

Intraspecific kleptoparasitism improves chick growth and reproductive output in Common Terns *Sterna hirundo*

GERMÁN O. GARCÍA,^{1*} PETER H. BECKER² & MARCO FAVERO¹

¹*Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET - Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ, Mar del Plata, Argentina*

²*Institute of Avian Research 'Vogelwarte Helgoland', An der Vogelwarte 21, D-26386, Wilhelmshaven, Germany*

Kleptoparasitism is a well-known foraging strategy used opportunistically by many seabirds. Here, we investigated the effect of intraspecific kleptoparasitism on chick growth and reproductive output in Common Terns *Sterna hirundo*. Effects were compared between two groups comprising (1) individuals using kleptoparasitism during the chick-rearing period (kleptoparasitic group, $n = 18$), and (2) individuals in pairs that never performed kleptoparasitism throughout the season ('honest' group, $n = 21$). The null models best described variation in mass at day 3 and the pre-fledging mass, indicating no significant effect of the explanatory variables. However, the best models describing the linear growth rate (days 3–13) and peak mass included the parents' foraging strategy (kleptoparasitic vs. honest parents) as an explanatory variable. These two growth parameters were higher in chicks of kleptoparasitic parents. Kleptoparasitic foraging strategy was also associated with higher pre-fledging survival, as the reproductive performance (i.e. number of fledglings) was significantly higher in the kleptoparasitic than in the honest group. We suggest that by stealing food (and consequently feeding offspring more frequently with high-quality prey), kleptoparasitic parents are able to produce higher quality chicks with enhanced survival.

Keywords: chick-rearing period, foraging strategy, parental performance, trophic parasitism, seabirds.

Kleptoparasitism, the stealing of food by one animal from another, is common in nature (Giraldeau & Caraco 2000) and occurs across a great variety of taxa, such as marine invertebrates (Iyengar 2004), insects and spiders (Vollrath 1984, Reader 2003), fish (Grimm & Klinge 1996, Hamilton & Dill 2003), reptiles (Cooper & Pérez-Mellado 2003), birds (Brockmann & Barnard 1979, Morand-Ferron *et al.* 2007) and mammals (Kruuk 1972, Brown *et al.* 2004), among others (see Iyengar 2008). Although kleptoparasitism can be either inter- or intraspecific, most studies have focused on interspecific kleptoparasitism (e.g. Brockmann & Barnard 1979, Morand-Ferron *et al.* 2007, Iyengar 2008). Observations of kleptoparasitism in

birds are particularly detailed and its occurrence is known to vary between taxa (e.g. Brockmann & Barnard 1979, Morand-Ferron *et al.* 2007).

Kleptoparasitism is common in seabirds (Furness 1987). Skuas (Stercorariidae) and frigatebirds (Fregatidae) can be specialized kleptoparasites and rely on this behaviour for most or all of their energy acquisition, at least during parts of the annual cycle (Brockmann & Barnard 1979, Furness 1987, Hockey & Steele 1990). In contrast, gulls and terns (Laridae) may perform kleptoparasitism opportunistically, using a range of foraging tactics, with kleptoparasitism being context-dependent and often performed during periods of low availability of primary food sources (Brockmann & Barnard 1979, Furness 1987, Triplet *et al.* 1999). Yet even in opportunistic kleptoparasites, some individuals may be more specialized as kleptoparasites

*Corresponding author.

Email: garciagerman@argentina.com

than others (Shealer & Spendlow 2002, Shealer *et al.* 2005, García *et al.* 2011) and this behaviour can be related to reproductive performance. Roseate Terns *Sterna dougallii* that use kleptoparasitism during the chick-rearing period have nestlings with better growth rates and have higher breeding success than non-kleptoparasitic individuals (Shealer *et al.* 2005). Common Terns *Sterna hirundo* can also kleptoparasitize food from conspecifics during the courtship period and females of kleptoparasitic males have higher body mass prior to egg-laying and lay larger last-laid eggs than non-kleptoparasitic parents (García *et al.* 2011). Both studies suggested that kleptoparasitic parents had higher breeding success than non-kleptoparasitic parents. However, the effect of intraspecific kleptoparasitism during the chick-rearing period on pre-fledging and fledging chick survival, and ultimately on the reproductive fitness of kleptoparasitic parents, remains to be addressed.

