J Ornithol (2015) 156:699–710
DOI 10.1007/s10336-015-1170-0

ORIGINAL ARTICLE

Intra-specific plasticity in parental investment in a long-lived single-prey loader

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Received: 2 April 2014 / Revised: 25 November 2014 / Accepted: 2 February 2015 / Published online: 6 March 2015
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Abstract Seabirds exhibit considerable behavioural flexibility in foraging investment in order to meet the nutritional needs of their chicks during variable environmental conditions. Although regulation of offspring provisioning is generally thought to be related to species-specific constraints imposed by central place foraging, some studies suggest different responses within the same species linked to local differences in foraging conditions. Under adverse conditions, seabirds are expected to be less flexible because they must secure their own survival chances first before investing in current reproduction. Short-ranging single-prey loaders are expected to show large intra-specific variation in time spent on foraging because their mode of foraging is energetically expensive, and because they face restricted possibilities to increase the numerical prey input to the colony compared to multiple prey loaders. In this study, we examined if and how the single-prey loading Sandwich Tern *Thalasseus sandvicensis* varies colony attendance based on the nutritional status of their chick as well as parental body condition in two study colonies. The proportion of time that a chick was left unattended at the colony negatively correlated with chick body condition, suggesting that the parents tried to counterbalance poor feeding conditions by investing more time in foraging. Energy transport rates to the chicks (corrected for time spent away from the colony) and body condition of the chicks were similar in both colonies. However, at Zeebrugge, where adults were in poor body condition, parental non-attendance was much lower than on Griend, even when chicks were in poor condition. Still, our results suggest that parental nest non-attendance in Sandwich Terns is merely a corrective response to food loss to kleptoparasitic gulls in order to meet the nutritional status of the chick, although an effect of adult body condition could not be excluded.

Keywords Sandwich Tern · Single-prey loader · Body condition · Parental nest attendance · Kleptoparasitism

Zusammenfassung

Innerartliche Anpassungsfähigkeit beim Elternaufwand in einem langlebigen Seevogel, der nur jeweils ein Beutetier im Schnabel transportieren kann

Seevögel zeigen sehr flexibles Verhalten im Aufwand der Futtersuche, um ihren Küken unter unbeständigen Umweltbedingungen ausreichend Nahrung zu beschaffen. Generell wird angenommen, dass die Regulation der Kükenversorgung abhängig ist von artspezifischen Einschränkungen bei der Futtersuche, die in einem Radius um die Brutkolonie stattfindet. Dennoch gibt es Studien, die auf innerartliche Unterschiede hinweisen, welche auf wechselnden Umweltbedingungen bei der Nahrungssuche beruhen. Es wird angenommen, dass Seevögel unter widrigen Bedingungen weniger flexibel reagieren, da sie zuerst ihr eigenes Überleben sichern müssen bevor sie in die Reproduktion investieren. Dabei wird erwartet, dass Arten mit kurzen Nahrungsflügen, die jeweils nur ein Beutestück transportieren können, eine hohe innerartliche Variation in

Communicated by O. Krüger.

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der Dauer der Nahrungsflüge aufweisen, da bei ihnen die Nahrungssuche wesentlich aufwändiger ist und sie wenig Möglichkeiten haben die Menge an Beutestücken zu erhöhen, die in der Kolonie ankommen. In dieser Studie untersuchten wir in zwei Brutkolonien, ob und wie die Brandseeschwalbe *Thalasseus sandvicensis* ihre Anwesenheit in der Brutkolonie in Bezug auf den Hungerzustand ihrer Küken sowie der Körperkondition der Eltern anpasst. Die Zeit, in der die Küken unbewacht in der Kolonie zurückgelassen wurden, korrelierte negativ mit der Körperkondition der Küken, was darauf hin deutet, dass die Eltern versuchten die schlechten Nahrungsbedingungen durch längere Futtersuche auszugleichen. Energietransportraten an die Küken (korrigiert für die Zeit, die entfernt von der Kolonie verbracht wurde) und Körperkondition der Küken waren in beiden Kolonien ähnlich. Allerdings waren Altvögel at Zeebrugge in schlechter Körperkondition und elterliche Abwesenheit deutlich geringer als in Griend, selbst wenn Küken in schlechter Verfassung waren. Dennoch deuten unsere Ergebnisse darauf hin, dass die elterliche Abwesenheit vom Nest in Brandseeschwalben nur eine ausgleichende Reaktion auf den Verlust von Beute an kleptoparasitische Möwen ist, um den Ernährungszustand der Küken zu erhalten. Ein Effekt auf die Körperkondition von Altvögeln kann allerdings nicht ausgeschlossen werden.

Introduction

Flexible time budgets allow individual animals to maintain the nutritional status of their offspring at an acceptable level. Many seabirds, for example, allocate more time to foraging when food density is low or when food availability decreases because of environmental conditions. Seabirds performing long feeding trips do not normally regulate their foraging investments very much to compensate for the current breeding requirements (but see, for example, Bolton 1995; Weimerskirch et al. 1997; Granadeiro et al. 2000) because the nutritional status of their chick is a poor indicator of the energetic needs during the next return to the colony (Hamer and Hill 1994; Weimerskirch et al. 1995). Many short-ranging seabirds, however, do exhibit considerable behavioural flexibility in foraging investment. In particular, Alcidae are known to modify foraging time at the expense of time spent at the colony in order to maintain provisioning rates or reproductive success (Monaghan et al. 1994; Harding et al. 2007; Ronconi and Burger 2008; Burke and Montevecchi 2009). They are able to fine-tune the provisioning to meet the nutritional needs of their chicks (e.g. Bolton 1995; Granadeiro et al. 2000) or to adapt to variable environmental conditions (Waugh and Weimerskirch 2003; Jodice et al. 2006; Burke and Montevecchi 2009).

While short-ranging seabirds that carry multiple prey items to the colony are known to adjust provisioning rates to compensate for a decrease in chick growth or body condition (Tveraa et al. 1998; Wernham and Bryant 1998; Harding et al. 2002), single-prey loaders can only adjust prey length, select for more energy-rich species or increase foraging effort (Harding et al. 2007; Limmer and Becker 2009; Dänhardt et al. 2011), but, compared to multiple-prey loaders, they face restricted abilities to increase the numerical prey input per unit of time. Single-prey loaders may thus show more variation in the time spent foraging, and may react sooner to a poor nutritional status of their offspring than multiple-prey loaders. On the other hand, life-history theory predicts that seabirds are fixed investors that should maximise their own survival independently of breeding requirements (Navarro and González-Solís 2007). Indeed, several studies with experimentally handicapped individuals have shown that seabirds do adjust their breeding efforts to compensate for the extra costs of the handicap, but not at the risk of incurred survival probabilities (Sæther et al. 1993; Weimerskirch et al. 1995, 1999; Navarro and González-Solís 2007; Bijleveld and Mullers 2009). None of these studies were performed on single prey-loaders, while their foraging methods are energetically more expensive as they must return to the colony each time they catch a suitable prey for their offspring, and as such they may reach a certain limit at which their future survival comes at risk more quickly.

