content of each prey species, we run the model assuming that chicks were fed only on one species at a time. For example, considering that an adult foraging trip for *Atherina* lasted 0.40 hours (Table 2), and assuming that parents could forage during the 13 daylight hours, they could feed their chicks with 32.5 *Atherina* preys. Also, we tested the impact of the absence of each prey species on chick growth by removing from the diet each one of the six prey types at a time, maintaining the other prey species and accounting for the extra foraging time (divided by the other preys) that is gained by not foraging on the omitted prey. This allowed us to understand the relative importance of shrimps vs. fishes or marine preys vs. lagoon prey items.

Statistical analysis

After checking for normality (Kolmogorov-Smirnov test) and homoscedasticity (Levene's test) we used *t*-tests to compare: (1) prey-length, (2) meal delivery rate and (3) chick linear growth rate between 2003 and 2005. Chi-square tests were carried out to test the null hypothesis that the number of items of each main prey delivered to chicks was similar between 2003 and 2005. For model calibration (with data from 2003) and validation (with data from 2005), we used Model II-regressions, a recommended procedure whenever both variables are subject to error (Sokal & Rohlf 1995). The significance of the regressions was tested with ANOVA (Fowler et al. 1998). We tested the null hypothesis that the intercept of the estimated regressions is not significantly different from 0 and the slope is not significantly different from 1, using Dent and Bleckie regression test (DBK), which simultaneously tests the slope and the intercept (Dent & Bleckie 1979). All analyses were performed with Statistica v6.0 (Statsoft 1996) with a significance level of $P < 0.05$. Data is presented as mean \pm standard error (SE).

RESULTS

Annual differences in diet and chick growth

The significant decrease in the percentage of *Fundulus* delivered to Little Tern chicks from 2003 to 2005 coincided with an increase in the delivery rates of *Atherina* and *Sardina pilchardus* (Fig. 3). The diet composition differed significantly between 2003 and 2005, namely *Atherina* ($\chi^2_1 = 39.58$; $P < 0.01$), *Sardina pilchardus* ($\chi^2_1 = 23.07$; $P < 0.0005$), *Scomberesox saurus* ($\chi^2_1 = 9.91$; $P < 0.01$), shrimps ($\chi^2_1 = 12.25$; $P < 0.01$) and *Fundulus* ($\chi^2_1 = 71.91$; $P < 0.01$). However, there was no significant difference in linear growth rate

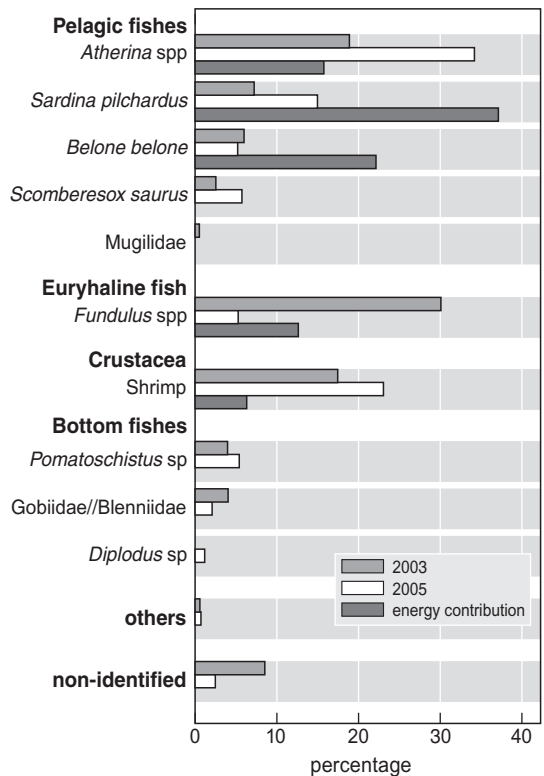


Figure 3. Diet composition of Little Tern chicks on the salinas in 2003 ($n = 857$, Paiva et al. 2006) and 2005 ($n = 1068$). The contribution of each food type to the energy pool that allows normal chick growth (based on the model) is indicated.