The Common Tern is a long-lived seabird with biparental care (Becker & Ludwigs 2004). At a colony site in Wilhelmshaven (Germany), we identified a small number of individual adult Common Terns that regularly (confirmed during all observation days) stole fish from conspecifics (García 2010). During the courtship period, kleptoparasitism was only observed in males (García *et al.* 2011). However, during the chick-rearing period (and in line with Shealer *et al.* 2005), kleptoparasitism was observed in both breeding males and females. Here we aim to assess the effect of intraspecific kleptoparasitism of Common Tern parents during the chick-rearing period on chick and pre-fledging chick survival, and so on parental reproductive output.

METHODS

Study area

The study was conducted during the 2008 breeding season in a Common Tern colony of 380 breeding pairs, located on the German North Sea coast in the harbour area of Wilhelmshaven ('Banter See'; 53°27'N, 08°07'E). The colony site consists of six artificial islands of equal size and rectangular shape (4.6 × 10.7 m each), arranged in a line with a distance of 0.9 m between islands. Each island is surrounded by a low concrete wall, preventing flooding and facilitating the finding and checking of chicks until fledging. Forty-four

elevated platforms (0.3 × 0.3 × 0.3 m) are installed on the walls for the adult Terns to land and rest on (Becker & Wendeln 1997). Since 1992, some adults and all fledglings have been marked with subcutaneously injected transponders as well as metal rings; no negative effects of this marking method have been observed (González-Solís *et al.* 1999). Resting platforms are equipped with an antenna to record remotely and automatically all transponder-marked birds attending the colony. Transponders are activated by the antenna, allowing recognition when the marked bird is within 10 cm of the antenna (Wendeln & Becker 1997). Adults were sexed by their courtship and copulation behaviour and, since 1998, all birds were sexed as chicks using standard molecular methods (Becker & Wink 2003).

Behavioural observation and characterization of individuals

With the aim of analysing the effect of kleptoparasitism on the reproductive performance of breeders, measured as their chicks' growth rate and number of fledglings, we compared two groups of individuals: (1) pairs in which at least one of the partners was observed to kleptoparasitize (hereafter 'kleptoparasitic group') and (2) parents where kleptoparasitism was never observed throughout the breeding season (hereafter 'honest group'; García *et al.* 2011). To account for seasonal changes in breeding performance (e.g. Arnold *et al.* 2004), only pairs that started laying within a period of 7 days were included (laying date as day of the year from 1 January: honest group = 133.4 ± 1.7 , $n = 21$; kleptoparasitic group = 132.2 ± 2.3 , $n = 18$). The modal laying date for the entire colony in 2008 was day 133 ($n = 309$).

Observations of foraging behaviour during the chick-rearing period were conducted for 97 h during daylight (08.00 to 20.00 h local time) and spread over 24 days. Observations were made from two hides in the colony (Wendeln & Becker 1996, García *et al.* 2011). For each observed kleptoparasitic attack, the aggressor was followed visually to its nest or to a resting platform and identified by transponders. Birds performing kleptoparasitism on a regular basis ($n = 18$) were remotely marked with yellow picric acid (Wendeln *et al.* 1996) and intensively followed through the breeding season to confirm the regular occurrence of this behaviour. Birds

belonging to the honest group ($n = 21$) were also marked with colour (silver nitrate) and intensively followed during the chick-rearing period to confirm that they never used kleptoparasitism.

Effect of kleptoparasitism on breeding performance

Egg size, brood size, hatching order and sex of chicks, all factors that are known to affect chick growth rate and reproductive success in Common Terns (Becker & Wink 2003), were measured for all kleptoparasitic and honest Common Tern nests. Data on egg size, brood size and hatching order were obtained from colony visits three times a week (Wagener 1998). We marked eggs by their laying sequence and measured their maximum length and breadth to the nearest 0.01 mm using Vernier callipers. We calculated an egg-volume index (= egg size) as egg length * breadth² * 1000⁻¹ (Harris 1964). All newly hatched chicks were ringed with steel rings from the Vogelwarte Helgoland ringing centre. When a chick was first observed, its age was assumed to be 0 day if the chick was freshly hatched, otherwise as 1 day. Brood size was defined as the number of chicks that hatched in a nest. If two or three newly hatched siblings were found in a nest on the same day, information on hatching order was inferred from the size of the yolk sac remains in the chick's abdomen (Wagener 1998). In each clutch, the first-hatched chick was denoted as A-chick, the second as B-chick and the third as C-chick. At the time the chicks were marked with transponders (on average 14 days old), two to five growing body feathers with blood were taken, stored in EDTA buffer at 4 °C, and DNA was isolated from them. These samples were used to identify the sex of the chicks using standard molecular methods (Becker & Wink 2003). The number of fledglings was recorded assuming that a chick fledged if it survived until at least the age of 25 days and was not found dead in the colony later in the season.

