Kleptoparasitism during courtship in *Sterna hirundo* and its relationship with female reproductive performance

Germán O. García · Peter H. Becker · Marco Favero

Abstract Kleptoparasitism is a well-known foraging tactic used opportunistically by many seabird species. However, little is known about this behaviour during the early stages of the breeding cycle and its effects on breeding performance. Here, we investigated the relationship between kleptoparasitism during the courtship period and female reproductive performance in Common Terns (*Sterna hirundo*). All identified kleptoparasites were males, and none of their mates performed such behaviour. We compared two groups of tern pairs, one where the males performed kleptoparasitism (kleptoparasitic group, $n = 10$), the other one where both mates were non-kleptoparasitic (honest group, $n = 22$). The body mass of kleptoparasitic females was between 8 and 15% higher than that of honest females. In kleptoparasitic females, the third egg was significantly bigger than in honest birds, and the egg-volume was not significantly different between the three eggs of the clutch in contrast to honest birds. We found no differences in the comparison among hatching success between both groups. The reproductive output, however, was significantly higher in the kleptoparasitic than in the honest group. Hence, we are providing the first evidence that kleptoparasitism during early stages of the breeding cycle has a strong link with egg size and reproductive output in Common Terns.

Keywords Kleptoparasitism · Courtship · Seabirds · Body mass · Egg size · Reproductive success

Introduction

Kleptoparasitism is defined as the stealing of food that has been caught by another individual (Brockmann and Barnard 1979). It occurs in a large variety of animals, including marine invertebrates (Iyengar 2004), insects and spiders (Vollrath 1984), fish (Grimm and Klinge 1996), reptiles (Cooper and Pérez-Mellado 2003), mammals (Kruuk 1972; Brown et al. 2004) and birds (Brockmann and Barnard 1979; Morand-Ferron et al. 2007). Observations of birds acting as kleptoparasites are amongst the most detailed, and Brockmann and Barnard (1979) provided a comprehensive list of observations and notes from different species. Kleptoparasitism is much more common in some groups of birds than in others, especially in seabirds (Furness 1987). Some birds such as skuas and jaegers (*Stercorarius* spp.) are considered obligate kleptoparasites, particularly during the breeding season or during migration. Others such as gulls and terns (Laridae) may kleptoparasitize opportunistically in breeding colonies or in areas where birds congregate for feeding (Hudson and Furness 1988; Steele and Hockey 1995). There is ample literature describing this behaviour and analysing mechanisms involved during different stages of the annual cycle in

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seabirds. However, little is known about kleptoparasitism during the early stages of the breeding cycle (e.g. courtship period) and its relationship with female reproductive performance.

Previous studies of long-lived birds, especially seabirds, have shown many aspects of reproductive performance, including probability of breeding (Cam et al. 1998), laying date (Catry et al. 1998), clutch size, egg size, hatching success, chick growth rates, and chick survival (Coulson and Porter 1985; Nisbet et al. 1998; Wendeln 1997). These aspects of reproductive performance are often correlated with each other and have been used as indices of parental quality (Coulson and Porter 1985; Mills 1989); for instance, larger eggs are more likely to produce larger offspring with higher chances of survival and faster growth, especially during the first few days after hatching (Reid and Boersma 1990; Williams 1994; Bize et al. 2002; Silva et al. 2007; Bonato et al. 2009).

Parental quality can be regarded as a phenotypic character that arises during development and is manifested during all or part of a lifetime, although it may also have a genetic component (Lindström 1999; Cam and Monnat 2000). However, little is known about its origins, ontogeny, or morphological, physiological, or behavioural characteristics that are correlated with it (Coulson 1968; Mills 1989; Wendeln 1997; Wendeln and Becker 1999). Shealer et al. (2005) provided the first evidence that birds which perform kleptoparasitism during the chick rearing period are associated with a superior growth performance in their nestlings. However, the relationship between intraspecific kleptoparasitism during the courtship period and reproductive traits such as egg size, clutch size, hatching success, and reproductive output were not explored.