The single-prey loading Sandwich Tern *Thalasseus sandvicensis* is restricted to foraging areas up to 15–25 km from the colony (Veen 1977; Fasola and Bogliani 1990; Stienen 2005). The parents alternate brooding and foraging duties (Veen 1977), and this synchronized behaviour results in a constant presence of one of the adults at the colony site. However, when food intake of the chicks is not sufficient, both parents may leave the colony for foraging and the brood is left unattended more often. Stienen and Brenninkmeijer (2002) suggest that this flexible foraging behaviour allows the parents to buffer against variation in feeding conditions and to counterbalance periods of food shortage for their offspring. In the Sandwich Tern colony of Griend, The Netherlands, kleptoparasitism or food robbery by Black-headed Gulls *Chroicocephalus ridibundus* seems to be the main driver of parental nest non-attendance. In some years, high proportions of the food that was brought to the tern chicks was robbed by the gulls, causing decreased energy intake by the chicks (Stienen et al. 2001; Stienen and Brenninkmeijer 2002). In such years, parents apparently tried to compensate for the loss by increasing the time spent foraging and leaving their chicks unattended at the nest more often (Stienen and Brenninkmeijer 2002). In this paper, we try to further unravel the decision rules that underlie the flexibility of time allocation to foraging in

Sandwich Terns using individually-based data (instead of averaged yearly values as was done by Stienen and Brenninkmeijer 2002) on chick body condition, chick feeding and parental nest attendance, and by comparing the Griend results with unpublished data from Zeebrugge, Belgium.

It is hypothesized that parental foraging effort increases with a decrease in the body condition of the chicks, and that parental colony attendance is likewise correlated to the body condition of their chicks. We further predict that parents use their own body mass to evaluate future fitness costs (cf. Navarro and González-Solís 2007) so that the degree of flexibility in parental foraging effort depends on adult body reserves. Although regulation of offspring provisioning is generally thought to be related to species-specific constraints imposed by central place foraging, some studies suggest different responses within the same species (Weimerskirch et al. 1999; Phillips and Croxall 2003). To test whether such intra-specific variations in parental responses are linked to different feeding conditions as suggested by Weimerskirch et al. (1999, 2001), we compared the foraging flexibility of Sandwich Terns at two major colony sites with very different feeding characteristics, both in terms of the rate of energy input into the colony and kleptoparasitism by neighbouring gulls.

Methods

Study sites

Research was conducted on Griend from 1992 to 1998 and at Zeebrugge between 2001 and 2007. Griend, an uninhabited island of about 57 ha in the Dutch Wadden Sea (53°15′N, 5°15′E), hosted 5600–8300 pairs of Sandwich Terns during the study period (Table 1). The Sandwich Tern colony at Zeebrugge held 46–4067 pairs and was situated within the port of Zeebrugge (51°21′N, 3°12′E). During the respective study periods, Griend held between 16,000 and 28,500 breeding pairs of Black-headed Gulls, whereas Zeebrugge hosted only 388–2390 pairs. On Griend, the numerical proportion of clupeids transported to the study chicks amounted to 30.8–74.7 %, while generally higher proportions (66.9–91.7 %) of clupeids were brought to the chicks at Zeebrugge (Table 1). Prey length was comparable between the two colonies and normally averaged between 9 and 11 cm. Only in 2006 and 2007, relatively small prey (average of less than 8 cm) were brought to the chicks at Zeebrugge. The number of prey brought to the colony varied between 4.8 and 17.9 prey per day, and was especially high at Zeebrugge in 2006 and 2007 when smaller prey items were brought to the chicks. Sandwich Terns breeding on Griend use the waters around the islands of Terschelling and Vlieland for foraging, and most individuals stay within 15 km distance from the colony (Stienen 2005). At Zeebrugge, smaller prey is caught within a few kilometres of the colony in the port itself or at the port entrance (own observations), while larger prey is caught at sea mainly within 25 km of the colony (Vanaverbeke et al. 2011).

Body condition of chicks

Each year, one more or less circular enclosure (diameter 3–8 m, height 50 cm) containing all study nests was constructed in/near the centre of a colony or a subcolony which

Table 1 Variation in the number of Sandwich Terns *Thalasseus sandvicensis* and Black-headed Gulls *Chroicocephalus ridibundus*, and some general feeding characteristics of the Sandwich Tern chicks in the colonies of Griend and Zeebrugge during the study period

Year	Colony	No. of Sandwich terns	No. of Black-headed Gulls	Prey delivery rate (*n* prey/day)	Prey length (cm)	Proportion of clupeids (%)
1992	Griend	6600	21,000	4.8 ± 0.24	10.1 ± 0.09	52.0
1993	Griend	7600	16,000	8.6 ± 0.19	9.4 ± 0.03	55.3
1994	Griend	8300	25,500	8.6 ± 0.19	9.1 ± 0.04	84.7
1995	Griend	8200	24,500	9.9 ± 0.29	10.6 ± 0.05	69.9
1996	Griend	5600	22,500	8.8 ± 0.20	10.2 ± 0.046	30.8
1997	Griend	5000	28,500	8.5 ± 0.21	9.2 ± 0.03	79.5
1998	Griend	6950	25,500	12.6 ± 0.29		73.4
2001	Zeebrugge	920	2390	7.1 ± 0.59	10.5 ± 0.20	90.2
2002	Zeebrugge	46	2127	8.2 ± 2.33	11.2 ± 0.69	75.6
2003	Zeebrugge	823	2272	8.3 ± 0.50	9.8 ± 0.22	71.4
2004	Zeebrugge	4067	740	7.5 ± 0.73	9.2 ± 0.27	66.9
2005	Zeebrugge	2538	600	8.10 ± 0.96	9.9 ± 0.21	91.5
2006	Zeebrugge	2062	844	15.4 ± 1.58	7.8 ± 0.20	86.0
2007	Zeebrugge	1127	388	17.9 ± 1.46	7.1 ± 0.12	91.7

Values of prey delivery rate and prey length are means ± SE

Table 2 The yearly number of chicks of which the nutritional state was monitored and observational protocols were made, and the yearly number of adults that were caught on the nest in the colonies of Griend and Zeebrugge in May and June

Year	Colony	Number of chicks	Number of adults
1992	Griend	8	27
1993	Griend	9	49
1994	Griend	18	64
1995	Griend	21	87
1996	Griend	23	123
1997	Griend	20	216
1998	Griend	20	83
2001	Zeebrugge	10	38
2002	Zeebrugge	7	0
2003	Zeebrugge	17	9
2004	Zeebrugge	21	40
2005	Zeebrugge	12	38
2006	Zeebrugge	20	41
2007	Zeebrugge	26	53

was established during peak laying. The enclosure was constructed just before hatching of the first eggs. During the pre-construction phase of the enclosures, the nests within the selected study sites were marked with numbered sticks, and eggs were marked in sequence of laying with a permanent marker and controlled every 2 or 3 days. At the first control post-hatching, the chicks were aged and individually ringed with a metal ring. For observations on chick feeding and parental behaviour, chicks were dyed with picric acid or ink for individual recognition. To prevent overcrowding and negative effects on chick growth, we regularly put some chicks that were not colour dyed out of the enclosure so that the density inside the enclosure resembled the density outside the enclosure.