During nest checks, chicks were weighed with a digital balance in a wind-protected weighing box (Wagener 1998, accuracy ± 1 g). To characterize the growth performance of chicks, the following parameters of the individual growth curve, corresponding to different stages of growth, were estimated for each chick:

- *Mass at day 3*: the body mass at day 3 (hatch = day 0), providing a measure of early growth, which is a good predictor of subsequent chick survival to fledging. In 2008, mass at day 3 showed a significant positive association with the probability to fledge (0 if chick died before fledged, 1 if it survived, logistic regression: $r = 0.173 \pm 0.031$, Wald = 9.66, $df = 1$, $P < 0.001$; constant $B = 1.188$, $r^2 = 0.269$, $n = 185$). Mass at day 3 also differed significantly between fledged chicks (26.5 ± 0.7 g, $n = 65$) and those that died before fledging (20.5 ± 0.5 g, $n = 120$; t -test = 6.84, $P < 0.001$). For nine chicks that were only weighed at days 1 and 5, mass at day 3 was estimated by linear interpolation (Hatch & Nisbet 2011).
- *Growth rate days 3–13*: the mean daily growth rate (g/days) during the linear phase of the body mass development between days 3 and 13. Growth rate shows strong inter-year variability and is linked to chick survival but is a poor predictor of peak and pre-fledging mass. It was calculated as an average of the mass differences between consecutive records divided by the interval in days between weighings, if at least two mass differences were available (≥ 3 mass records between 3 and 13 days of age; Becker & Wink 2003).
- *Peak mass*: the maximum mass a chick reached in the nest, on average reached at 22.6 ± 2.6 sd days of age, which can be a good predictor of the future adult body mass (Becker *et al.* 2001).
- *Pre-fledging mass*: the last mass recorded before fledging and departure from the colony. The pre-fledging recession in weight was assumed to reflect the physiological and behavioural constraints of fledging. Pre-fledging mass is *c.* 7 g lower than peak mass in Common Terns (Becker *et al.* 1997, Becker & Wink 2003).
- *Fledging age*: the age of a chick when it was observed for the last time during daily colony visits. If the chick was not found dead thereafter we assumed that it had fledged successfully.

Growth rate at 3–13 days, peak mass and pre-fledging mass were calculated only for chicks that fledged; mass at day 3 was determined for chicks that survived to at least 9 days of age (Hatch & Nisbet 2011).

Statistical analysis

The effects of predictor variables (parent's foraging strategy, egg size, hatching order, brood size and offspring sex) on chick's growth parameters were analysed using linear mixed models (hereafter LMMs) with a Gaussian error structure and identity link function (Pinheiro & Bates 2000, Crawley 2007, Zuur *et al.* 2009). Because of non-independence between siblings, brood identity was included in all mixed models as a random effect. The mass at day 3 was modelled with egg size as a continuous variable, and foraging strategy (kleptoparasitic vs. honest parents), hatching order (A, B, C) and brood size (2, 3) as fixed effects. The growth rate at 3–13 days was modelled with parent's foraging strategy, hatching order (A, B) and brood size (2, 3) as fixed effects. Offspring sex does not influence early growth (Becker & Wink 2003) and therefore offspring sex was not included in these models. The peak mass and pre-fledging mass were modelled as a function of parental foraging strategy, hatching order (A, B), brood size (2, 3) and chick sex (female, male) as fixed effects. To fit the last three models (growth rate at days 3–13, peak mass and pre-fledging mass), C-chicks were not considered because none fledged within the honest group (Nicholls 1989, García *et al.* 2010). Egg size was also not included because of the lack of data on egg size for some chicks included in the modelling.

