

Stealing food from conspecifics: spatial behavior of kleptoparasitic Common Terns *Sterna hirundo* within the colony site

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Abstract Amongst seabirds, kleptoparasitism is one of the most common types of exploitation in which individuals compete for food already procured by another forager. Here, we analyzed the within-colony spatial movements and foraging of transponder-marked Common Terns (*Sterna hirundo*) during the chick-rearing period in relation to the terns' trophic strategy (kleptoparasitic vs. honest). Attendance patterns (time spent at the colony site per day, number and locations of resting platforms used) were compared between kleptoparasitic ($N = 11$) and honest individuals ($N = 26$). A total of 725 kleptoparasitic attacks were recorded during the chick-rearing period at the colony site. We found sex differences in the tactic used for stealing food and the area chosen for attacks: females attacked in the vicinity of their nest, while males attacked further away. Significant differences were found between both groups in the spatial pattern: kleptoparasites (particularly males) used more resting platforms and moved more widely across the colony site than honest individuals, and parasitic females were present in the colony longer during the day than honest ones. Our results show a differential use of the colony site dependent on the foraging strategy. Parasitic birds used the colony site as a foraging patch, monitoring the colony and looking for kleptoparasitic feeding opportunities without compromising their parental

roles. In contrast, honest individuals spent much time outside the colony foraging for their chicks.

Keywords Chick-rearing period · Foraging strategy · Parental role · Trophic parasitism · Seabirds

Zusammenfassung

Futter stehlen bei Artgenossen: Räumliches Verhalten von kleptoparasitischen Flusseeeschwalben *Sterna hirundo* innerhalb der Kolonie

Kleptoparasitismus ist bei Seevögeln eine wichtige Strategie zur Nahrungsbeschaffung, wobei Individuen um Nahrung konkurrieren, die ein anderer Vogel bereits erbeutet hat. In dieser Studie haben wir das räumliche Verhalten von transponder-markierten Flusseeeschwalben (*Sterna hirundo*) in der Kolonie während der Küken-Aufzuchtphase untersucht. Zusätzlich wurden Fütterungsbeobachtungen in Relation zur Strategie der Individuen (kleptoparasitisch vs. nicht-kleptoparasitisch) durchgeführt. Die Anwesenheitsmuster (verbrachte Zeit pro Tag in der Kolonie, Anzahl der aufgesuchten Rastplätze) zwischen kleptoparasitischen ($N = 11$) und nicht-kleptoparasitischen ($N = 26$) Individuen wurden verglichen. Insgesamt konnten 725 kleptoparasitische Attacken während der Aufzuchtphase in der Kolonie registriert werden. Bei den Kleptoparasiten haben wir geschlechtsabhängige Unterschiede sowohl bei der angewandten Taktik als auch dem Gebiet, indem die Attacken stattfanden, beobachtet: Während die Weibchen den Artgenossen die Beute vorwiegend in der Nähe ihres eigenen Nestes streitig machten, nutzen Männchen auch weiter weg gelegene Gebiete der Kolonie. Außerdem wurden auch Differenzen im räumlichen Verhalten der beiden Gruppen gefunden: Kleptoparasitische Männchen

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nutzen mehr Rastplätze und bewegten sich weiter durch die Kolonie als nicht-kleptoparasitische Männchen. Auf der anderen Seite hielten sich die kleptoparasitischen Weibchen pro Tag länger in der Kolonie auf als die nicht-kleptoparasitischen. Unsere Ergebnisse zeigen deutlich eine unterschiedliche Nutzung der Kolonie abhängig von der Strategie bei der Nahrungssuche. Kleptoparasitische Individuen nutzen die Kolonie selbst als Jagdgebiet und warteten bis sich eine Gelegenheit zum Futter stehlen ergab, ohne dabei die elterliche Fürsorge ihrer Jungen zu beeinträchtigen. Im Gegensatz dazu müssen die ehrlich jagenden Flussseeschwalben viel Zeit außerhalb der Kolonie zur Nahrungssuche aufwenden, um den Nachwuchs aufzuziehen.