In Common Terns (*Sterna hirundo*), kleptoparasitism is widespread (Belisle 1998; Ludwigs 1998; González-Solís et al. 2001; Stienen 2006). Until recently, it was not known whether kleptoparasitism in this species is practised either regularly by only a small percentage of the population or occasionally by most or all individuals. At a colony site in Wilhelmshaven during the breeding season 2008, we identified a group of adult Common Terns that regularly stole fish either for themselves or to feed their partners during the courtship period, indicating that for this species kleptoparasitism was practised by only a small number of specialised individuals. Given this background, our main objective was to analyse the relationship between kleptoparasitism during courtship and female reproductive performance in Common Terns. Here, we provide the first evidence that kleptoparasitism is associated with enhanced reproductive performance during the early stage of the breeding season in terms of egg size and with reproductive output.

Methods

Study area

We conducted the study during the breeding season 2008 in a monospecific colony of Common Terns (380 breeding pairs) located in the harbour area of Wilhelmshaven, Germany. The colony site (Banter See, 53°27′N, 08°07′E) consists of six artificial islands (sub-colonies A–F) of equal size and rectangular shape (each 4.6 × 10.7 m), arranged in a line with a distance of 0.9 m between the islands. Each island is surrounded by a low concrete wall, preventing flooding. Forty-four elevated places (0.3 × 0.3 × 0.3 m) are installed on the walls for the terns to land and rest on (resting platforms; for details see Becker and 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 antennae to remotely and automatically record all transponder-marked birds. Transponders are activated by an antenna, allowing recognition when the marked bird is within 10 cm to the antenna. Sixteen antennae were combined with electronic balances (Sartorius BL6, PT6, TE 6100) to record the body mass of transponder-marked individuals throughout the season (Wendeln and Becker 1996). Adults were sexed by their courtship and copulation behaviour. Moreover, the sex of many adults was known because since 1998 they have been sexed as chicks using molecular methods (Kahn et al. 1998).

Observations and data collection

With the aim of analysing the relationship between kleptoparasitism and reproductive performance of females (measured by egg size, clutch size, hatching success and reproductive output), we identified and compared two groups of terns, one with pairs where at least one of the partners performed kleptoparasitism (hereafter kleptoparasitic group) and the other with non-kleptoparasitic partners (hereafter honest group). We only considered pairs from both groups that were breeding synchronously (in order to avoid confounding effects in the analysis of clutch volumes and breeding performance allied to laying dates). These pairs were early laying birds, beginning their breeding attempt between days 128 and 135 (in Julian days, i.e. 1 May = 121), before the mean laying date of the colony (135.6 ± 5.5 days, n = 283 pairs).

To identify kleptoparasitic birds, we made observations during the courtship period (95 h of observation distributed over 19 days; throughout daylight hours, 0800–2000 hours local time) from hides located along the walls at the colony

(see Wendeln and Becker 1996). The observation period was individually defined from arrival in the colony to the laying date of the first egg, including only first clutches and not replacement clutches. For each observed kleptoparasitic attack, the bird was visually followed to its nest or to a resting platform and identified by transponders or by reading the metal rings. We marked all kleptoparasitic birds ($n = 10$) remotely with colour (yellow picric acid; see Wendeln and Becker 1996; Sudmann and von Rienen 2000) and observed them intensively during the courtship period to confirm their behaviour. Birds belonging to the honest group ($n = 22$) were also marked with colour (silver nitrate) and were observed intensively during the courtship period to confirm that they never performed kleptoparasitism.

Birds considered kleptoparasites were regularly recorded performing kleptoparasitic attacks during the courtship period. To estimate kleptoparasitism efficiency (i.e. percentage of successful attacks out of total kleptoparasitic attacks registered) we followed kleptoparasitic attacks ($n = 414$) and registered the result as successful or unsuccessful. An attack was considered successful when the kleptoparasite took the fish from the host. When a kleptoparasitic attack was successful, the kleptoparasite was followed until the prey was swallowed or delivered to its partner.

To analyse the development of body mass in females belonging to the honest or kleptoparasitic group, the weights of six individuals were available (to the nearest 1 g, three individuals from each group), monitored through the pre-laying stage (see Wendeln and Becker 1996 for methods). Body mass was repeatedly recorded per individual and stored along with date, number of resting place with balance, transponder code and time of day for each individual at every balance placed in the colony. As data were not constantly available over time, weights were pooled for two periods prior to egg laying: (1) between the 5th and 6th day before laying the first egg, and (2) between the 3rd and 4th day before laying.