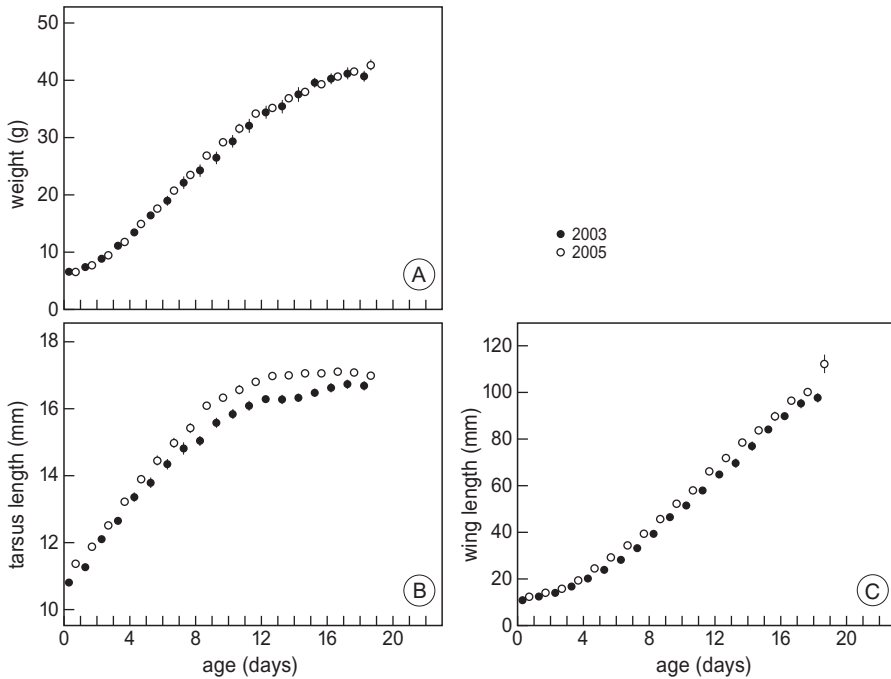


Figure 4. Chick growth curves of Little Tern compared between 2003 ($n = 32$) and 2005 ($n = 28$; means \pm SE) based on weight (A), tarsus length (B) and wing length (C). In 2003 14 A-chicks, 11 B-chicks and 7 C-chicks (after day 5 dropping to 2) were sampled; corresponding numbers in 2005 were 12, 11 and 5 (after day 10 dropping to 2).

between 2003 ($2.42 \pm 0.09 \text{ g day}^{-1}$, $n = 24$) and 2005 ($2.33 \pm 0.11 \text{ g day}^{-1}$, $n = 19$; $t_{41} = 0.63$, $P = 0.53$). Energy contribution of *Sardina pilchardus* and *Belone belone* to normal chick growth was much higher than that of other prey types (Fig. 3). In addition, linear growth of tarsus (2003: $0.29 \pm 0.01 \text{ mm day}^{-1}$ in 2005: 0.27 ± 0.01 ; $t_{40} = 1.42$; $P = 0.16$) and wing length (2003: $6.05 \pm 0.14 \text{ mm day}^{-1}$ in 2005: 5.95 ± 0.20 ; $t_{40} = 0.42$; $P = 0.68$) did not differ significantly between years (Fig. 4).

Model validation

Chick body mass growth predicted by the model for A-, B- and C-chicks agreed well with observed data of 2003 and 2005. In 2003, A-chicks grew faster than B-chicks but both attained the same mass at 18 days. The same pattern was obtained for predicted growth curves with C-chicks reaching