To assess differences in pre-fledging survival among groups, we used chi-squared tests and generalized linear mixed models (hereafter GLMMs) with a binomial error structure (two possible values for the response variable: 1 if chick died before fledging, 0 if it survived to fledging), log link function and Laplace approximation method (Crawley 2007, Bolker *et al.* 2009). Pre-fledging survival was modelled with hatching order (A, B), parental foraging strategy (kleptoparasitic vs. honest), brood size (2, 3) and chick sex (female, male) as fixed effects, while brood identity was included as random effect. C-chicks were excluded because no C-chick fledged in the honest group (Nicholls 1989, García *et al.* 2010).

Model selection used an information-theoretic approach (Burnham & Anderson 2002). Models with all possible combinations of predictor variables were considered. This resulted in eight (for growth rate at 3–13 days) and 16 (for mass at day 3, peak mass, pre-fledging mass and pre-fledging survival) candidate models (Tables 1 and 2).

Akaike's information criterion (AIC) was calculated for each model (Burnham & Anderson 2002). Due to small sample sizes (mass at day 3: $n = 43$, growth rate 3–13 days, peak mass and pre-fledging mass: all $n = 27$, pre-fledging survival: $n = 61$) we used corrected AIC (AIC_c). Model comparisons were made with ΔAIC_c , which is the difference between the lowest AIC_c value (i.e. best of suitable models) and AIC_c from all other models. In general, ΔAIC_c between 0 and 2 indicate substantial support for the model, ΔAIC_c between 4 and 7 indicate less support for the model, and $\Delta AIC_c > 10$ indicate no support for the model (Burnham & Anderson 2002). The weight of a model (w_i) signifies the relative likelihood that the specific model is the best of the suite of all models. If model uncertainty existed, we evaluated the support for predictor variables summing w_i across all models that contained the parameter being considered (parameter likelihood; Burnham & Anderson 2002). Predictor variables with good support have high parameter-likelihood values (i.e. near 1). Parameter estimates were calculated using model-averaged parameter estimates based on w_i for all candidate models. Unconditional variances of those candidate models were used to calculate standard errors. To supplement evidence of important effects with parameter likelihoods, we also assessed the degree to which the 95% confidence intervals of parameter estimates overlapped zero. We calculated upper and lower confidence limits by adding or subtracting $2 \times se$, respectively.

LMM with Gaussian structure and identity link function were used to assess differences between kleptoparasitic and honest groups (fixed effects) in fledging age (Pinheiro & Bates 2000, Crawley 2007). To assess differences between kleptoparasitic and honest groups in breeding success (i.e. number of chicks fledged per pair) a generalized linear model (GLM) with Poisson structure and log link function was used (Pinheiro & Bates 2000, Crawley 2007).

All statistical analyses were carried out using R software version 2.13.1 (R Development Core Team 2011). All values are given as mean \pm se and all tests were two-tailed with a significance level of $\alpha \leq 0.05$.

RESULTS

In total, 444 kleptoparasitic attacks were recorded during the chick-rearing period, of which 47%

Table 1. Summary of model selection results for models explaining the variation of chick growth in relation to egg size (ES), hatching order (HO), brood size (BS), parental foraging strategy (FS) and sex (S) for the Common Tern colony 'Banter See' in 2008.