Each year, the body mass (±1 g) of the enclosed chicks was measured with an electronic balance preferably every 3 days until the chicks left the enclosure (fledged), died or were preyed upon. Because measurements of body mass were often not performed on days when observations on food were made, body mass was imputed for each missing measurement assuming linear growth between two successive measurements. For each observation day and for each chick (Table 2), body condition index (BCI) was computed using the relative deviation from the average body mass of all chicks (at both study sites and during all study years) that were of similar age and that ultimately fledged (i.e. max. age ≥25 days).

Body condition of adults

Since body mass of parents of individually followed chicks was largely lacking, we used averaged yearly values of adult body mass (BMA^{avg}) as a proxy for yearly body condition. Each year, 9–216 adults (mean = 66.6 ± 53.7 SD) were randomly caught at the nest during May and June of which the body mass (±1 g) was measured with an electronic balance (Table 2). In 2002, when the Zeebrugge colony was reduced to just 46 pairs, no attempts were made to catch adults. All adults were caught a few days before expected hatching during the pipping process of the egg(s). In this way, we accounted for possible confounding effects of decreasing body mass during incubation (Wendeln and Becker 1996).

Chick feeding and parental attendance

Food transport to the chicks was followed from a hide placed at a few metres from the enclosure. Observational protocols lasted 60–1084 min per day (mean = 642.1 min ± 336.4 SD); protocols of less than 1 h were omitted from the analyses. We recorded prey species (two types, namely Clupeidae *Clupea harengus*/*Sprattus sprattus* and Ammodytidae *Ammodytes* spp./*Hyperoplus lanceolatus*), prey length and the fate of the prey (consumed or not consumed by the chick). Prey species, other than Clupeidae and Ammodytidae, were omitted from the analyses since they amounted to less than 1.1 % of all food items supplied to the chicks (Stienen et al. 2000). Prey size was estimated in quarters of the parent's bill size (bill length = 5.43 ± 0.25 cm; Stienen et al. 2000), and estimating prey size was calibrated among the observers. The first author (E.S.) participated in observations at both study sites during all years while A.B. and W.C., respectively, participated in observations on Griend and at Zeebrugge. Other more occasional observers (seven on Griend and three at Zeebrugge) are mentioned in the Acknowledgements.

The fate of the food items brought to the colony was categorized as consumed or not consumed by the chick. A very small proportion of the prey items brought to Sandwich Tern chicks (<2 % of all prey brought to the chicks on Griend) was dropped on the ground or was eaten by the parent itself, but the main reasons for not consuming a prey were robbery of food items by Black-headed Gulls or sometimes other kleptoparasites, losing prey out of the observer's sight when the prey-carrying parent was chased by a kleptoparasite or eating of prey by the parent when it was attacked by a kleptoparasite (Stienen et al. 2000). The proportion of prey items that was consumed by the chick can thus be used as an estimate of the kleptoparasitic pressure. To calculate the daily amount of energy transported to the chicks (DET), the daily amount of energy actually consumed by the chick (DEI) and the proportion of energy that was consumed by the chick (CP), prey were transformed into energy values according to the allometric relationships given by Stienen and Brenninkmeijer (2002).

During the protocols, the presence of one or more parents near the nest was monitored continuously. If one or more parents were present in the (sub)colony under study, there was regular interaction with the chick or among partners so that parents could be easily linked to an individual chick. When no parent was present near the nest, most often the chick was hiding in the vegetation or crouched motionless on the ground. In this paper, we distinguish between the presence (one or two parents present near the nest) and absence (no parent present near the nest) of parents, in the latter case assuming that both parents went out foraging. Daily energy supply per parent ($\mathrm{DET}^{\mathrm{par}}$) was computed as follows:

$$\mathrm{DET}^{\mathrm{par}} = (\mathrm{DET})/(2 \times \mathrm{PU} + P) \times 100$$

where PU = proportion of the time the chick was left alone at the colony site and P = the proportion of the time the chick was attended by one parent.

Statistical analysis

Data on chick body condition as well as observational data on parental nest attendance and food were restricted to nests with only one chick. Chicks younger than 15 days were excluded from all statistical analysis as they are usually attended by at least one parent (cf. Stienen and Brenninkmeijer 2002). Since most second-hatched chicks die within 2 weeks post-hatching (Stienen and Brenninkmeijer 2006), a restriction to singletons only led to a relatively small reduction of the entire dataset (in this study, 2.3 % of the data were not used).

The data on singletons ≥15 days old (Table 2) consisted of 1418 measurements of 232 individual chicks of chick body condition (BCI) and parental nest non-attendance (PU). For analyses of daily energy transport (DET), daily energy consumption (DEI) and the proportion consumed (CP = DEI/DET × 100 %), the year 1998 was omitted because in that year we had no reliable estimates of prey length, leaving 1246 measurements of 211 individual chicks for analysis of DET, DEI and CP.

The effects of chick age (AGE), BCI, colony site (KOL entered as a factor variable) and a random effect of INDIVIDU (to control for repeated samples of individuals) on the proportion of time the chick was left unattended at the nest (logit transformed PU), daily energy transport to the chick (DET), daily energy consumption of the chicks (DEI) and the proportion of the energy actually consumed by the chick (CP) were analysed using a generalised linear mixed model (GLMM) in S-PLUS v.6.2.

To examine the combined effects of the nutritional state of the chicks and the adult body condition on the proportion of parental non-attendance, for each year the average body mass of adults caught on the nest in May and June ($\mathrm{BMA}^{\mathrm{avg}}$), the averaged condition of chicks ($\mathrm{BCI}^{\mathrm{avg}}$) and the averaged parental nest non-attendance ($\mathrm{logitPU}^{\mathrm{avg}}$) were entered into a linear regression model. To control for