the mass of A-chicks at 16 days. Most of the predicted mass values for the three chicks were within standard error lines of observed weights (though less well for C-chicks), ensuing significant Model II-regressions for A-, B- and C-chicks in 2005 (model validation, ANOVA: $F_{1,18} = 5.43$, $P = 0.001$, $r^2 = 0.98$; $F_{1,17} = 4.34$, $P = 0.001$, $r^2 = 0.97$ and $F_{1,20} = 3.2$, $P = 0.01$, $r^2 = 0.96$; Fig. 5). Furthermore, the slope of the regression was not significantly different from 1 and the intercept was not significantly different from 0 for A-, B- and C-chicks (DBK-regression test: $F_{1,18} = 3.22$, $P = 0.001$; $F_{1,17} = 2.45$, $P = 0.001$ and $F_{1,18} = 1.24$, $P = 0.01$), giving credibility to our model. In addition there were also significant Model II-regressions for A-, B- and C-chicks in 2003 (model calibration, ANOVA: $F_{1,17} = 5.67$, $P = 0.001$, $r^2 = 0.98$; $F_{1,17} = 3.88$, $P = 0.001$, $r^2 = 0.98$ and $F_{1,16} = 2.34$, $P = 0.01$, $r^2 = 0.96$; Fig. 5).

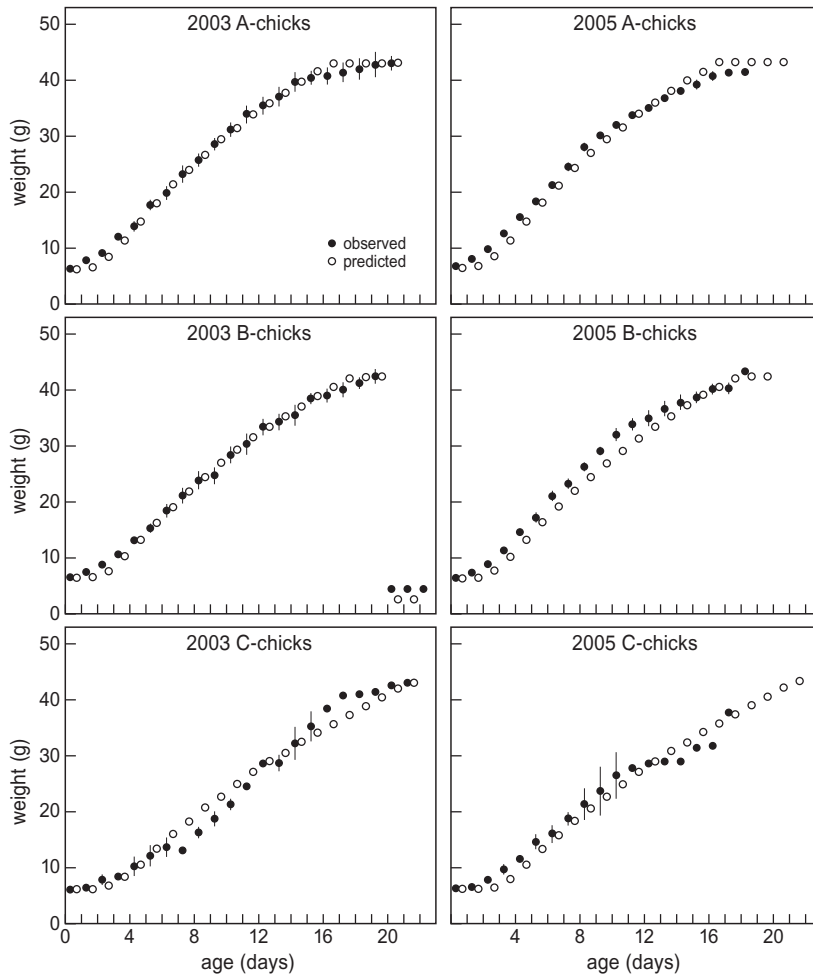


Figure 5. Observed and predicted growth curves of A- (top), B- (mid), and C- chicks (bottom) of Little Tern (mean weight \pm SE) in 2003 and 2005. Correlations between observed and predicted values were all highly significant for all chicks (model validation, see Results).

Sensitivity analysis

Sensitivity analysis revealed that growth rates were most sensitive to the number of daylight hours that parents delivered food to chicks and to the factor converting dry into wet body mass (Table 3), while changes in the other parameters did not affect chick growth. C- and B-chicks were the most sensitive to those parameters, followed by A-chicks. Changes of $\pm 10\%$ on these three parameters caused $\pm 10\%$ of variation on the weight of the chicks.