Response variable	Model	No. of parameters	AIC _c	ΔAIC _c	w _i	Model likelihood
Mass at day 3	Null model	2	273.69	0.0	0.348	1.000
	BS	3	275.20	1.5	0.163	0.469
	ES	3	275.96	2.3	0.112	0.320
	FS	3	275.98	2.3	0.111	0.318
	BS + FS	4	277.52	3.8	0.051	0.147
	HO	4	277.54	3.9	0.051	0.146
	BS + ES	4	277.58	3.9	0.050	0.143
	ES + FS	4	278.39	4.7	0.033	0.095
	BS + HO	5	279.23	5.5	0.022	0.062
	BS + ES + FS	5	280.06	6.4	0.014	0.041
	HO + FS	5	280.08	6.4	0.014	0.041
	ES + HO	5	280.09	6.4	0.014	0.041
	BS + HO + FS	6	281.79	8.1	0.006	0.017
	BS + ES + HO	6	281.91	8.2	0.006	0.016
	ES + HO + FS	6	282.79	9.1	0.004	0.011
	Global model	7	284.65	11.0	0.001	0.004
Growth rate 3–13 days	HO + FS	4	107.77	0.0	0.491	1.000
	Global model	5	109.27	1.5	0.232	0.472
	HO	3	110.20	2.4	0.145	0.296
	BS + HO	4	112.08	4.3	0.057	0.116
	FS	3	112.85	5.1	0.039	0.079
	Null model	2	114.38	6.6	0.018	0.037
	BS + FS	4	115.09	7.3	0.013	0.026
Peak mass	BS	3	116.60	8.8	0.006	0.012
	FS	3	180.98	0.0	0.350	1.000
	FS + S	4	183.00	2.0	0.127	0.363
	HO + FS	4	183.72	2.7	0.089	0.254
	BS + FS	4	183.75	2.8	0.088	0.250
	HO + FS + S	5	184.64	3.7	0.056	0.160
	S	3	184.68	3.7	0.055	0.157
	BS	3	185.17	4.2	0.043	0.123
	HO	3	185.18	4.2	0.043	0.123
	Null model	2	185.18	4.2	0.043	0.122
	BS + FS + S	5	186.04	5.1	0.028	0.080
	HO + S	4	186.75	5.8	0.020	0.056
	BS + HO + FS	5	186.76	5.8	0.019	0.056
	BS + S	4	187.45	6.5	0.014	0.039
	Global Model	6	187.94	7.0	0.011	0.031
	BS + HO	4	187.95	7.0	0.011	0.031
	BS + HO + S	5	189.79	8.8	0.004	0.012
Fledging mass	Null model	2	181.93	0.0	0.327	1.000
	S	3	182.69	0.8	0.223	0.681
	FS	3	184.47	2.5	0.092	0.281
	HO	3	184.47	2.5	0.092	0.280
	HO + S	4	185.01	3.1	0.070	0.214
	FS + S	4	185.38	3.5	0.058	0.178
	BS	4	186.36	4.4	0.036	0.109
	BS + S	5	186.72	4.8	0.030	0.091
	HO + FS	4	187.24	5.3	0.023	0.070
	HO + FS + S	5	187.88	6.0	0.017	0.051
	FS + S	6	188.92	7.0	0.010	0.030
	BS + FS	5	189.22	7.3	0.009	0.026
	BS + HO	5	189.38	7.5	0.008	0.024
	BS + FS + S	6	190.03	8.1	0.006	0.017
	BS + HO + FS	6	192.55	10.6	0.002	0.005
	Global model	7	192.61	10.7	0.002	0.005

Models are listed in decreasing order of support. Models with strong support ($\Delta\text{AIC}_c \leq 2$) are highlighted in bold. AIC_c: corrected Akaike's information criterion, w_i: Akaike weight.

Table 2. Summary of model selection results for models explaining the variation of chick's pre-fledging survival in relation to hatching order (HO), brood size (BS), parent's foraging strategy (FS) and sex (S) for the Common Tern colony 'Banter See' in 2008.

Model	No. of parameters	AIC _c	ΔAIC _c	w _i	Model likelihood
FS + HO + S	5	62.22	0.0	0.572	1.000
Global model	6	64.31	2.1	0.201	0.352
HO + S	4	64.85	2.6	0.154	0.269
HO + BS + S	5	66.71	4.5	0.061	0.106
FS + S	4	72.24	10.0	0.004	0.007
FS + HO	4	72.63	10.4	0.003	0.006
FS + BS + S	5	74.06	11.8	0.002	0.003
S	3	74.37	12.2	0.001	0.002
HO	3	74.73	12.5	0.001	0.002
FS + HO + BS	5	74.86	12.6	0.001	0.002
BS + S	4	76.00	13.8	0.001	0.001
HO + BS	4	76.84	14.6	0.000	0.001
FS	3	83.63	21.4	0.000	0.000
Null model	2	85.04	22.8	0.000	0.000
FS + BS	4	85.67	23.4	0.000	0.000
BS	3	86.95	24.7	0.000	0.000

Models are listed in decreasing order of support. Models with strong support ($\Delta\text{AIC}_c \leq 2$) are highlighted in bold. AIC_c: corrected Akaike's information criterion, w_i: Akaike weights.

were successful. In only one of the 18 pairs belonging to the kleptoparasitic group did both parents show kleptoparasitic behaviour. In the remaining 17 pairs, only one of the mates was the kleptoparasite (males in nine and females in four pairs; the sex could not be determined in the remaining four).