Laying date, clutch size, egg size, hatching success, and reproductive output were obtained from checks of the colony every 2 or 3 days during the breeding season (Wagener 1998). Laying date is given as day of the year (number of days elapsed from 1 January to the laying date of the first egg). We marked the eggs by their laying sequence (=order of eggs) and measured their maximum length and breadth to the nearest 0.01 mm using Vernier callipers. We defined egg-volume index as egg length × breadth^2/1.000 (Harris 1964), and average egg-volume index as the mean egg volume index per clutch. Hatching success was calculated as the number of hatched eggs per clutch. To determine reproductive output (number of chicks fledged per pair), after hatching chicks were ringed

with steel rings from the ringing centre "Vogelwarte Helgoland". Chicks were assumed to be fledged if they were observed alive ≥18 days of age and not found dead in the colony later in the season.

Statistical analyses

To investigate differences between kleptoparasitic and honest group in clutch size, hatching success and reproductive output we used Mann–Whitney U test. As only 1 of the 22 clutches of the honest group was a two-egg clutch, this was excluded from the further analyses.

To analyse the relationship of kleptoparasitism with average egg-volume index, we employed general linear mixed models (GLMM) with normal error structure and identity link function (Pinheiro and Bates 2000; Crawley 2007). This analysis was performed using GLMM to consider the non-independence of the eggs within a three-egg clutch. The relationship between the average egg-volume index and kleptoparasitism was modelled with nest identity as a random effect and parent group as fixed effect (Crawley 2007). In order to analyse the relationship of order of egg with egg-volume index within each parent group, and the relationship of kleptoparasitism with egg-volume index within each particular order of egg, we employed GLMM with normal error structure and identity link function (Pinheiro and Bates 2000; Crawley 2007). The relationship between the egg-volume index and order of egg was modelled with nest identity as a random effect and parent group/order of egg as fixed effects; and the relationship between the egg-volume index and kleptoparasitism was modelled with nest identity as a random effect and order of egg/parent group as fixed effects (Crawley 2007). All statistical analyses were performed using R software (R Development Core Team 2008). The level of significance in all tests was set to $P \leq 0.05$.

Results

General characteristics of kleptoparasitism in the colony

In general terms, the kleptoparasitic behaviour of Common Terns observed during the study can be described as follows. Kleptoparasitic terns remained seated on the resting places or overflew the tern colony looking for robbing opportunities. The kleptoparasitic attacks consisted of (1) aerial pursuits, (2) attacks while the food was transferred from male to female (bill to bill), or (3) attacks to females that did not swallow fish immediately after the transfer. A total of 414 kleptoparasitic attacks was observed, 15% of which were successful (kleptoparasitism efficiency).
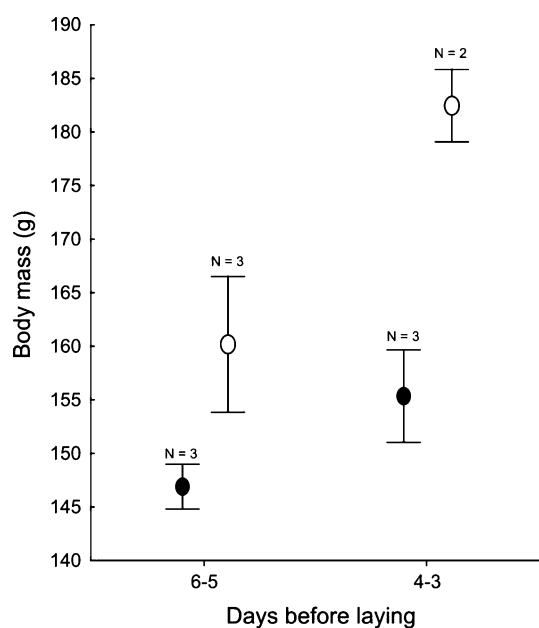
Kleptoparasites delivered 20% of the stolen prey to their partner. All kleptoparasites ($n = 10$) were males, and none of their mates performed such behaviour.