Theoretical scenarios

Assuming that parents feed their chicks solely on *Atherina* (spending 0.40 hours to deliver one item of this species to the nest), the model predicts that at an age of 22 days A-, B- and C-chicks attain a body mass of 43.0, 42.5 and 40.6 g, respectively. If we remove *Atherina* from the chicks' diet, while keeping the foraging day at 13 h and assuming the other prey types are delivered in relation to the duration of their specific foraging trip (Stienen &

Table 3. Sensitivity analysis of the principal parameters entered into the model. See text for explanation of sensitivity computations.

Parameters	Value	Sensitivity		
		A-chicks	B-chicks	C-chicks
Basal metabolism rate	0.0470	0.0049	-0.0041	-0.0048
Feeding hours/day	13	0.3441	0.3583	0.4580
Loss factor	0.5	-0.0012	-0.0013	-0.0013
Assimilation efficiency coefficient	0.8	0.0626	0.0616	0.0683
Conversion factor (wet weight of bird)	7.995	-0.3372	-0.3558	-0.4521

Brenninkmeijer 2002), A-, B- and C-chicks would achieve 43.1, 42.4 and 43.09 g, respectively. If the chicks were only fed *Sardina pilchardus*, A-, B- and C-chicks would attain asymptotic mass at an age of 7, 8 and 10 d, respectively. However, if no *Sardina pilchardus* were fed at all, none of the chicks would attain asymptotic weight. If fed only on *Belone belone* the chicks would achieve an asymptotic weight at an age of 9, 10 and 13 d, respectively. If no *Belone belone* is fed, the model predicts that C-chicks would be slightly under the asymptotic mass at fledging, weighing 41.6 g at day 22 (Fig. 6).