Introduction

Parasitic interactions over food resources are one of the most widespread forms of exploitation throughout the animal kingdom, and there is a vast body of literature describing the many variations of such behavior (Giraldeau and Caraco 2000). Different forms of social parasitism have been reported in a number of taxa, including snails (Iyengar 2004), insects (Bentinen and Preisser 2009), spiders (Kerr 2005), fish (Hamilton and Dill 2003), lizards (Cooper and Pérez-Mellado 2003), birds (García et al. 2010), and carnivorous mammals (Carbone et al. 2005). In birds, social parasitism is mostly associated with kleptoparasitism (Brockmann and Barnard 1979), in which one individual steals food captured by another individual of the same or a different species (Rothschild and Clay 1952).

Most species of terns (Laridae) breed in dense colonies (Cabot and Nisbet 2013). In contrast to many other seabirds, while they transport food for their chicks or partners, terns hold the prey in their bill, making it visible to other birds and increasing the likelihood of either inter- or intraspecific kleptoparasitic attacks (Fuchs 1977; García et al. 2010, 2011). These seabirds are considered opportunistic kleptoparasites that generally use a range of foraging tactics but often show kleptoparasitic behavior during periods of low food availability (Brockmann and Barnard 1979; Furness 1987; Oro 1996; Triplet et al. 1999). In Common Terns *Sterna hirundo*, kleptoparasitism is widespread and has been considered opportunistic (Belisle 1998; Ludwigs 1998; González-Solís et al. 2001; Stienen et al. 2001). However, it appears to be a strategy that is consistently employed by a specialized proportion of the common tern population that spend most of their time stealing fish from conspecifics within their breeding colony (García et al. 2013).

Different studies have investigated the relationship between kleptoparasitism in terns and factors such as prey availability and quality (Ludwigs 1998; Dies and Dies 2005), weather conditions (García et al. 2010), and breeding performance (Shealer et al. 2005; García et al. 2011, 2013), among others. Previous studies have shown that kleptoparasitic individuals within a population are more productive than non-kleptoparasitic ones (Shealer et al. 2005; García et al. 2011, 2013). However, the relationship between this foraging strategy and the spatial use of the colony site is yet to be explored.

In the study reported in the present paper, we used a novel technology to study the spatial movements of transponder-marked individuals that were automatically monitored by an antenna network deployed at the colony site (see Ludwig and Becker 2006). Our main goal was to compare the spatial patterns of colony site use and the attendance of kleptoparasitic and non-kleptoparasitic Common Terns (in terms of time spent at the colony per day and the number and locations of resting sites used). The kleptoparasitic Common Terns studied during this investigation regularly stole fish from conspecifics to feed their partners (during courtship) or chicks (during chick rearing), and had been identified and monitored since 2008 at the colony site Banter See in Germany (García et al. 2011, 2013). We expected that the foraging strategy would have consequences for the terns' spatial movements within the colony area, and we predicted that kleptoparasites—which monitor the colony, searching for opportunities to steal food from conspecifics—would be registered for longer periods in the colony and use more resting sites than honest individuals.

Methods

Study area

The study was conducted during the 2011 breeding season at a Common Tern colony holding 435 breeding pairs and located on the German North Sea coast in the harbor area of Wilhelmshaven (“Banter See,” 53°27'N, 08°07'E), which has been studied since 1984. The colony site consists of six artificial islands (i.e., subcolonies) 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 that prevents flooding, facilitates the discovery of chicks, and allows them to be checked until fledging. The breeding habitat is homogeneous; the only difference between the subcolonies is the increasing distance from the shore. 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). On the walls surrounding the islands, 44 elevated resting platforms ($0.3 \times 0.3 \times 0.3$ m) were mounted and equipped with antennae for remote and automated registration of transponder-fitted birds. Wires between the resting platforms prevented the birds from sitting directly on the walls. The individual transponder codes, recorded automatically by the antennae every 5 s, were stored along with date, time, and location (number of the resting platform). Adults were sexed by their courtship and mating behavior, and all birds have been sexed as chicks using standard molecular methods since 1998 (Becker and Wink 2003).