Body mass and breeding parameters for kleptoparasitic and honest birds

Body mass of females belonging to the kleptoparasitic group (i.e. with partners performing kleptoparasitism) was higher than that of honest females, both at 5–6 and 3–4 days before laying the first egg. The former group showed body masses 8.3 and 14.7% higher for 5–6 and 3–4 days before laying, respectively (Fig. 1).

All clutches of kleptoparasites contained three eggs ($n = 10$), and only one clutch of the honest group contained two eggs ($n = 22$). The mean honest clutch size was 2.95 ± 0.21, and modal clutch size was 3. We found no differences among clutch sizes of the two groups (Mann–Whitney U test: $U = 120.00$, $P > 0.05$).

The average egg volume index was 40.1 ± 1.2 mm^3 in the kleptoparasitic group ($n = 10$) and 38.3 ± 2.3 mm^3 in the honest group ($n = 21$; GLMM: $F_{1,294} = 5.19$, $P = 0.032$). The egg-volume index within the kleptoparasitic group did not differ significantly between the three eggs with respect to their laying order; however, within the honest group, the third egg was significantly smaller than the first one (Table 1; Fig. 2). The volume of the first and second egg did not differ significantly between groups, but the third egg was significantly larger in kleptoparasites (Table 2; Fig 2).

The number of hatched eggs per clutch was 2.70 ± 0.48 in the kleptoparasitic group ($n = 10$) and 2.73 ± 0.70 in the honest group ($n = 22$; Mann–Whitney U test: $U = 98.50$, $P > 0.05$). The reproductive output was 1.30 ± 0.82 fledglings pair^{-1} in kleptoparasitic parents ($n = 10$) and 0.59 ± 0.50 fledgling pair^{-1} in the honest group ($n = 22$). Reproductive output was significantly higher in the kleptoparasitic group than in honest group (Mann–Whitney U test: $U = 54.50$, $P = 0.02$).

Discussion

Different studies have shown that kleptoparasitism is a widespread behaviour in Common Terns during the breeding season (Hays 1970; Belisle 1998; Ludwigs 1998; Shealer and Spendelow 2002; Stienen 2006). However, this is the first study where individuals of this species were identified regularly stealing fish, and where the relationship with their breeding performance was assessed. Only 10 out of some 300 pairs observed during the courtship period, all of them males, were identified as kleptoparasites, suggesting that during this period kleptoparasitism is regularly practised by a small proportion of specialised individuals. The fact that all identified kleptoparasites were males can be the result that only males perform courtship feeding. Therefore, during the days before egg laying, females do not need to be active kleptoparasites when they depend completely on their mates' food (Nisbet 1977; Wendeln 1997). In addition, the increased body weight in females immediately before egg laying (up to 65% compared to the weight on arrival at the colony) might handicap them in foraging (Nisbet 1977).

The Common Tern is one species where males deliver food to their partners during the courtship period (Nisbet 1973; González-Solís et al. 2001). The nutritional significance of this courtship feeding has received considerable attention because significant amounts of food are transferred from the male to the female during the pre-laying stage (Tasker and Mills 1981). Although originally thought to participate primarily in the formation of the pair bond (Lack 1940), the primary function of courtship feeding in seabirds is to provide or enhance the nutrition of the female (Hunt 1980; Wendeln 1997; González-Solís et al. 2001). Hence, a decreased courtship feeding rate may result in reduced nutrient intake and smaller egg or clutch size (Reid 1987).

Previous investigations in the same Common Tern colony studied the relationship between laying date, age, previous breeding experience and body condition (Wendeln 1997; González-Solís et al. 2004). These studies showed

Fig. 1 Mean body mass of female Common Terns (*Sterna hirundo*) with (*open circles*) and without (*black circles*) kleptoparasitic partners at days 6–5 and 4–3 days prior to egg laying. Average values are shown along with $\pm$ 1SE (*lines*)

Table 1 Coefficients (±SE) from general linear mixed model describing the relationship between order of egg and egg-volume index within a parent group of Common Terns (*Sterna hirundo*), respectively