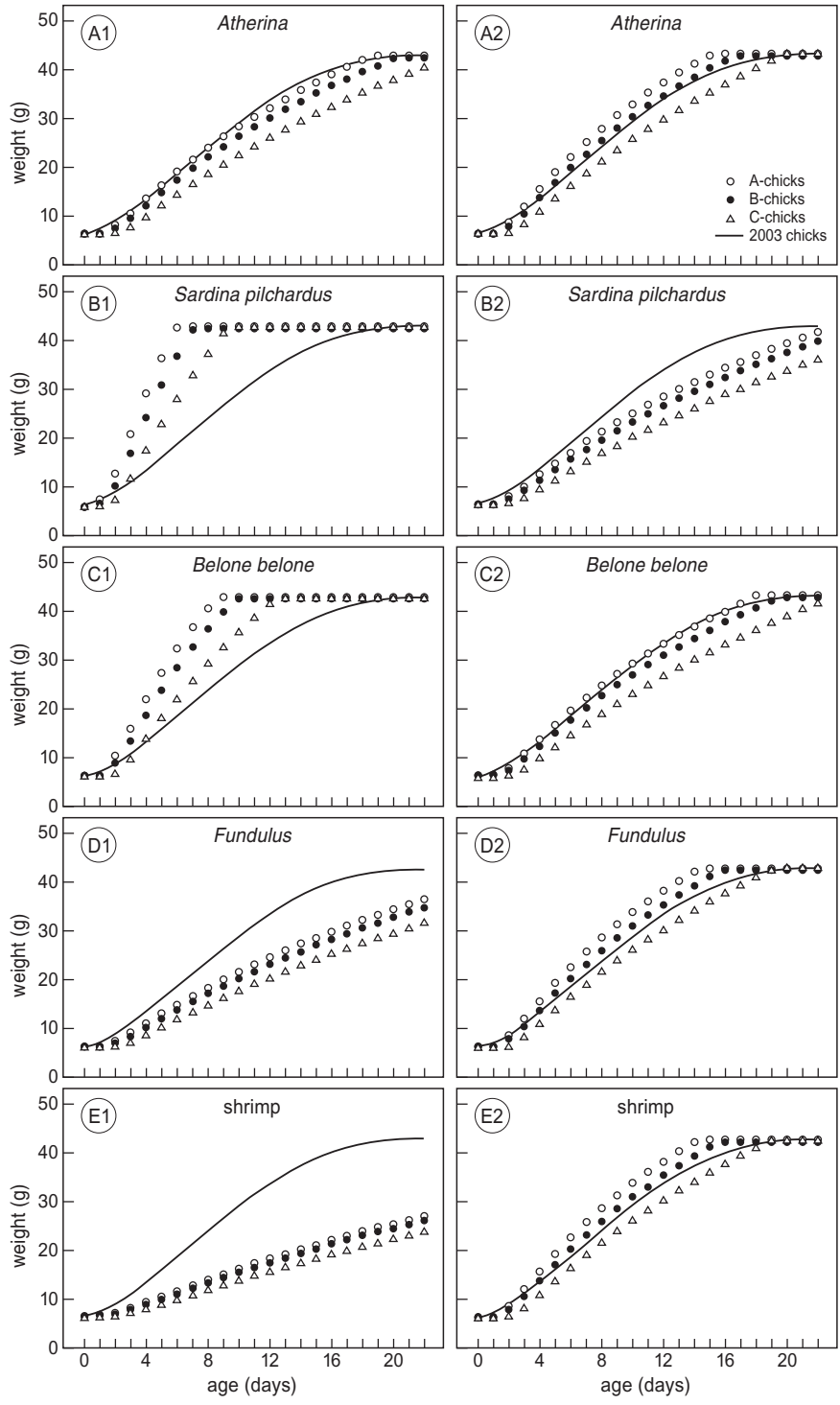
If only *Fundulus* was delivered to the chicks, A-, B- and C-chicks would weigh 36.7, 35.1 and 31.9 g at an age of 22 d; i.e. they would not reach asymptotic mass. When no *Fundulus* was delivered to the chicks, A-, B- and C-chicks would reach asymptotic weights at an age of 15, 16 and 20 d, respectively. Finally, if the chicks would only ingest shrimps all would starve since A-, B- and C-chicks would weight only 27.1, 26.0 and 23.9 g at an age of 22 d. When shrimps were removed from the diet, A-, B- and C-chicks would attain asymptotic mass at an age of 15, 16 and 19 d (Fig. 6).

If the chicks ingested only marine prey (*Sardina pilchardus* and *Belone belone*) they would

achieve asymptotic mass at an age of 12, 13 and 17 d for A-, B- and C-chicks, respectively (Fig. 6). From these theoretical scenarios it follows that, in order to deliver sufficient food for normal growth of chicks, corresponding to 118 kJ per day per chick as based on the 2003 observations, parents that fed chicks only with *Fundulus*, shrimps and *Atherina* were to increase feeding rate by 79.2%, 287.4% and 2.40%, respectively. On the contrary, parents feeding their chicks only with *Sardina pilchardus* or *Belone belone*, could reduce feeding rate by 70.1% and 52.3%, respectively.

The removal of each of the five main prey types from the diet of chicks (maintaining other items with their specific delivery rates) modified the predicted chick growth. The removal of *Fundulus* and/or shrimps did not prevent chicks from reaching asymptotic weight. When *Atherina* or *Belone belone* were removed, only C-chicks did not achieve their maximum weight, reaching only 41.3 and 38.0 g, respectively. On the other hand, when removing *Sardina pilchardus* from the chicks' diet, none of the chicks would attain asymptotic weight, unless the delivery rate of other prey increased by 20, 30 or 50% for A-, B- and C-chicks to reach asymptotic weight.

Figure 6. (right) Effects of the most abundant prey species on the growth of Little Tern chicks in 2003. Observed growth curves for 2003 chicks, represented by a polynomial cubic function is shown for purpose of comparison. Lefthand panels indicate growth curves when chicks are simulated to have a mono-species diet: (A1) *Atherina*, (B1) *Sardina pilchardus*, (C1) *Belone belone*, (D1) *Fundulus* and (E1) shrimp. Observed asymptotic weights attained by A-, B- and C-chicks, at an age of 20, 19 and 21 d, were 43.0, 42.4 and 43.0 g, respectively. The righthand panels show growth curves when the simulated diet is without the indicated species: (A2) *Atherina*, (B2) *Sardina pilchardus*, (C2) *Belone belone*, (D2) *Fundulus* and (E2) shrimp.