Chick growth

None of the analysed predictor variables described variation in the mass at day 3 (Table 1, Fig. 1a). The best-supported model of variation of growth rate at 3–13 days included hatching order and parent's foraging strategy as explanatory variables ($w_i = 0.491$, likelihood ratio test, comparison with null model: $\chi^2_3 = 11.92$, $P < 0.01$, Tables 1 and 3) and both had the highest likelihood parameter values (Table 3). The mean growth rate at 3–13 days was higher in A-chicks than in B-chicks (7.1 ± 1.8 g/day, $n = 20$; 5.8 ± 2.4 g/day, $n = 7$, respectively). Growth rate at 3–13 days was higher in chicks from kleptoparasitic parents than from the honest group (7.4 ± 1.9 g/day, $n = 16$; 5.8 ± 1.9 g/day, $n = 11$, respectively). As indicated by the low parameter likelihood values and the confidence interval including zero, brood size was not related to the growth rate at 3–13 days (Table 3, Fig. 1b).

The model best describing variation of peak mass included only parental foraging strategy ($w_i = 0.350$, likelihood ratio test, comparison with

null model: $\chi^2_1 = 4.20$, $P < 0.05$, Table 1) and showed the highest likelihood parameter value (Table 3). The mean peak mass was higher in chicks of kleptoparasitic parents than of honest parents (129.4 ± 8.7 g, $n = 16$; 123.3 ± 5.5 g, $n = 11$, respectively). As indicated by the low parameter likelihood values and confidence intervals including zero, hatching order, brood size and sex of the chick were all unassociated with peak mass (Table 3, Fig. 1c).

The model best describing variation of pre-fledging mass was the null model, indicating no significant effect of hatching order, parental foraging strategy, brood size or chick sex on pre-fledging mass (Table 1, Fig. 1d).

Pre-fledging survival, fledging age and breeding success

Chick survival to fledging was affected by hatching order and parental foraging strategy. Although B- and C-chicks did not show significant differences in survival probability (0.18 ($n = 39$) and 0.06 ($n = 33$), respectively; $\chi^2_1 = 2.31$, $P = 0.13$), these chicks had a lower survival than A-chicks (0.51 ($n = 39$); A–B-chicks: $\chi^2_1 = 9.57$, $P < 0.001$; A–C-chicks: $\chi^2_1 = 17.23$, $P < 0.001$). The survival probability was significantly lower in chicks of honest parents compared with chicks of kleptoparasitic parents (0.18 ($n = 60$) and 0.35 ($n = 51$), respectively; $\chi^2_1 = 4.11$, $P < 0.05$).

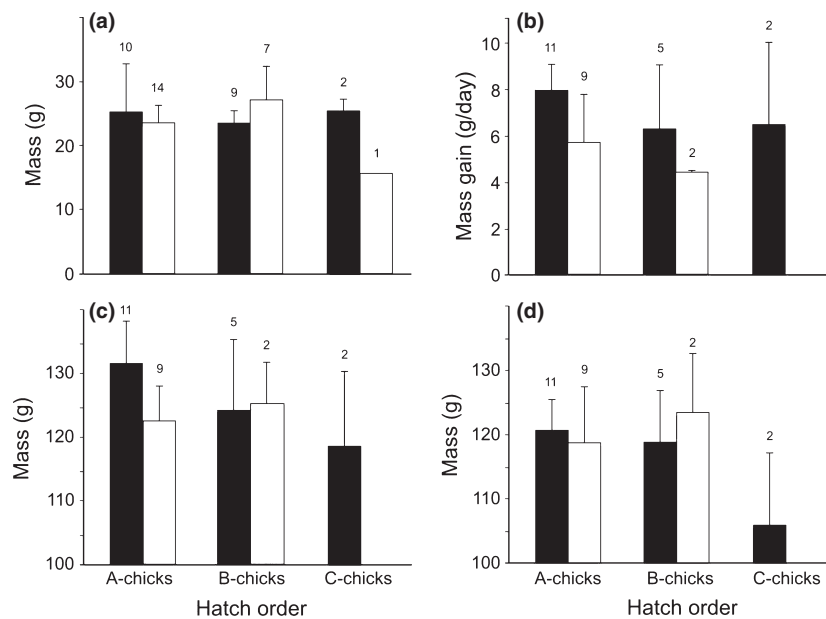


Figure 1. Growth performance of first (A-chicks), second (B-chicks) and third (C-chicks) Common Tern chicks with kleptoparasitic (black bars) and honest (white bars) parents in the 'Banter See' colony in 2008. (a) Mass at day 3 as an indicator of early growth, (b) growth rate at 3–13 days as the average daily mass gain during the middle linear growth period, (c) peak mass as a predictor of future adult body mass and (d) pre-fledging mass reflecting the physiological and behavioural constraints of fledging. Means are shown \pm 1 sd, with sample size (number of chicks) above bars.

