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Original Article

The costs of kleptoparasitism: a study of mixed-species seabird breeding colonies

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Mixed-species assemblages are common in nature, providing mutual benefits to associating species including anti-predator advantages or resource facilitation. However, associating with other species may also impose costs through kleptoparasitism (food theft). Identification of these costs, and how they vary when different species breed alongside one another, is essential to understand the payoffs of mixed-species assemblages. We explore the costs of kleptoparasitism for greater crested terns *Thalasseus bergii* provisioning offspring at a single-species colony, where individuals suffer kleptoparasitism from conspecifics, and at a mixed colony where terns breed alongside Hartlaub's gulls *Chroicocephalus hartlaubii* and are vulnerable to both intra and interspecific kleptoparasitism. Gull presence likely contributes to increases in both kleptoparasitic attacks and the proportion of prey lost or stolen during provisioning, relative to the single-species colony. Provisioning adults suffered additional energetic costs in response to gull kleptoparasitism, requiring more attempts to deliver prey, taking longer to do so, and swallowing more prey (to the detriment of their offspring). Gulls also appear to increase the duration of tern vulnerability to kleptoparasitism, because they continued to steal food from adults and chicks after precocial chicks left the nest, when intraspecific kleptoparasitism is negligible. Terns breeding in a mixed colony, therefore, suffer direct and indirect costs through decreased provisioning and increased provisioning effort, which may ultimately affect reproductive success, resulting in colony decline where kleptoparasitism is frequent. This study illustrates how forming a mixed-species seabird breeding assemblage has costs as well as benefits, potentially fluctuating between a parasitic and a mutualistic relationship.

Key words: **kleptoparasitism, greater crested terns, mixed assemblage, Hartlaub's gull, energy cost, non-invasive, Robben Island.**

INTRODUCTION

Many species form associations with others, termed mixed-species assemblages. Typically, such assemblages provide net benefits to associating species and are thus considered to be mutualistic relationships (Bronstein 2001; Leigh 2010). In particular, mixed-species breeding colonies, typical among many seabird species, are commonly thought to provide mutual anti-predator benefits to component species or to facilitate access to the same favorable local environmental resources (e.g. Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Danchin et al. 1998; Broinsten 2001). However, many species also impose costs on associating species, and the relationships may tend towards parasitism when these costs are high (Rathcke 1992; Baigrie et al. 2014). Food theft, or kleptoparasitism, is common in some seabird colonies, where breeders returning to provision their young are vulnerable to attack, both by conspecifics (intraspecific kleptoparasitism) and other species (interspecific kleptoparasitism) (Brockmann and Barnard 1979; Iyengar 2008). Interspecific kleptoparasitism may represent a significant cost of associating with other species, both through food loss and through changes to adult provisioning behavior to reduce robberies with a resultant increase in energy expenditure (Nettleship 1972; Stienen et al. 2001). Consequently, to understand the trade-offs of mixed-species assemblages there is a need to identify the costs arising from kleptoparasitism and to assess how these differ when a species breeds alone or alongside other species.

Prey stealing is likely to be particularly acute where kleptoparasitic species breed alongside "host" species in mixed-breeding colonies, potentially resulting in decreased individual survival and

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breeding success (Fuchs 1977; Furness 1987). For example, in mixed colonies of breeding sandwich terns *Thalasseus sandvicensis* and black-headed gulls *Chroicocephalus ridibundus* in the Netherlands, kleptoparasitism by gulls substantially decreased food provisioned to tern chicks and overall productivity (Stienen et al. 2006). Interspecific kleptoparasitism may also diminish feeding rates due to a greater time spent airborne in order to evade kleptoparasites (Le Corre 1997; Stienen et al. 2001; Blackburn et al. 2009). Direct comparison of kleptoparasitism rates between breeding colonies of puffins *Fratercula arctica*, with or without gulls, illustrated that chick-feeding rates were higher in gull-free colonies (Finney et al. 2001). To better understand the costs imposed by kleptoparasitism (e.g. increased provisioning costs for adults), further comparisons are needed of colonies that differ only in the presence of a kleptoparasitic species. For these studies, key factors to investigate include the total amount of food stolen and the costs of attempting to feed offspring under the threat of kleptoparasitism. In addition, detailed information on what is stolen and when is necessary to determine which factors make birds vulnerable to robbery and therefore more likely to be the targets of kleptoparasitic attacks. Specifically, direct comparison of inter- versus intraspecific kleptoparasitism is crucial to determine the relative costs they impose, how they differentially affect behavior and whether they interact to affect the outcome of kleptoparasitism (Ens et al. 1990). For example, where provisioning adults are vulnerable to intra and interspecific kleptoparasitism in different contexts, this has the potential to drive different behaviors in single-species versus mixed colonies. Such investigations would help to elucidate the dynamics underlying interactions within mixed-species aggregations and shed light on the evolution of these relationships, particularly when there are potential shifts between mutualism and parasitism.