Foraging habitat use by breeding location

Both main feeding habitats (lagoon and sea) were equally used by adults breeding on salinas (at sea $n = 18$ observations, in the lagoon $n = 19$) and on sandy beaches (at sea $n = 17$, in the lagoon $n = 15$; $\chi^2_1 = 0.14$; $P = 0.71$). On the other hand, birds breeding on sandy beaches were not observed feeding on salinas, whereas adults breeding in salinas were (Fig. 1).

DISCUSSION

The differences in abundance of the main prey items ingested by chicks between 2003 and 2005 were not translated into differences in chick growth parameters. The inter-annual diet comparison revealed that *Fundulus* almost disappeared from the diet of chicks in 2005, whereas in 2003 it was the most delivered species. Very little is known about the distribution of this euryhaline species, introduced from the United States into Portugal. This species was never collected in the Ria Formosa lagoon (Erzini *et al.* 2002), and it may occur only in salinas and adjacent channels. Changes in the salinity of the salinas in 2005 due to semi-industrial salt extraction purposes (pers. obs.) could be a reason for such a decline (although *Fundulus* is resistant to pollution, Wirgin & Waldman 2004, Meyer *et al.* 2005, Liu *et al.* 2005). The decrease in the abundance of *Fundulus* may also explain the increase in the amount of shrimps delivered to chicks in 2005; *Fundulus* is one of their natural predators (Carson & Merchant 2005). Our results show that marine preys were more important in the diet in 2005: adults delivered significantly larger items of *Sardina pilchardus* and *Belone belone*, and a higher number of *Sardina pilchardus*, *Scomberesox saurus* and *Diplodus* sp. A variety of factors, such as sea currents, population stock fluctuations (Steele & Henderson 1984), may have been responsible for more individuals swimming into the lagoon in 2005.

The relatively low correlation between observed and predicted growth curves for C-chicks may be related to the fact that after day 5 only two

C-chicks were present within the fences. The high mortality of C-chicks has been well documented in Little Terns (Davies 1981, Norman 1992) as well as in other tern species with 3-chicks broods such as the Common Tern *Sterna hirundo* (Nisbet *et al.* 1995, Nisbet *et al.* 1998). Nevertheless, our Little Tern chick growth model used growth parameters that appeared to simulate chick growth very well and we can say that it is possible, with high accuracy, to obtain a Little Tern chick growth model based on differential energy of each prey species. Moreover, sensitivity analysis suggests a high dependence of chick growth on high food delivery rates, which are directly and exclusively related to parental performance and experience. Using this sort of growth models has a large advantage above protocols where chicks are raised in the laboratory on a known amount of a specific fish species (e.g. Massias & Becker 1990, Negro *et al.* 1994, Dahdul & Horn 2003).

Because calorific content varied little between delivered prey species (although *Fundulus* had a significantly higher calorific content, Paiva *et al.* 2006), the main differences in energy received by chicks were related to prey delivery rates. Our results suggest that in years in which foraging conditions in the salinas are good (2003 when *Fundulus* dominated the diet), Little Terns derive an important part of their daily energy demands from food caught in the salinas. Although *Fundulus* was the prey most delivered by parents it was, together with shrimps, less important in terms of energy contribution. These unexpected results seem to be related to the biomass-total length ratios of fish prey species, as also found by Martins *et al.* (2004). Prey items like *Sardina pilchardus* and *Belone belone* have higher biomass content per total length than *Fundulus* or shrimps. On the other hand, *Atherina*, which is the most abundant prey species in the lagoon of Ria Formosa (Erzini *et al.* 2002), had a moderate importance for chick growth, although it ranked as third in the meal delivery rate. In case of food limitation (removing one species at a time), only the growth of C-chicks was affected (they did not reach asymptotic weight at an age of 22 d) when *Belone belone* or

Atherina were removed from the diet. However, when *Sardina pilchardus* was removed, the growth of all chicks was severely affected.