Table 3. Parameter estimates (\pm se) from generalized linear mixed models describing variation in the growth rate at 3–13 days, the peak mass and the pre-fledging survival in Common Tern chicks at the 'Banter See' colony in 2008. Parameter likelihoods are corrected Akaike's information criterion weights (w_i) summed across all models that contained that parameter and are indicative of the importance of the variable. Parameter estimates are weighted averages (using w_i) from all models, and se are calculated from all candidate models using unconditional variances.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimated \pm se	CI	
				Lower	Upper
Growth rate 3–13 days	Intercept	1.000	5.91 \pm 0.79	4.33	7.49
	Hatching order ^a	0.925	–1.20 \pm 0.36	–1.92	–0.47
	Foraging strategy ^b	0.774	1.65 \pm 0.72	0.21	3.09
	Brood size ^c	0.307	0.98 \pm 0.91	–0.84	2.79
Peak mass	Intercept	1.000	123.80 \pm 2.89	118.02	129.58
	Hatching order ^a	0.253	–0.66 \pm 1.45	–3.56	2.23
	Foraging strategy ^b	0.744	6.22 \pm 3.03	0.15	12.29
	Brood size ^c	0.190	0.08 \pm 3.88	–7.68	7.83
Pre-fledging survival	Sex ^d	0.282	2.62 \pm 0.84	–1.65	4.47
	Intercept	1.000	0.40 \pm 0.87	–1.330	2.131
	Hatching order ^a	0.993	–2.55 \pm 0.80	–4.147	–0.961
	Foraging strategy ^b	0.781	1.72 \pm 0.82	0.084	3.349
	Brood size ^c	0.264	–0.71 \pm 1.13	–2.969	1.557
	Sex ^d	0.993	2.62 \pm 0.84	0.938	4.305

Upper and lower confidence interval limits (CI 95%) were calculated by adding or subtracting 2 se, respectively. Explanatory variables with CI excluding zero are in bold. ^aRelative variable to value of hatching order (A-chicks). ^bValue of parent's foraging strategy (honest). ^cValue of brood size (2). ^dValue of sex (female).

Generalized linear mixed model analysis of pre-fledging survival in a subset of 61 chicks of known sex also demonstrated significant effects of hatching order and parental foraging strategy on pre-fledging survival and in addition an effect of offspring sex ($w_i = 0.572$, likelihood ratio test, comparison with null model: $\chi^2_3 = 29.70$, $P < 0.01$, Table 2). The three variables included in the best supported model were important predictors of pre-fledging survival showing the highest likelihood parameter values (Table 3). Multi-model inference showed that the survival of chicks was lower in B-chicks than in A-chicks, female chicks had a lower survival than male chicks, and chicks of honest parents survived less well than chicks of kleptoparasitic parents (Table 3).

Fledging age did not differ between parental foraging strategy (kleptoparasites: 27.5 ± 0.9 days ($n = 18$), honest: 27.3 ± 1.3 days ($n = 11$); LMM: $t_{24} = 0.48$, $P = 0.63$). Breeding success was significantly higher for kleptoparasitic parents than for honest parents (1.06 ± 0.73 fledglings per pair ($n = 18$) and 0.52 ± 0.51 fledglings per pair ($n = 21$), respectively; GLM: $Z = 1.94$, $P < 0.05$).

DISCUSSION

Kleptoparasitic Common Terns had enhanced parental performance compared with parents that were not seen kleptoparasitizing, showing higher growth rates, peak mass and survival, resulting in a higher reproductive output compared with honest conspecifics.