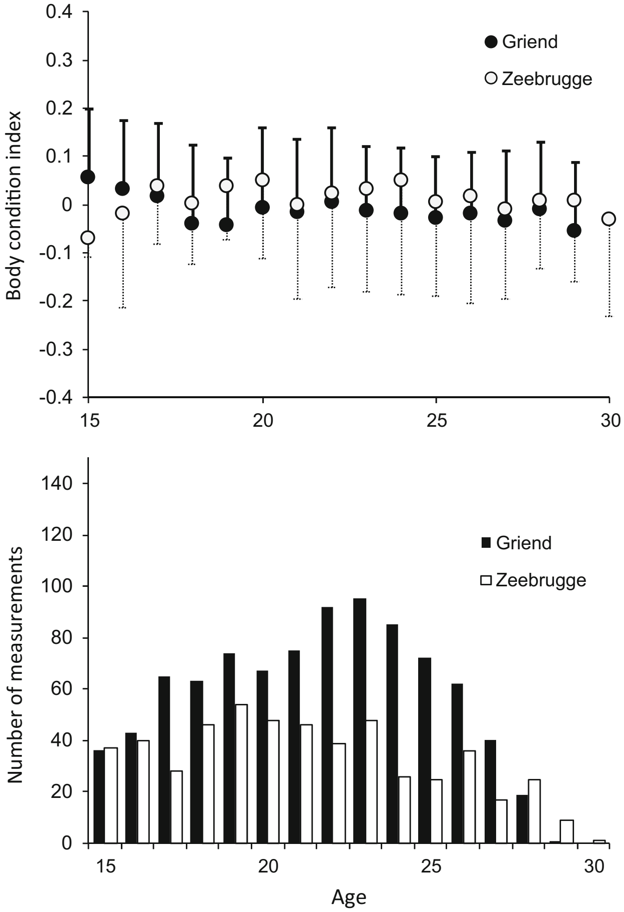


Fig. 1 Body condition index BCI (average ± SD, respectively for Griend and Zeebrugge) of Sandwich Tern *Thalasseus sandvicensis* chicks at Zeebrugge and on Griend in relation to the age (in days) of the chicks (*above*). *Below* the number of measurements

Table 3 GLMM coefficient estimates for the effect of chick age (AGE), chick body condition index (BCI) and colony site (KOL: Griend vs. Zeebrugge) on parental nest non-attendance (logitPU; $n = 1418$ observation days)

Variable	Parameter estimate ± SE	t value	P
Intercept	−6.57 ± 0.31	−21.0	<0.0001
AGE	0.24 ± 0.01	17.7	<0.0001
BCI	−7.24 ± 2.60	−2.8	0.005
KOL	1.28 ± 0.47	2.7	0.007
AGE × BCI	−0.04 ± 0.12	−0.3	0.74
AGE × KOL	−0.16 ± 0.02	−7.6	<0.0001
BCI × KOL	8.60 ± 3.93	2.2	0.03
AGE × BCI × KOL	−0.17 ± 0.20	−0.9	0.39

Individual identity was used as a random grouping factor ($n = 232$ individuals)

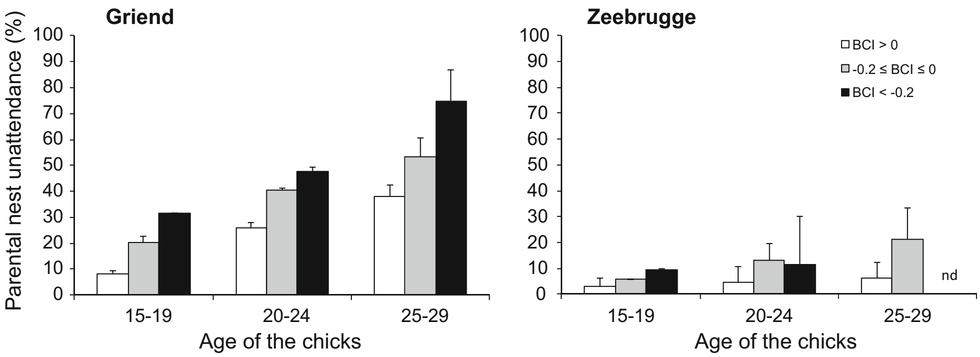


Fig. 2 The effects of chick age (in days) and chick body condition index (BCI) on parental nest non-attendance in the colonies of Griend and Zeebrugge. Values represent averages + SE. *Nd* no data

repeated measurements of BCI and logitPU on individual chicks, these parameters were first averaged per individual chick after which these values were averaged per year.

Results

Nutritional state of the chicks

Individual measurement of body condition index (1246 measurements) of the studied Sandwich Tern chicks ranged from −0.70 to 0.35. Average body condition of chicks was slightly higher at Zeebrugge (Fig. 1), but the difference was not significant (BCI = −0.02 ± 0.11 SD and 0.00 ± 0.12 SD, respectively, on Griend and at Zeebrugge; $n = 231$ chicks, Student's t test, $t = 1.48$, $P = 0.17$). Also, averaged yearly body condition of the chicks (BCI^{avg}) did not differ between the two colonies (−0.03 ± 0.05 and −0.01 ± 0.09 SD, respectively, on Griend and at Zeebrugge; $n = 14$, Student's t test, $t = 0.5$, $P = 0.60$).

Parental colony attendance

Parental non-attendance (logitPU) at the colony significantly increased with chick age (AGE), and was negatively correlated with body condition index (BCI) of the chick (Table 3; Fig. 2). Furthermore, we found significant effects of the colony site (KOL) and the interaction term AGE × KOL. On Griend, the probability of being left alone at the colony strongly increased with chick age and with decreasing BCI, whereas at Zeebrugge the effect of age was much smaller (Fig. 2).

Averaged yearly parental non-attendance ($logitPU^{avg}$) was significantly higher on Griend than at Zeebrugge (corresponding PU, respectively, 29.8 % ± 24.5 and 8.4 % ± 10.7 SD; $n = 14$, Student's t test, $t = 2.9$, $P = 0.01$).

Effects of parental condition

Body mass of individual adult Sandwich Terns (BMA) varied between 195 and 312 g. Averaged yearly BMA

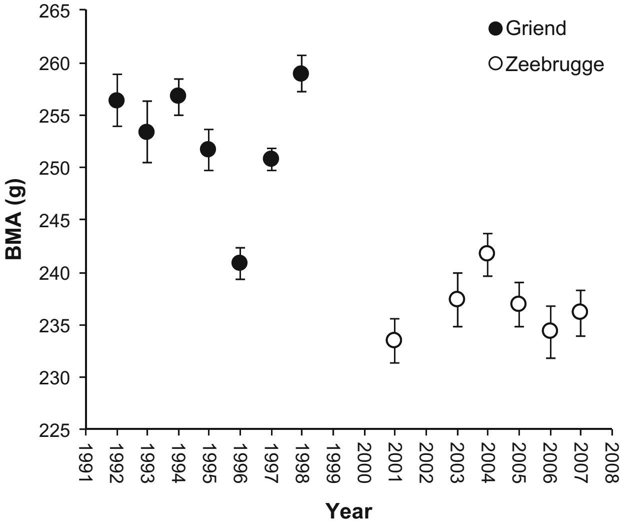


Fig. 3 Average body mass of adult Sandwich Terns (BMA ± SE) on Griend (1992–1998) and at Zeebrugge (2001, 2003–2007)

Table 4 Linear regression analysis testing the combined effect of the averaged yearly adults' body mass (BMA^{avg}) and the averaged yearly body condition index of the chicks (BCI^{avg}) on averaged yearly parental nest non-attendance ($logitPU^{avg}$)