Characterization of individuals and behavioral observations

With the aim of analyzing the effect of foraging strategy on the terns' spatial behavior, we compared two groups of birds: (1) the “kleptoparasitic group” consisted of individuals that frequently performed intraspecific kleptoparasitic attacks during the chick-rearing period, and (2) the “honest group” constituted of individuals in which kleptoparasitism was never observed throughout the breeding season (see García et al. 2011, 2013). Both groups have been monitored with respect to these foraging strategies since 2008, and have shown consistency in the use (or not) of kleptoparasitism.

Observations of foraging behavior during the chick-rearing period were conducted from two hides in the colony for 99.5 h during daylight (08.00 to 20.00 h local time) over 27 days (Wendeln and Becker 1996). For each observed kleptoparasitic attack, the parasite was visually followed to its nest or to a resting platform, where it was identified by the transponder. Birds performing kleptoparasitism on a regular basis ($n = 11$) were individually marked from a remote location with yellow picric acid (see Wendeln et al. 1996; García et al. 2011) and intensively monitored throughout the breeding season to confirm the regular occurrence of this behavior. Birds belonging to the honest group ($n = 26$) were also individually marked from a remote location with color (silver nitrate) and intensively monitored during the breeding season to confirm that they never performed kleptoparasitism.

For each registered kleptoparasitic attack, the following variables were recorded: (1) the identity of the kleptoparasite (visually by the color mark, or by the transponder), (2) the area where the attack was performed, and (3) the attack tactic used by the kleptoparasite. Regarding the spatial use in the colony, we considered whether the kleptoparasitic attack occurred (a) in the subcolony where the kleptoparasite was breeding, (b) in a different subcolony from where the individual was breeding, and/or (c) at the periphery of

the colony site. Regarding the kleptoparasitic tactic used, we distinguished whether or not the bird used aerial pursuit.

Colony attendance patterns

The mean number of registrations per bird on the resting platforms during the chick-rearing period was 3.615 ± 3.892 for kleptoparasites ($N = 11$) and 2.645 ± 6.164 for honest birds ($N = 26$). The chick-rearing period was individually defined as 30 days after the hatching date of the first chick of a focal breeder, including only first clutches and excluding replacement or second clutches. At this site, chicks fledged on average when they were 26–28 days old (Becker and Wink 2003). For further analysis, this period was divided into 10-day periods (1–10 days, 11–20 days, and 21–30 days after hatching). Given that the number of resting platforms attended per bird proved to be significantly and positively correlated with the number of subcolonies visited (Spearman's rank correlation; honest birds: $r_s = 0.844$, $N = 26$, $P < 0.001$; kleptoparasites: $r_s = 0.603$, $N = 11$, $P < 0.05$), the former was used as an indicator of a given individual's spatial use of the colony. In addition, we calculated the proportion of days in which a bird was registered in the colony (number of days registered in the colony divided by the 30 days of the chick-rearing period), the number of resting platforms that a bird used in different subcolonies, as well as the time spent at the colony site (calculated as the number of hours per day in which the bird was registered at least once). Birds that were registered for a minimum of 8 days during the study period were the only ones considered for attendance (mean days registered: 23.4 ± 7.7 , $N = 11$ for kleptoparasites; 20.2 ± 7.1 , $N = 26$ for honest birds).

Statistical analyses

The frequency of aerial pursuits used by the kleptoparasites of the two sexes and the distribution of the areas in which they carried out their attacks were tested using the chi-square test (Zar 1999). The differences in (1) the proportion of registered days, (2) the total number of resting platforms used per individual, and (3) the time spent at the colony site per day between kleptoparasitic and honest individuals were tested with Student's *t* test or the Mann–Whitney *U* test. Differences in the number of resting platforms used by kleptoparasitic and honest individuals inside their own subcolony or in other subcolonies were tested with the Wilcoxon signed-rank test for related samples. The variation in the use of resting platforms throughout the chick-rearing period (10-day periods: 1–10, 11–20, and 21–30 days after hatching) was tested for honest birds and kleptoparasites separately using the Friedman test. All

statistical analyses were carried out using the R software package, version 2.13.1 (R Development Core Team 2011). All values are the mean \pm one standard error (SD), and all tests were two-tailed with a significance level of $\alpha \leq 0.05$.