In southern Africa, greater crested terns *Thalasseus bergii* often breed in mixed colonies with Hartlaub's gulls *Chroicocephalus hartlaubii* (Uys 1978). Greater crested terns generally lay 1 egg, and for the first 2–4 days after hatching parents feed their chick in the nest cup. Thereafter, feeding occurs progressively away from the nest cup as the chicks become mobile. Mobile chicks gather in crèches until they fledge and can accompany adults to feeding and roosting areas (Heydorn and Williams 1993). Terns returning to provision offspring are often victims of kleptoparasitism by other terns, but also by Hartlaub's gulls (Gaglio and Sherley 2014). However, the impact of kleptoparasitism on the terns has not been explored. In this study, we investigate the direct costs of kleptoparasitism by comparing the frequency of kleptoparasitic attempts, and the amount of food stolen between a single-species tern colony, and a mixed-species colony where terns breed in association with Hartlaub's gulls. We explore whether patterns of intraspecific kleptoparasitism vary between these colonies, to better understand whether any differences are potentially driven by the presence of gulls. We then investigate the relative costs of intra versus interspecific kleptoparasitism within a mixed colony, specifically considering the factors affecting when terns are vulnerable to kleptoparasitism. Finally, we investigate the indirect costs borne by terns to prevent loss of prey and whether this differs between inter and intraspecific kleptoparasitism.

METHODS

Study system

Data were collected on Robben Island (33° 48' S, 18° 22' E; 500 ha), South Africa, from February to May during 3 breeding seasons (2013, 2014, and 2015). Two colonies occurred in 2013 and 2014. The single-species (tern only) colony was situated on the north side of the island and consisted of ca 7500 pairs in 2013 and ca 8000 in 2014. The mixed colony was an association of greater crested terns (hereafter "terns") and Hartlaub's gulls (hereafter "gulls"), 2 km away at the southeast end of the island. The mixed colony totaled ca 2500 tern and 1000 gull breeding pairs in 2013 and ca 800 terns and 1300 gulls in 2014 (Department of Environmental Affairs [DEA], unpublished data). In 2015, all terns bred in a single mixed colony of ca 8000 pairs of terns and 1400 gulls surrounding the tern nests (DEA unpublished data) and comparison between colonies was not possible. The single-species and mixed colonies were similar in terms of substratum, vegetation and nesting density (ca 7.0 ± 2.5 nests m^{-2}; Gaglio et al. 2015). Being only 2 km apart, the 2 colonies also experienced similar environmental conditions (e.g. access to food resources, influence of wind, tide, and temperature). Despite these similarities, the colonies differed in size and we do not possess data on feeding site preferences between colonies. To account for the potential effect of such factors, the study should have been performed across multiple islands home to both single and mixed colonies, but this was not feasible. Nevertheless, we considered that comparison between the single and mixed-species colony on Robben Island was appropriate, acknowledging the above constraint.

Throughout the study period, breeding activity at the colonies were monitored daily, with the number of breeding pairs of terns and gulls recorded from the moment the first birds arrived on site. The development of the mixed-species colony followed the same steps in each year, with terns settling first. Terns occupied an area for several days before laying eggs (Gaglio et al. 2015). Once the first terns laid eggs (17–23 February in 2013 and 22–28 February in 2014 and 2015), other pairs were observed courting and copulating. During this period, gulls were present, but did not lay eggs until 2–4 days later, when the first nests were recorded surrounding the incubating terns.