Variable	Parameter estimate ± SE	t value	P
Griend			
Intercept	22.67 ± 11.93	1.9	0.13
BMA^{avg}	−0.10 ± 0.05	−2.1	0.11
BCI^{avg}	−22.78 ± 6.25	−3.6	**0.02**
Zeebrugge			
Intercept	−41.24 ± 32.94	−1.3	0.29
BMA^{avg}	0.15 ± 0.13	1.2	0.31
BCI^{avg}	−7.66 ± 8.85	−0.9	0.45
Both colonies			
Intercept	−24.64 ± 9.54	−2.6	**0.02**
BMA^{avg}	0.07 ± 0.04	2.3	**0.04**
BCI^{avg}	−8.50 ± 5.38	−1.6	0.15

The upper two sections of the table show the results separately for both colonies, and the bottom section shows the results for a single analysis using data from both colonies

Significant values are shown in bold

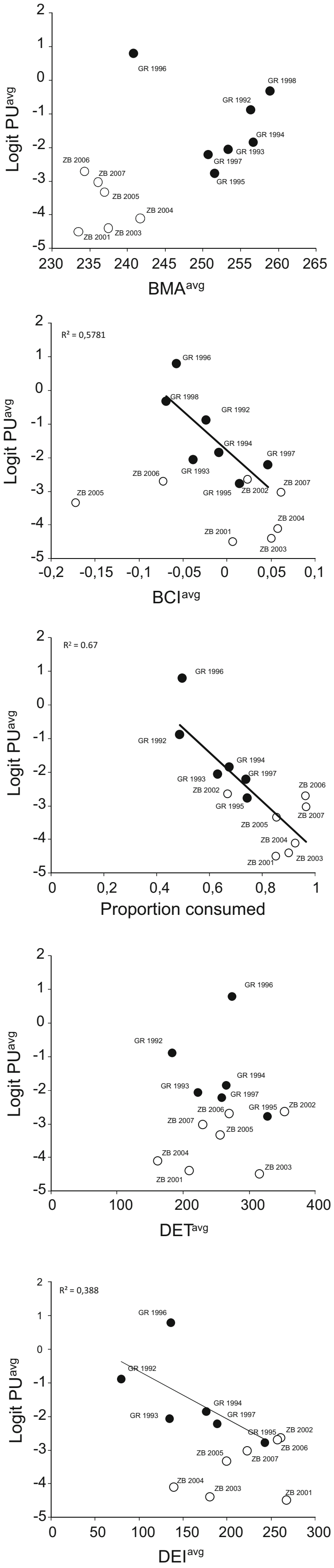


Fig. 4 Relationship between averaged yearly parental nest non-▶ attendance (logitPU^{avg}) and averaged yearly body mass of adults (BMA^{avg}), body condition index of the chicks (BCI^{avg}), food consumption probability, daily energy transport (DET^{avg}) and daily energy intake (DEI^{avg}) at Zeebrugge (ZB; *circles*) and on Griend (GR; *dots*). Significant correlations are shown by *lines*. Note that if the year 1996 is omitted all relationships become stronger and even the relationship between BMA^{avg} and logitPU^{avg} becomes highly significant

(BMA^{avg}) was consistently higher in the Griend colony (Fig. 3) where adults weighed on average 14.5 g more than at Zeebrugge ($n = 868$, Student's t test, $t = 11.4$, $P < 0.001$). There was no relationship between the averaged yearly BMA^{avg} and the averaged yearly body condition of chicks (BCI^{avg}; Pearson regression, $R^2 = 0.005$, $P = 0.81$).

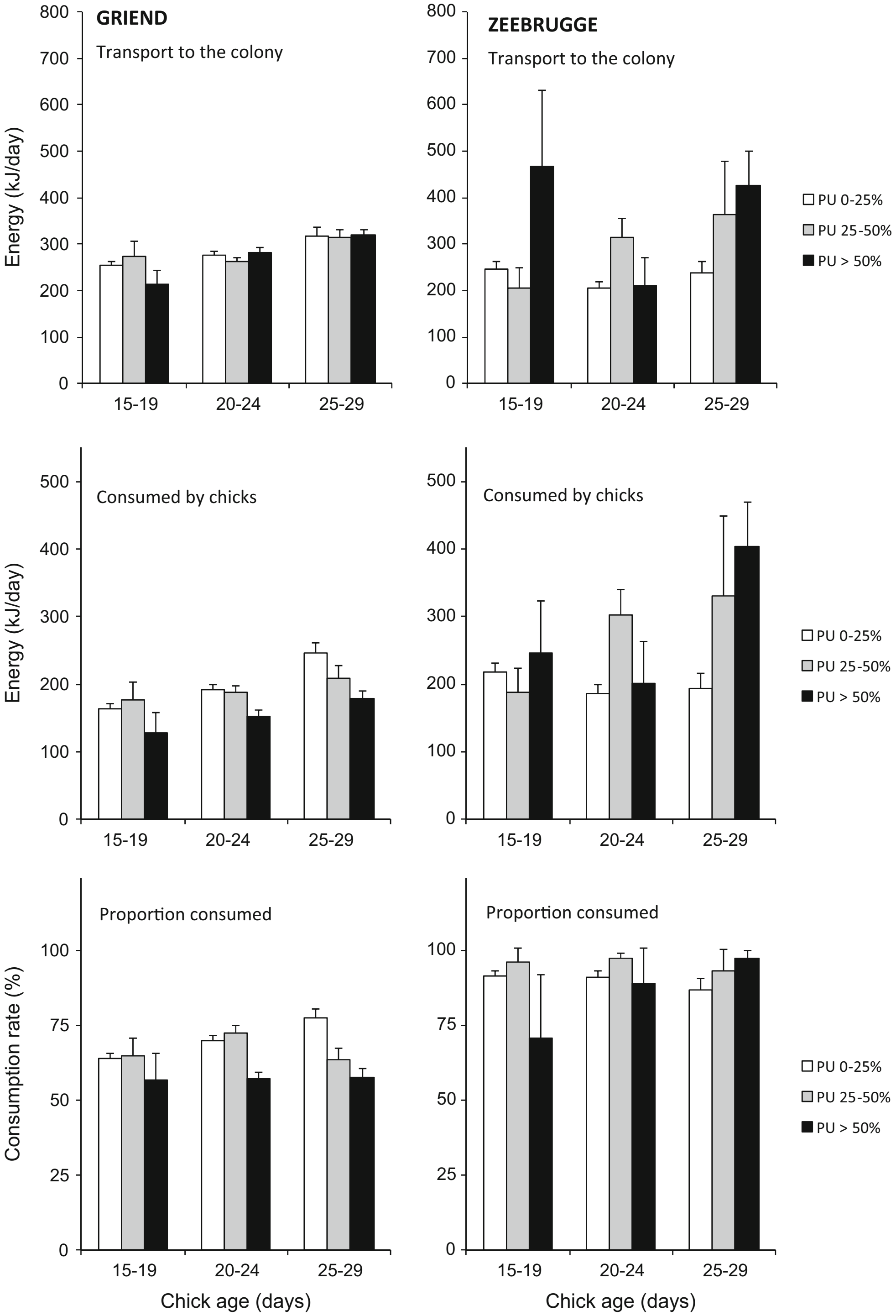
On Griend logitPU^{avg} correlated with BCI^{avg} but not with BMA^{avg}, whereas at Zeebrugge neither BCI^{avg} or BMA^{avg} significantly contributed to explain the variation in logitPU^{avg} (Table 4; Fig. 4). When data of both colonies were entered into a single regression analyses, logitPU^{avg} significantly correlated with BMA^{avg}, but no longer with BCI^{avg} (Table 4). Further adding the factor variable colony (KOL) resulted in a significant effect of KOL ($P = 0.01$), while BMA^{avg} and BCI^{avg} were no longer significant ($P = 0.27$ and 0.10, respectively).