Response variable	Fixed effects	Categories	Coefficient ± SE	P
Egg volume index (n = 93)	Intercept		39.00 ± 0.49	0.000
	Parent group/order of egg	Honest/order 1		
		Honest/order 2	−0.44 ± 0.39	0.381
		Honest/order 3	−1.69 ± 0.39	0.000
		Kleptoparasite/order 1		
		Kleptoparasite/order 2	−0.08 ± 0.56	0.877
		Kleptoparasite/order 3	−0.70 ± 0.56	0.222

This relationship was modelled with nest identity as a random effect and parent group/order of egg as fixed effect. Either for honest or kleptoparasitic grousp, the first egg was used as reference category
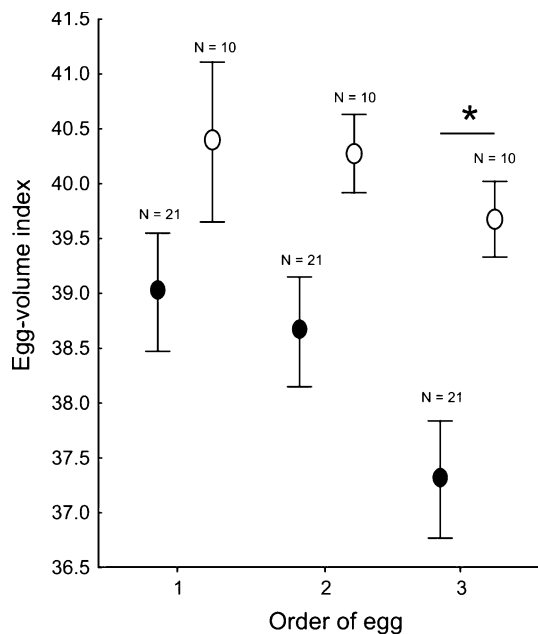
Fig. 2 Relationship between kleptoparasitism in Common Terns and egg-volume index. Average values (*circles*) are shown along with ± 1SE (*lines*). *Open circles* represent the kleptoparasitic group and *closed circles* the honest group. The *line with asterisk* indicates a significant difference ($P \leq 0.05$) between groups. See text and Tables 1 and 2 for statistics

that late laying pairs are those where males deliver less energy to their mates, hence females show lower body mass at laying (Wendeln 1997). We found that the body mass of kleptoparasites' females was between 8 and 15% higher than that of honest females. This provides the first evidence that kleptoparasitism performed by males during courtship could be affecting body mass of kleptoparasites' females. However, these results should be considered preliminary given the small sample size. Also, we could not address the question of whether this was only the result of enhanced courtship feeding or a combination of this plus other factors such as the fact that male kleptoparasites could be able to attract better mates than non-kleptoparasites. These results

should be a matter of further studies with more adequate sample sizes.

On the other hand, several factors have been shown to correlate with intra-specific variation in egg size, including laying order (Slagsvold et al. 1984), clutch size (Parsons 1976), the age and experience of the reproductive female (Järvinen and Vaisanen 1983; González-Solís et al. 2001), heritability (Ojanen et al. 1979), physiological and environmental parameters (Ojanen et al. 1981; Nager and Zandt 1994), and supplemental food (Christians 2002). Our results showed that in the kleptoparasitic group the third egg was significantly bigger than in honest birds, and the egg-volume index was constant for the three eggs. The hypothesis that nutrient acquisition during egg synthesis influences size of the clutch and of the third egg in Larids is supported by several lines of evidence (Wooller and Dunlop 1981; Winkler 1985; Salzer and Larkin 1990). We hypothesise that specialised kleptoparasitic birds (males) deliver larger amounts of food to their females—and later to their chicks (Nisbet 1973)—than honest males, thus increasing nestling survival and reproductive success.

Different studies have shown that besides the quantity of food the quality of available prey is the main factor affecting the occurrence of kleptoparasitism in seabirds (e.g. Ludwigs 1998; García et al. 2010). Kleptoparasitic Common Terns show a strong selectivity in relation to type and size of fish stolen, selecting larger marine fish with higher energetic values (Ludwigs 1998). Previous studies conducted during the courtship period in the colony under study showed that males use both marine and freshwater foraging areas. Males foraging in marine areas carry out long foraging flights, but benefit from marine prey having higher energetic value than limnetic prey. Furthermore, the same study showed that birds foraging in marine areas had higher body mass and started laying earlier (Wendeln 1997). During the last 10 days before laying, kleptoparasitic males identified in our study were observed for long periods (even throughout the whole day) in the colony without taking long foraging trips to marine areas (Germán