Measuring rates of kleptoparasitism on nestling and mobile chicks

Feeding and kleptoparasitism rates of tern nestlings still confined to their nest cup were assessed from 800 h of video recordings (40% in 2013, 32% in 2014, and 26% in 2015). Filming took place from February to March in 2013, 2014, and 2015 at all colonies, using video cameras (Sony DCR-SX22E) affixed to tripods and powered via 2 deep-cycle 12 V batteries and an AC/DC power inverter. The camera system was placed 20–50 m from the colony edge and focused on 6–8 nests; the camera system was moved daily to record a different area of the colony with non-overlapping nests and a total of 229 nests were monitored during 35 days of video-recording. As chicks became mobile, video-recording was not possible; feeding frequencies and rates of kleptoparasitism were gathered from a hide, using focal observations on individual chicks (distance 10–30 m) banded with metal and engraved color rings as part of routine ringing operations (carried out for the DEA). Each chick was followed for at least 2 consecutive feeds. Data for mobile young were collected at the mixed-colony only. Only mobile chicks were ringed, so analyses comparing nestling and mobile chick data could potentially include individual chicks recorded both within the nest and when mobile. However, the probability that individuals were sampled at both chick stages was low due to the large number of chicks monitored (229 nestlings monitored out of a total of ca 26 700 nestlings at both colonies and 149 mobile chicks monitored out of a total of ca 11 200 mobile chicks [1250 banded] at the mixed colony). Hence, age classes were compared directly in the same analysis within the mixed colony. Breeding by greater crested terns is highly synchronous within the same colony (Crawford et al. 2005), and most chicks were already out of their nest-cup when visual observations of mobile chicks took place (25 days of observations), so there was little temporal overlap in data collected for nestlings and mobile chicks.

A kleptoparasitism attempt was defined as a movement by an individual bird toward a tern holding a prey item (either an adult or chick), and aiming to seize the item, or the aerial pursuit of an adult tern carrying prey (following Finney et al. 2001). No aerial chases were observed on terns not carrying prey and we did not observe chicks stealing food from one another. Intraspecific kleptoparasitism typically occurred on the ground between neighbors at the nest, usually when chicks were handling prey items, which often fell to the ground. These attempts were differentiated from attacks that did not target prey. For example, attacks over territory were observed largely by incubating terns, which use their beaks to chase away intruders and defend their nest. By comparison, interspecific kleptoparasitism by gulls occurred in the air as well as on the ground, and adults with prey were targeted as they approached their nest or while transferring prey to chicks. We also recorded the number of feeding passes per food item by adults attempting to deliver prey. A feeding pass occurred when an adult approached its chick with a food item at a distance of ≤1 m, but then flew away. Finally, for a subset of successful food deliveries, irrespective of whether there was a kleptoparasitism attempt, we recorded "delivery + handling time" as the time elapsed (in seconds) from when a tern landed near the nest (≤1 m) with a prey item in its bill until the prey was swallowed by its chick.

Video recordings were analyzed using VLC media player (VideoLAN project). Fate of prey and kleptoparasitism events were documented as follows: 1) delivered (when the prey was successfully delivered to and eaten by a chick); 2) tern kleptoparasitism (intraspecific, when the prey was stolen by another tern); 3) gull kleptoparasitism (interspecific, when the prey was stolen by a gull); 4) focal adult consumed the prey (typically, but not always, when the prey was swallowed by an adult undergoing a kleptoparasitic attack); 5) prey given to another tern (courtship or display); and 6) prey lost or stolen outside the observer's view (when the provisioning adult, invariably under attack, was forced to fly away from the nest and returned without its prey; in these cases the outcome of the kleptoparasitic attack was unknown, but the feeding attempt failed). Generally, adults that lost their prey came back to the nest and interacted with their partner and/or chick, before departing on a new foraging trip or switching with the partner. In the event, the adult was not observed returning to the nest (22%), the prey was considered lost after 10 min, as this duration corresponds to a short foraging trip for greater crested terns (McLeay et al. 2010).

Prey items returned to chicks were categorized as "silver" or "other" prey. Silver prey included fish such as anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, redeye round-herring *Etrumeus whiteheadi*, Atlantic saury *Scomberesox saurus*, and other less common silver-colored fish. Other prey included "non-silver" fish (e.g. long-snout pipefish *Syngnathus temminckii*), and invertebrate prey (e.g. insects, crustaceans, squid; Gaglio et al. 2017). Prey size was estimated relative to the adult tern's bill length (ca 60 mm), and categorized as "small" (≤90 mm: prey ≤1.5 times adult culmen length) and "large" (>90 mm: prey >1.5 times culmen length).