During the courtship period, kleptoparasitism was only performed by a small proportion of specialized males (García *et al.* 2011), although during the chick-rearing period (and in agreement with Shealer *et al.* 2005), kleptoparasitism occurred in both fathers and mothers (two-thirds and one-third of kleptoparasitic breeders, respectively). All identified males that stole food during the chick-rearing period had shown kleptoparasitic behaviour during the courtship period as well; however, females stealing food during chick-rearing had never shown such behaviour during the earlier stages of the reproductive cycle (G. García unpubl. data). This pattern of behavioural expression could be explained by the differential roles of the two sexes at different stages of the season. During mating and incubation, male courtship feeding of the female plays an important role in pair bond formation and maintenance as well as in

egg production, so males are more dedicated to obtaining food whereas females allocate larger amounts of time to incubation (Nisbet 1977, Tasker & Mills 1981, Wendeln 1997, Moore *et al.* 2000). Although during the first week of chick development food provisioning is still mostly carried out by males (Wendeln 1997), preliminary observations suggest that during early development kleptoparasitic females are also able to feed their offspring by stealing fish from conspecifics in the vicinity of their nests. This requires further investigation. The efficiency of kleptoparasitism was three times higher during chick-rearing than during courtship and incubation (47 vs. 15%; García *et al.* 2011). These differences could be at least partially attributed to the fact that during chick-rearing, kleptoparasitism was often performed during the susceptible transfer of food from parents to chicks, and an important number of prey items were actually stolen from chicks.

The effect of parental foraging behaviour (kleptoparasites vs. honest) on chick growth was modelled while accounting for other factors known to be related to growth at different stages of the ontogeny in Common Terns, such as egg size, hatching order, brood size and sex of chicks (Becker & Wink 2003). None of these factors was a significant predictor of early growth (mass at day 3). However, during the middle (growth rate at 3–13 days) and late (peak mass) stages of chick development, chicks from kleptoparasitic parents consistently grew better than chicks from honest parents. Although we did not test for an interaction between parental foraging strategy and hatching order, it is worth highlighting the similarities found in the growth rate at 3–13 days of B- and C-chicks from the kleptoparasitic group and A-chicks from the honest group (Fig. 1b). However, peak mass of chicks (considered to be a good predictor of future adult body mass; Becker *et al.* 2001) from the kleptoparasitic group was significantly higher than in chicks from the honest group. This pattern was clear in A-chicks; B-chicks from the kleptoparasitic group showed similar peak mass as A- and B-chicks from the honest group (Fig. 1c). These findings are in agreement with those reported by Shealer *et al.* (2005), linking the kleptoparasitic behaviour of Roseate Tern adults to offspring growth. It is also worth noting that a few C-chicks survived in the kleptoparasitic group, whereas none survived in the honest group.

This study provides evidence that intraspecific kleptoparasitism during the breeding season enhances the reproductive success of kleptoparasites, at least during the 2008 breeding season, which was characterized by average conditions (Dänhardt & Becker 2011). Kleptoparasitic parents produced about 1.5–2 times more fledglings than honest breeders. Earlier studies at this colony conducted during the courtship period showed that kleptoparasitic courtship-feeders also had higher performances during egg formation than honest ones (García *et al.* 2011). It is worth highlighting the similarity of our results with those from the study by Shealer *et al.* (2005) on Roseate Terns, in which the number of chicks fledged relative to clutch size was 20% higher in kleptoparasites than in those with honest parents (for a modal clutch size of 2, kleptoparasitic and honest Roseate Tern parents fledged 1.20 and 0.83 chicks, respectively, whereas for a clutch size of 3, Common Tern parents fledged 1.06 and 0.52 chicks, respectively). Thus, both studies showed a significant effect of the kleptoparasitic behaviour on the probability of fledging.

We suggest that kleptoparasitic parents are high-quality individuals with respect to age, breeding experience and body mass that are able to deliver larger amounts of high-quality food (and at a more frequent rate) to their chicks than honest parents only foraging at sea. Owing to the relationships between fledging survival, sub-adult survival and recruitment in Common Terns (Becker & Zhang 2011) and other species (e.g. Bouwhuis *et al.* 2010), the higher reproductive output combined with an improved quality of fledglings (cf. Braasch *et al.* 2009) most likely enhances the fitness of kleptoparasitic parents. The link between the expression of kleptoparasitism and life-history parameters which are indicative of parental quality were not addressed in this study and deserve further exploration, as well as which are the factors limiting the number of kleptoparasites in a Common Tern colony.

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