Results

Kleptoparasitic behavior

A total of 725 kleptoparasitic attacks were recorded during the chick-rearing period, 64 % of which were performed by males and the remaining 36 % by females. In general terms, the kleptoparasitic behavior of Common Terns observed during this study can be described as follows: kleptoparasitic terns remained on the resting platforms, next to the nest, or overflowed the colony looking for robbing opportunities. Kleptoparasitic attacks occurred mainly while prey was being transferred from adults to chicks, or when prey was already handled by chicks. Less frequently, kleptoparasites also stole food from terns in flight; females used aerial tactics less frequently than males (females 5.4 %, males 14.6 %; chi-square test: $\chi^2_2 = 14.19$, $P < 0.001$). Furthermore, the distribution of colony areas in which kleptoparasites attacked differed between sexes (see Fig. 1); females attacked most commonly at their breeding subcolony (64 %, see Fig. 1, $\chi^2_2 = 161.45$, $P < 0.001$), while males attacked more frequently outside their subcolony (50 %, see Fig. 1, $\chi^2_2 = 101.07$, $P < 0.001$).

Spatial behavior and attendance patterns

In general terms, the proportion of days registered in the colony and the time that each individual spent per day on the resting platforms were not affected by their foraging strategy (Table 1; Mann–Whitney U test, $U = 104.00$,

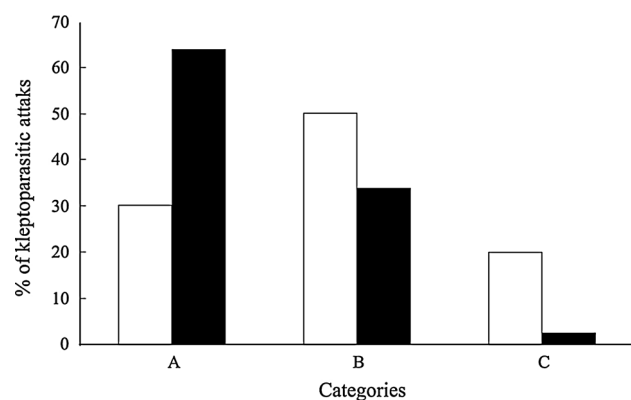


Fig. 1 Frequency (%) of observed kleptoparasitic attacks by sex (open bars males, black bars females) in relation to the area of the colony: A at the breeding subcolony, B outside the breeding subcolony, and C outside the colony area

$N = 37$, $P = 0.199$ and $U = 99.00$, $N = 37$, $P = 0.148$, respectively) or sex ($U = 147.00$, $N = 37$, $P = 0.587$ and $U = 144.50$, $N = 37$, $P = 0.481$, respectively). Even within each foraging group, there were no significant differences between the sexes (registered days in honest birds: $U = 65.50$, $N = 26$, $P = 0.459$; in kleptoparasites: $U = 14.50$, $N = 11$, $P = 0.931$; registered hours per day in honest birds: $U = 65.00$, $N = 26$, $P = 0.406$; in kleptoparasites: $t = -0.20$, $N = 11$, $P = 0.846$) (Table 1). However, the time spent per day on the resting platforms by terns of each sex differed in relation to foraging strategy; kleptoparasitic females spent more time in the colony than honest females (4.89 ± 3.16 h/day vs. 1.79 ± 1.36 h/day, $t = 2.80$, $N = 16$, $P = 0.014$), whereas male attendance at the colony did not differ (kleptoparasitic males: 4.51 ± 4.00 h/day, honest males: 3.95 ± 3.93 h/day, $U = 41.00$, $N = 21$, $P = 0.785$; Table 1).