Energy transport to the colony and energy consumption by the chicks

Daily energy transport to the chick (DET) was significantly higher on Griend than at Zeebrugge (respectively 269.5 ± 98.9 and 239.4 ± 101.7 kJ/day, $t = 2.47$, $n = 211$ chicks, $P = 0.01$), but because prey loss was much higher on Griend (compare CP in Fig. 5) daily energy intake (DEI) was significantly lower than at Zeebrugge (173.2 ± 62.5 and 211.3 ± 89.9 kJ/day, $t = 3.52$, $n = 211$ chicks, $P < 0.001$). Because of the lower colony attendance on Griend, the daily energy transport that was realised per parent (DET^{par}) did not differ between the two colonies under study (respectively 217.7 ± 69.6 and 230.6 ± 98.0 kJ/day for Griend and Zeebrugge, $t = 1.1$, $df = 209$, $P = 0.28$).

On Griend but not at Zeebrugge, DET increased with chick age (Table 5; Fig. 5). In none of the colonies did increased parental non-attendance result in a significant increase of the energy transport to the chick. On Griend, consumption probability (CP) of the prey significantly correlated with logitPU and with the interaction term logitPU × AGE, with the latter reflecting an increasingly negative effect of parental non-attendance on CP with increasing age of the chick (Fig. 5).

Fig. 5 Daily energy transport to the chick, daily energy intake by the chick and the proportion of energy consumed by the chick in relation to chick age and parental nest non-attendance (PU) in the colonies of Griend (*left*) and Zeebrugge (*right*). Values represent averages + SE



The positive effect of chick age on DET and CP (although not always significant) resulted in a significant effect of AGE on the daily energy intake (DEI) in both colonies (Table 5; Fig. 5). At Zeebrugge, the interaction term AGE × logitPU also had a significant effect on DEI, showing an increasingly positive effect of parental nest non-attendance on the energy intake with aging of the chick (Fig. 5).

The averaged yearly proportion of energy that was actually consumed by the chick (CP^{avg}) strongly correlated with parental non-attendance ($logitPU^{avg}$), whereas DET^{avg} was not related to $logitPU^{avg}$ (Fig. 4). Only for Griend was

Table 5 GLMM coefficient estimates for the effect of chick age (AGE) and parental nest non-attendance (logitPU) on the daily energy transport (DET), energy intake (DEI) and consumption probability (CP) of chicks on Griend (left panels) and at Zeebrugge (right panels)

Variable	Griend (721 obs, 98 chicks)			Zeebrugge (525 obs, 113 chicks)		
	Estimate ± SE	*t* value	*P*	Estimate ± SE	*t* value	*P*
Daily energy transport (DET)						
Intercept	104.76 ± 40.00	2.6	**0.01**	156.37 ± 125.16	1.2	0.21
AGE	7.92 ± 1.70	4.7	**<0.0001**	7.73 ± 5.42	1.4	0.15
logitPU	−12.18 ± 11.98	1.0	0.31	−22.27 ± 30.69	0.7	0.47
AGE × logitPU	0.60 ± 0.54	1.1	0.27	2.10 ± 1.35	1.6	0.11
Daily energy intake (DEI)						
Intercept	60.00 ± 34.03	1.7	0.07	61.24 ± 113.66	0.5	0.59
AGE	5.46 ± 1.45	3.8	**0.0002**	10.15 ± 4.91	2.1	**0.03**
logitPU	14.46 ± 10.17	1.4	0.15	−41.98 ± 27.87	1.5	0.13
AGE × logitPU	−0.81 ± 0.46	1.8	0.08	2.86 ± 1.23	2.3	**0.02**
Variable	Griend (719 obs, 98 chicks)			Zeebrugge (448 obs, 111 chicks)		
	Estimate ± SE	*t* value	*P*	Estimate ± SE	*t* value	*P*
Consumption probability (CP)						
Intercept	60.78 ± 8.50	7.2	**<0.0001**	80.85 ± 15.12	5.3	**<0.0001**
AGE	0.19 ± 0.36	0.5	0.60	0.47 ± 0.65	0.7	0.47
logitPU	7.86 ± 2.56	3.1	**0.002**	−5.50 ± 3.78	1.5	0.15
AGE × logitPU	−0.43 ± 0.12	3.7	**0.0003**	0.27 ± 0.17	1.6	0.11

Significant values are shown in bold

DEI^{avg} significantly, but negatively, correlated with $\mathrm{logitPU}^{avg}$.

Discussion

Importance of chick body condition

The main finding of this study is that, in Sandwich Terns, the proportion of time that chicks were left unattended at the nest negatively correlated with chick body condition. Assuming that time spent outside the colony is used for foraging, this suggests that Sandwich Terns do adjust parental foraging effort to the nutritional status of their chicks. This was expected, as seabirds, and especially short-ranging seabirds (Hamer and Hill 1994; Weimerskirch et al. 1995), must be flexible and adjust foraging effort in response to variable conditions that affect the growth and survival of their offspring in order to be successful (Cairns 1987). Such plasticity in parental investment has already been found in many other short-ranging seabirds (Monaghan et al. 1994; Bolton 1995; Hamer et al. 1998; Tveraa et al. 1998; Wernham and Bryant 1998; Granadeiro et al. 2000; Harding et al. 2002; Ronconi and Burger 2008; Burke and Montevecchi 2009). Only a few studies on short-ranging seabirds have not found a relationship between parental foraging effort and the body condition of their chicks (Ricklefs and Schew 1994; Takahashi et al. 1999).