Salinas are suitable breeding habitats (Catry *et al.* 2004) but our results suggest that proximity to marine/coastal lagoon areas is important for successful breeding, due to the significance of marine species (*Sardina pilchardus* and/or *Belone belone*) for chick growth. This hypothesis was corroborated by sightings of marked adults from the salinas travelling to feed in marine areas. Therefore, there seems to be an active effort of individuals to capture marine prey species. However, salinas may provide an important foraging habitat during certain years and in periods of strong winds or decreased visibility in the lagoon habitat (Paiva *et al.* 2006). Our results underline the importance of marine prey species for chick growth, and help to understand why Little Terns prefer sandy beaches to breed (Catry *et al.* 2004). Presently, the loss of sandy beaches occurs at an alarming rate throughout the world due to human recreation and tourism.

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- voordeel van een geringere kans op verstoring staat echter dat de afstand van de voedselvluchten naar zee langer is. De vogels kunnen echter ook voedsel zoeken in de zoutpannen. Er is weinig bekend of de prooien die er voorkomen, voldoen aan de voedingseisen van de opgroeiende jongen. Om dit te onderzoeken werd in de Algarve, Portugal, een kolonie Dwergsterns in een van de zoutpannen geselecteerd, waar gedurende twee seizoenen het door de ouders aangebrachte voedsel en de groei van de jongen werden geregistreerd. Hiertoe werden jaarlijks 12 nesten (aantal jongen gemiddeld 2,3) met gaas afgeschermd, zodat de jongen gemakkelijk te vinden waren om te wegen. Uit waarnemingen bij de nesten bleek dat uit zee kleine vissen werden aangebracht, vooral koornaarvissen *Atherina* spp., Sardien *Sardina pilchardus* en Geep *Belone belone*. De zoutpannen leverden vissen op – vooral *Fundulus* spp. – en garnalen (*Paleomonetes* spp. en *Paleomon* spp.). De zoutpannen waren voedselrijk. De ouders waren dan ook sneller terug bij het nest met een prooi uit de zoutpannen dan wanneer ze naar zee vlogen om te vissen. Maar de prooien uit de zoutpannen bleken aanzienlijk kleiner dan de aangebrachte zeevissen, waardoor ze als voedsel voor jongen minder aantrekkelijk bleken. Het kostte 16 minuten om een garnaal van 42 mg uit de zoutpan te halen, terwijl een Sardien van gemiddeld 380 mg in 23 minuten uit zee werd gehaald. Mede op basis van het gewicht en de energetische waarde van de prooitypes werd een theoretisch model opgesteld dat een schatting maakt van de hoeveelheid energie die de kuikens tijdens het opgroeien binnenkregen, en hoeveel daarvan voor lichaamsgroei beschikbaar was. Dit model vormde een onderbouwing voor het grote belang van zeevissen voor de jonge sterns. Het liet zien dat zonder zeevissen sternkuikens amper in staat waren een voldoende uitvlieggewicht te bereiken. Vooral de jongste, kleinste kuikens in een nest bleken gevoelig voor de kwaliteit van het aangebrachte voedsel: het theoretisch model voorspelde dat bij het ontbreken van zeevissen een aanzienlijke groeiachterstand zou ontstaan. Deze voorspelling werd ondersteund door de waarneming dat veel van de jongste kuikens in het nest verhongerden. (JP)

SAMENVATTING

De Europese populaties van de Dwergstern *Sterna albifrons* staan onder druk, onder meer als gevolg van verstoring van de nesten door intensieve recreatie langs de kusten van dit continent. In Portugal is recent een opmerkelijke verschuiving in broedverspreiding opgetreden, namelijk van drukke zandstranden naar zoutpannen ('salinas'), een kunstmatig habitat om zout te winnen. De sterns kunnen hier relatief rustig broeden. Tegenover het

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