Table 2 Coefficients (±SE) from general linear mixed model describing the relationship between parent group and egg-volume index

Response variable	Fixed effects	Categories	Coefficient ± SE	P
Egg volume index ($n = 93$)	Intercept		39.00 ± 0.49	0.000
	Order of egg/parent group	Order 1/honest		
		Order 1/kleptoparasite	1.36 ± 0.87	0.125
		Order 2/honest		
		Order 2/kleptoparasite	1.62 ± 0.87	0.069
		Order 3/honest		
		Order 3/kleptoparasite	2.36 ± 0.87	0.009

This relationship was modelled with nest identity as a random effect and order of egg/parent group as fixed effect. The honest group was used as the reference category in all cases

García, unpublished data). However, through their kleptoparasitic activities males might be able to deliver larger amounts of food to their females and ensure a more constant provisioning than individuals foraging at sea. The increase in food delivered to their partner would be acting as additional food for the female at the critical time of egg formation, may affect reproductive performance as well as females' body mass growth, and the final weight at laying as the individual weight data indicate.

In our study, we did not find differences in the hatching success between kleptoparasites and honest birds. However, we are providing the first evidence that kleptoparasitism during early stages of the breeding season is strongly associated with high reproductive output, with a higher number of chicks fledged per pair in the kleptoparasitic group. Our results concerning differences in this fitness component greatly exceed those found by Shealer et al. (2005), where kleptoparasitic Roseate Terns (*Sterna dougallii*) produced about 45% more fledglings than honest birds. Assuming equal reproductive lifetimes, kleptoparasitic terns could produce about twice as many fledglings than honest ones, representing a considerable fitness advantage.

In this study, we are providing the first evidence that kleptoparasitism during the courtship period is strongly associated with high parental quality in terms of egg size and reproductive output. In Common Terns, this relationship increased the survival of nestlings, thus enhancing the reproductive output and likely the fitness of kleptoparasitic parents.

Zusammenfassung

Kleptoparasitismus während der Balzfütterungsphase von Flussseeschwalben Sterna hirundo in Bezug zur Reproduktionsleistung der Weibchen

Kleptoparasitismus während der Balzfütterungsphase von Flussseeschwalben *Sterna hirundo* in Bezug zur Reproduktionsleistung der Weibchen. Kleptoparasitismus ist eine Ernährungstaktik, die opportunistisch von vielen Seevogelarten eingesetzt wird. Kenntnisse über dieses Verhalten und seine Effekte auf die Brutbiologie zu Beginn des Brutzyklus aber sind rar. Während der Balzfütterungsperiode von Flussseeschwalben (*Sterna hirundo*) untersuchten wir den Zusammenhang zwischen Kleptoparasitismus und Reproduktionsleistungen der Weibchen. Alle identifizierten Kleptoparasiten waren Männchen, während keine ihrer Partnerinnen dieses Verhalten zeigte. Wir verglichen zwei Gruppen von Paaren: Bei der ersten waren die Männchen Kleptoparasiten (kleptoparasitische Gruppe, $N = 10$), bei der zweiten waren beide Partner nicht kleptoparasitisch aktiv (Kontrollgruppe, $N = 22$). Die Partnerinnen von Kleptoparasiten erzielten zwischen 8% und 15% höhere Körpergewichte, und ihr drittes Ei war signifikant größer als das von Kontrollweibchen. Im Gegensatz zu den Kontrollvögeln unterschied sich das Eivolumen der kleptoparasitischen Gruppe nicht signifikant zwischen den drei Eiern des Geleges. Wir fanden keine Unterschiede im Schlüpferfolg beider Gruppen, aber der Reproduktionserfolg war bei der kleptoparasitischen Gruppe signifikant höher. Am Beispiel der Flussseeschwalbe unterbreiten wir damit den ersten Beleg, dass Kleptoparasitismus auch während früher Stadien des Brutzyklus in engem Zusammenhang mit den Reproduktionsleistungen steht und die Eigröße und den Reproduktionserfolg steigert.

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