However, the relationship between body condition and parental non-attendance strongly differed between the two study sites, with Sandwich Tern parents from Griend apparently reacting much more pronounced to a backlog in the development of their chicks than parents at Zeebrugge. Consequently, averaged yearly parental non-attendance on Griend was significantly higher than at Zeebrugge, while the average body condition of the chicks did not differ between the two colonies. On Griend, but not at Zeebrugge, averaged yearly parental non-attendance strongly correlated with the average body condition of the chicks. Our results thus suggest that, within the same species, parents may respond differently to changes in the body condition of their offspring. Studies on other seabirds found that the differences in the degree of parental investment may depend on the build-up of energy reserves of the parents themselves as well as on the body condition of their chicks (e.g. Erikstad et al. 1998; Navarro and González-Solís 2007). When having sufficient body mass reserves and with their own future survival not at risk, seabirds can increase foraging effort in an attempt to counterbalance a backlog in the body condition of their offspring. Weimerskirch et al. (1999, 2001) therefore suggested that parental foraging flexibility in seabirds critically depends on local conditions influencing food abundance, which could explain why some studies found different responses within the same species (Phillips and Croxall 2003; this study). In the closely related Common Tern *Sterna hirundo*, Wendeln (1997a, b) found that intra-specific differences in adult body mass as well as in colony attendance were strongly related to different foraging strategies. Prior to egg-laying, birds using marine feeding areas were heavier and started laying earlier than limnetic foraging adults (Wendeln 1997b). During incubation, body mass of females that specialised on marine prey strongly decreased (Wendeln 1997a), so that during chick feeding adults at marine sites were lighter, and colony attendance was lower than at freshwater sites (Becker et al. 1997). Also, in this study, we found a pronounced and consistent difference in adult body condition between the two breeding sites with incubating parents on Griend weighing on average 14.5 g more than at Zeebrugge, suggesting strong site-specific differences in food availability. It is, however, not clear whether and how this relates to the strong differences in colony attendance of the parents. If we used data of both colonies, and included chick body condition and adult body mass in a linear regression analysis, parental nest non-attendance did correlate with adult body mass. However, the relationship did not hold when the analyses were performed separately for the two colonies under study. On Griend, there was one year (1996) in which adult body mass was exceptionally low while parental non-attendance was the highest recorded in this study, suggesting that factors other than adult body mass played an even more important role in determining foraging effort.

Additional costs of food robbery

In most years, Sandwich Terns on Griend brought proportionally more sandeels and longer prey items to their chicks than at Zeebrugge (Table 1). Although longer prey are more susceptible to robbing, the difference in prey length cannot explain the large difference in the proportion of energy that was actually consumed by the chicks. Given the average prey lengths as presented in Table 1, and using the relationship between prey length and consumption probability as found by Stienen et al. (2001), average consumption probability would amount to 0.70 ± 0.03 on Griend (close to the values shown in Fig. 5) and 0.72 ± 0.07 at Zeebrugge (much lower than in Fig. 5). We instead believe that the higher consumption probability at Zeebrugge was due to the fact that this colony held much lower numbers of Black-headed Gulls (Table 1). During incubation and the onset of chick-rearing, the gulls protect the terns against predators (Veen 1977), but, with the aging of the tern chicks, a number of gulls develop into specialised parasites of fish meant for the tern chicks (Stienen et al. 2001). The lower gull density and the fact that the tern colony at Zeebrugge was never located within the gull colony as was always the case on Griend, but instead at the edge, make it less likely that neighbouring gulls would develop into specialised pirates. On Griend, on average more than three Black-headed Gulls tried to rob a fish from an arriving Sandwich Tern parent (Stienen and Brenninkmeijer 1999), while at Zeebrugge normally none or only one pirate was active (own observations). Despite the fact that daily energy transport to the chicks on Griend was higher, the low energy consumption probability even resulted in a lower energy intake rate than at Zeebrugge.

The strong relationship between parental nest non-attendance and energy consumption probability suggests that Sandwich Tern parents react to high rates of food loss to kleptoparasites by increasing the time spent foraging and by leaving the chick unattended at the colony more often. When a prey is successfully delivered to the chick, brooding and foraging duties are normally changed between the partners (own observations). When the prey was stolen, however, the parent that was initially carrying the prey normally returned to the foraging area, and when its subsequent return took too long, the attending parent often left the colony to forage (own observations). The low nest attendance on Griend might thus merely be a response to high rates of food loss which in turn causes a decrease in chick body condition.

Effects of adult body condition

Since we found a significant relationship between adult body mass and energy consumption probability, it cannot be excluded that the relationship between parental nest non-attendance and energy consumption probability reflects a difference in the degree of parental foraging investment due to variation in the build-up of energy reserves of the parents. Here, one must bear in mind that the correlation between parental nest attendance and adult body mass was much weaker than the correlation with consumption probability (Fig. 4), mainly because the data from Griend in 1996 (relatively low adult body mass and high parental nest non-attendance) did not fit very well. Nevertheless, one can think of several plausible explanations for a direct effect of adult body mass on parental nest non-attendance and a possible link with food consumption probability. Firstly, this can be expected when parents have already incorporated the expected additional costs for rearing young (i.e. expected increase in foraging effort due to food loss to kleptoparasites) before hatching of the eggs by investing in extra body mass (Sénéchal et al. 2011), and by assuming that parents on Griend in 1996 did not correctly predict the robbing pressure. The rate of kleptoparasitism experienced during courtship feeding or the number of Black-headed Gulls present in the colony might, for example, be used as a proxy for the robbing pressure expected during chick rearing. Also, differences in the age composition or experience of the adults may explain the difference in provisioning rates and parental plasticity between Griend and Zeebrugge as was found in Common Terns *Sterna hirundo* (Limmer and Becker 2009).

Another explanation would be that parents use their own body mass to evaluate future fitness costs and adjust parental foraging effort accordingly (cf. Navarro and González-Solís 2007). If at the same time high non-attendance at the colony evokes high rates of food parasitism, a high parental body condition would eventually result in low food consumption probabilities of their offspring. The latter is plausible, since prey delivery seems easier when one of the parents attends the chick (own observations). When a prey-carrying parent arrives at the colony, the attending parent normally repositions the chick to an open spot where the prey-carrying parent can land easily. After landing, the chick is normally positioned inbetween the two parents who form a protective shield around the chick with their open wings. When no parent is attending the chick, not only will this protective behaviour be absent but in addition neighbouring adults often do not allow an unattended chick to wait for the arriving parent at an open spot, making successful delivery of the prey less easy.

We therefore conclude that our study strongly suggests that parental nest non-attendance in Sandwich Terns is basically a response to compensate for the food loss to kleptoparasitic gulls in order to meet the energy requirements for the growth of the chicks, but that an additional role of adult body condition cannot be excluded.

Acknowledgments We like to thank all the people involved in collecting biometrical data and doing observations on Griend and at Zeebrugge. Especially, Hans Schekkerman, Hilbran Verstraete, John Habraken, John Schobben, Karin Geschiere, Nicolas Vanermen, Peter van Beers, Piet van Tienen, René Oosterhuis and Marc Van de walle spend many hours of observations in a hide near the colony. We thank Cees de Boer, Dirk de Boer, Dirk van Hollik, Dirk Kuiper, Jan van Dijk and Peter van Tellingen for their logistic support. The Agency of Nature and Forest (ANB) undertook regular maintenance of the colony site at Zeebrugge. The Port Authority Zeebrugge (MBZ) kindly gave permission to access the breeding sites. The Flanders Marine Institute (VLIZ) provided storage facilities for the field equipment. Ivy Jansen (INBO) gave statistical advice. Financial support for this study was provided by the Department of Maritime Access of the Flemish Government (AMT: 16EP/HS/4/2005 and related contracts) and the Belgian Science Policy Office (projects TROPHOS EV-BNZ-03 and Westbanks SD/BN/01A).