The number of resting platforms used by terns did not differ significantly between males and females ($U = 127.00$, $P = 0.244$). However, this parameter was affected by the foraging strategy; kleptoparasites used more resting platforms than honest birds ($U = 33.50$, $P < 0.001$). The effect of foraging strategy was stronger in males than in females (Table 1): Kleptoparasitic individuals used more resting platforms outside than inside their breeding subcolony (mean number in breeding subcolony: 4.82 ± 2.36 ; in other subcolonies: 10.91 ± 8.40 ;

Table 1 Mean number of resting platforms (\pm SD) used by Common Terns, mean hours registered per day (\pm SD), and percentage of days (\pm SD) on which the individuals were registered at the colony in relation to foraging strategy (kleptoparasite, honest) and sex (female, male)

| Factor | Number of resting platforms | Hours/day | Percentage of registered days (%) |
|------------------------------|-----------------------------|-----------------------------|-----------------------------------|
| Foraging strategy | | | |
| Kleptoparasite (11) | 15.7 ± 8.5 | 4.7 ± 3.5 | 77.7 ± 25.9 |
| Honest (26) | 6.8 ± 6.4 | 3.0 ± 3.3 | 67.4 ± 23.6 |
| P^a | <0.001 | 0.148 | 0.199 |
| Sex | | | |
| Female (15) | 10.8 ± 8.1 | 2.8 ± 2.5 | 68.8 ± 24.5 |
| Male (22) | 8.5 ± 8.1 | 4.1 ± 3.9 | 71.7 ± 24.9 |
| P^a | 0.244 | 0.481 | 0.587 |
| Sex/foraging strategy | | | |
| Female kleptoparasite (5) | 14.4 ± 5.2 | 4.9 ± 3.2 | 77.7 ± 30.6 |
| Female honest (10) | 9.0 ± 8.9 | 1.8 ± 1.4 | 64.3 ± 21.3 |
| P | 0.071 ^a | <0.02^b | 0.486 ^b |
| Male kleptoparasite (6) | 16.8 ± 10.9 | 4.5 ± 4.0 | 77.8 ± 24.4 |
| Male honest (16) | 5.4 ± 3.8 | 3.9 ± 3.9 | 69.4 ± 25.5 |
| P^a | <0.01 | 0.481 | 0.399 |

Sample sizes are given in parentheses

^a Mann–Whitney U test. ^b Student's t test

Wilcoxon test: $Z = -2.26$, $N = 11$, $P = 0.045$). This difference was not significant in honest birds (in breeding subcolony: 3.15 ± 1.32 ; in other subcolonies: 3.62 ± 5.64 ; $Z = -0.529$, $N = 26$, $P = 0.606$). The number of resting platforms used by terns within each foraging group did not differ between the three periods of chick rearing (Friedman test; number of resting platforms used by kleptoparasites, 1–10 days: 9.64 ± 8.10 , 11–20 days: 10.82 ± 8.64 , 21–30 days: 9.00 ± 5.74 ; $\chi^2_2 = 2.47$, $N = 11$, $P = 0.289$; by honest birds, 1–10 days: 3.23 ± 3.2 , 11–20 days: 3.73 ± 4.59 , 21–30 days: 4.42 ± 4.23 ; $\chi^2_2 = 0.62$, $N = 26$, $P = 0.731$).

Discussion

In this study, we explored the relationship between within-colony spatial use and individual foraging strategy in a colonial seabird. We tested whether kleptoparasitic and honest foraging Common Terns show differing spatial use of their colony. The sample size of 11 kleptoparasitic individuals is relatively small, but this minority of Common Terns could not be enlarged; hence, no more individuals that used this specific foraging strategy were found in the colony despite our extended observation times. However, for behavioral field studies in colonial breeders, detailed observations and high numbers of spatial records of parasitic and honest birds have documented their individual foraging tactics exceptionally well. Another shortcoming is that we restricted our observations to the colony site and were not able to study the foraging behavior at sea, where kleptoparasitism also might occur. Three major conclusions can be drawn from the results of this study: (1) kleptoparasites moved more actively in the colony, (2) kleptoparasitic females spent more time within their subcolonies than honest ones, and (3) females and males used different tactics and areas to steal food. Ours results present evidence that the conflict between parental care and foraging was better solved by parasitic parents than honest parents.