References

Bijleveld A, Mullers RC (2009) Reproductive effort in biparental care: an experimental study in long-lived Cape Gannets. Behav Ecol 20:736–744

Becker PH, Frank D, Wagener M (1997) Luxury in freshwater and stress at sea? The foraging of the Common Tern *Sterna hirundo*. Ibis 139:264–269

Bolton M (1995) Experimental evidence for regulation of food delivery to Storm Petrel, *Hydrobates pelagicus*, nestlings: the role of chick body condition. Anim Behav 50:231–236

Burke CM, Montevecchi WA (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. J Zool 278:354–361

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–272

Dänhardt A, Fresemann F, Becker PH (2011) To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea. J Ornithol 152:347–357

Erikstad KE, Fauchald P, Tveraa T, Steen H (1998) On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79:1781–1788

Fasola M, Bogliani G (1990) Foraging ranges of an assemblage of Mediterranean seabirds. Colon Waterbirds 13:72–74

Granadeiro JP, Bolton M, Silvam MC, Nu-Nesa M, Furness RW (2000) Responses of breeding Cory's Shearwater *Calonectris diomedea* to experimental manipulation of chick condition. Behav Ecol 11:274–281

Hamer KC, Hill JK (1994) The regulation of food delivery to nestling Cory's Shearwaters *Calonectris diomedea*: the roles of parents and offspring. J Avian Biol 12:198–204

Hamer KC, Lynnes AS, Hill JK (1998) Regulation for chick provisioning rate in Manx Shearwaters: experimental evidence and implications for nestling obesity. Funct Ecol 12:625–630

Harding AMA, van Pelt TI, Piatt JF, Kitaysky AS (2002) Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the Horned Puffin *Fratercula corniculata*. Condor 104:842–847

Harding AMA, Piatt JF, Schmutz JA, Shultz MT, van Pelt TI, Kettle AB, Speckman AB (2007) Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). Ecology 88:2024–2033

Jodice PGR, Roby DD, Suryan RM, Irons DB, Turco KR, Brown ED, Thedinga KR, Visser GH (2006) Increased energy expenditure by a seabird in response to higher food abundance. Mar Ecol Prog Ser 306:283–293

Limmer B, Becker PH (2009) Improvement of chick provisioning with parental experience in a seabird. Anim Behav 77:1095–1101

Monaghan P, Walton P, Wanless S, Uttley JD, Burns MD (1994) Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. Ibis 136:214–222

Navarro J, González-Solís J (2007) Experimental increase of flying costs in a pelagic seabird: effects on foraging strategies, nutritional state and chick condition. Behav Ecol 151:150–160

Phillips RA, Croxall JP (2003) Control of provisioning in Grey-headed Albatrosses (*Thalassarche chrysostoma*): do adults respond to chick condition? Can J Zool 81:111–116

Ricklefs RE, Schew WA (1994) Foraging stochasticity and lipid accumulation by nestling petrels. Funct Ecol 8:159–170

Ronconi RA, Burger AE (2008) Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. Mar Ecol Prog Ser 366:245–258

Sæther BE, Andersen R, Pedersen HC (1993) Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic Petrel *Thalassoica antarctica*. Behav Ecol Sociobiol 33:147–150

Sénéchal E, Bêty J, Gilchrist G (2011) Interactions between lay date, clutch size, and postlaying energetic needs in a capital breeder. Behav Ecol 22:162–168

Stienen EWM (2005) Living with gulls: trading off food and predation in the Sandwich Tern *Sterna sandvicensis*. Alterra Scientific Contributions 15. PhD thesis, Rijksuniversiteit Groningen, Groningen

Stienen EWM, Brenninkmeijer A (1999) Keep the chicks moving: how Sandwich Terns can minimize kleptoparasitism by Black-headed Gulls. Anim Behav 57:1135–1144

Stienen EWM, Brenninkmeijer A (2002) Foraging decisions of Sandwich Terns in the presence of kleptoparasitising gulls. Auk 119:473–486

Stienen EWM, Brenninkmeijer A (2006) Effect of brood size and hatching sequence on prefledging mortality of Sandwich Terns: why lay two eggs? J Ornithol 147:520–530

Stienen EWM, Brenninkmeijer A, Geschiere CE (2001) Living with gulls: the consequences for Sandwich Terns of breeding in association with Black-headed Gulls. Waterbirds 24:68–82

Stienen EWM, van Beers PWM, Brenninkmeijer A, Habraken JMPM, Raaijmakers MHJE, van Tienen PGM (2000) Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*. Ardea 88:33–49

Takahashi A, Kuroki M, Niizuma Y, Watanuki Y (1999) Parental food provisioning is unrelated to manipulated offspring food demand in a nocturnal single-provisioning alcid, the Rhinoceros Auklet. J Avian Biol 30:486–490

Tveraa T, Sæther BE, Aanes R, Erikstad KE (1998) Regulation of food provisioning in the Antarctic Petrel: the importance of parental body condition and chick body mass. J Anim Ecol 67:699–704

Vanaverbeke J, Braarup AB, Braeckman U, Courtens W, Cuveliers E, Deneudt K, Goffin A, Hellemans B, Huyse T, Lacroix G, Larmuseau M, Mees J, Provoost P, Rabaut M, Remerie T, Savina M, Soetaert K, Stienen EWM, Verstraete H, Volckaert F, Vincx M (2011) Understanding benthic, pelagic and airborne ecosystem interactions in shallow coastal seas. “Westbanks”: final report. Belgian Science Policy Office, Brussels

Veen J (1977) Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). Behav Suppl 20:1–193

Waugh SM, Weimerskirch H (2003) Environmental heterogeneity and the evolution of foraging behaviour in long ranging greater albatrosses. Oikos 103:374–384

Wendeln H, Becker PH (1996) Body mass change in breeding Common Terns *Sterna hirundo*. Bird Study 43:85–95

Wendeln H (1997a) Allocation of parental duties and foraging behavior influence body condition of adult Common Terns, *Sterna hirundo*. Bird Behav 12:47–54

Wendeln H (1997b) Body mass of female Common Terns (*Sterna hirundo*) during courtship: relationships to male quality, egg mass, diet, laying date and age. Colon Waterbirds 20:235–243

Wernham CV, Bryant DM (1998) An experimental study of reduced parental effort and future reproductive success in the Puffin, *Fratercula arctica*. J Anim Ecol 67:25–40

Weimerskirch H, Chastel O, Ackermann L (1995) Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the Thin-billed Prion *Pachyptila belcheri*. Behav Ecol Sociobiol 36:11–16

Weimerskirch H, Fradet G, Cherel Y (1999) Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic Prion. J Avian Biol 30:165–174

Weimerskirch H, Mougey T, Hindermeijer X (1997) Foraging and provisioning strategies of Black-browed Albatrosses in relation to the requirements of the chicks: natural variation and experimental study. Behav Ecol 8:635–643

Weimerskirch H, Zimmermann L, Prince PA (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the Yellow-nosed Albatross. Behav Ecol 12:22–30