Our study showed that kleptoparasites (particularly kleptoparasitic males) used more resting platforms than honest individuals. The number of resting platforms visited by an individual was considered an indicator of its range of movement within the colony. The difference between kleptoparasitic and honest individuals can be attributed to the fact that kleptoparasitic birds explore more widely in search for potential hosts from which to steal food. Kleptoparasites patrolled the colony looking for hosts with prey, and used different resting platforms in the colony as lookout posts. Honest individuals, in contrast, spent more time outside the colony foraging (i.e., fishing) to feed their chicks, used fewer resting platforms, and were more restricted to their own breeding subcolony. There were no

differences, however, in the time spent on resting platforms between kleptoparasitic and honest birds. This result indicates that honest birds were not excluded from using the platforms by kleptoparasitic individuals, which presumably were not dominant at these preferred sites. Parasitic females, however, spent more time on the platforms than honest ones, which can (at least partly) be attributed to different strategies of kleptoparasitic and honest mothers during the chick-rearing period. Although it has been reported that food provisioning is mainly carried out by males during the first week of chick development (Wendeln 1997), kleptoparasitic females are able to feed their offspring by stealing fish from hosts in the vicinity of their nests (García et al. 2013). During this study, we observed that, after their chicks had hatched, kleptoparasitic females waited on the resting platforms close to their nests for kleptoparasitic opportunities (e.g., when other chicks were handling fish offered by their parents). Honest females, in contrast, regularly remained on the ground of the nesting territory during the first week of the chick period; after that, the honest females started foraging at sea to feed their chicks (Wiggins and Morris 1987; Wendeln 1997).

The foraging tactics used by Common Terns during this study were in line with those described recently by Cabot and Nisbet (2013). In our study, we found sex differences in the use of aerial pursuit and in the colony area chosen for kleptoparasitic attacks. Males used aerial pursuit more frequently than females, and females attacked more in the vicinity of their nests. These differences in parasitic behavior can be, at least partly, attributed to the described differences in parental roles. Previous studies of Common Terns have shown that, during the first week of chick development, females spend more time than males at the nest brooding chicks (Wiggins and Morris 1987; Wendeln 1997). During this week, chicks are vulnerable to attacks from adult terns: intraspecific kleptoparasitism can cause unguarded chicks to be removed from the colony together with the stolen fish (Ludwigs 1998; Sudmann 1998). The vulnerability of small chicks may increase when inexperienced adults deliver prey that are too large for their chicks and that require long handling times (G.G., unpubl. data). In the Banter See colony, such chick-removal events were frequently observed during the first week of life, and were likely the main cause of the disappearance of chicks, as predation is very rare in this colony. We suggest that the behavior of females kleptoparasitizing close to their nest site may be advantageous, as it allows them to (1) avoid compromising the parental role of protecting the chicks from predators and/or kleptoparasites and (2) improve the feeding rate of their chicks by circumventing their normal strict dependence on provisioning by the father. This is in line with previous findings (see García et al. 2011, 2013; Shealer et al. 2005) that kleptoparasitic terns show higher

breeding performance than honest ones in terms of egg size, growth rates, chick survival, and reproductive output, among other parameters. With respect to a potential fitness benefit of kleptoparasitic individuals via fecundity selection, it would be interesting to know whether kleptoparasitism is an inherited trait or whether it is a cultural tradition passed on from parents to their young through mimicking and learning this tactic.

Conclusions

Our observations reveal that, whereas honest individuals spent much time foraging outside the colony, parasitic individuals used the colony site as a foraging patch, monitoring the colony and looking for feeding opportunities without compromising their parental role. Because of this foraging tactic, kleptoparasitic fathers used larger areas of the colony site than did honest fathers. In mothers, kleptoparasitic foraging resulted in extra time to spend in their breeding subcolonies compared with honest mothers. This enabled them to protect chicks against predators or conspecifics and to brood them without neglecting the chicks' food demands, which were covered by the mothers' concomitant stealing of food from colony members. Specialized kleptoparasites represent a minority in the colony and reflect a different foraging niche that is also manifested by a shift in their spatial behavior at the colony site. The parental kleptoparasitic lifestyle is successful, as indicated by the resulting improvement in reproductive performance (see above). This indicates that the conflict between parental care and foraging is better solved by parasitic parents than by honest parents.

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