Statistical analyses

Fewer data were available on prey type and size per feeding attempt at the single-species colony than at the mixed one. Chi-squared goodness-of-fit tests were used to determine whether prey sizes and types provisioned at the 2 colonies were comparable. The impact of a kleptoparasitic attack on prey handling time was compared using a 2-sample *t*-test with data $\log_{10}$ transformed to fulfil assumptions of normality.

To further investigate the outcome and consequences of kleptoparasitism, generalized linear mixed models (GLMMs) were performed using the package lme4 (Bates and Maechler 2009), allowing for the inclusion of both fixed and random terms. ID code (nestling or mobile chick identity) nested within year, was used to fit random intercepts in all models to account for repeated measures. We used a hypothetico-deductive approach and created maximal models from which terms were sequentially dropped in order of significance and retained in the model only when log-likelihood ratio tests indicated that their removal significantly reduced the model's explanatory power. The residuals for each model were checked for over-dispersion and visually for homogeneity of variance.

The impact of gulls at mixed versus single-species breeding colonies

To investigate whether terns suffered increased kleptoparasitism pressure in the presence of gulls, we first used a GLMM (binomial error, logit link) to determine: (i) the overall likelihood of a kleptoparasitism attempt and (ii) whether food was stolen or lost following kleptoparasitism (tern and gull kleptoparasitism combined), at the 2 colonies. We then used a GLMM (binomial error, logit link) to determine the likelihood of (iii) a tern kleptoparasitism attempt only and (iv) whether food was stolen following the attempt at the 2 colonies. It was not possible to investigate colony differences in gull kleptoparasitism alone, because this was not observed at the single-species site. Explanatory variables were colony (single-species, mixed) and prey item size (small, large). We first undertook an analysis with the subset of feeding attempts where prey size was known, to determine whether prey size affected kleptoparasitism. Where this did not significantly improve model fit (likelihood-ratio test), we removed prey size and then analyzed the full dataset. Similar methods were used in all subsequent analyses where prey size was included as an explanatory variable.

Comparison of intraspecific and interspecific kleptoparasitism at the mixed colony

For the mixed colony only, we first used GLMMs (binomial error, logit link) to test whether terns or gulls more frequently kleptoparasitise food. For this, we investigated the proportion of parental feeding passes per nestling or mobile chick on which there were (i) kleptoparasitism attempts by either terns or gulls and (ii) the proportion of occasions when food was stolen or lost. Explanatory variables were kleptoparasitism type (tern, gull), chick stage (nestling, mobile) and their interaction. We then used GLMMs (binomial error, logit link) to further investigate the factors affecting the likelihood of (iii) a tern or (iv) gull kleptoparasitism attempt, and whether food was stolen or lost following (v) a tern or (vi) gull kleptoparasitism attempt at the mixed-species colony. Explanatory variables were prey size and chick stage.

Finally, to explore when gull versus tern kleptoparasitism attempts were successful, and therefore why they may target specific provisioning contexts, we used a GLMM (binomial error, logit link) to determine (vii) what factors affect the likelihood that a kleptoparasitism attempt is successful. Explanatory and random terms were the same as above, with the inclusion of the species attempting kleptoparasitism (gull, tern, both) and their interaction; species attempting kleptoparasitism was classified as follows per kleptoparasitism attempt for a single prey item: (i) gull only, (ii) tern only, (iii) both terns and gulls.

Parental costs due to kleptoparasitism avoidance tactics

We used GLMMs to investigate (i) whether kleptoparasitism attempts increased the number of feeding passes adults took to deliver food to their young at the 2 colonies. The number of feeding passes was fitted as the response variable in a GLMM (Poisson error, log link). Explanatory terms included prey size and chick stage, with the addition of whether or not there was a kleptoparasitism attempt (attempt, no attempt). We then additionally used a GLMM (Poisson error, log link) to investigate the effect of chick stage and food item size on number of delivery passes using data for the mixed-species colony (ii). Finally, we used GLMM's (binomial error, logit link) to investigate the factors affecting whether adults ate food themselves comparing between colonies (iii) and within the mixed colony (iv) with the same explanatory variables as the previous analyses of feeding attempts. All analyses were conducted using R (version 3.3.1, R Core Team 2016), with the significance level set at $P < 0.05$.

RESULTS

Prey size and type

Among all prey returned by terns to the mixed colony, 22% were scored as "large" (>1.5 times adult bill length) and 78% "small," with similar proportions when compared to the single-species colony (16% large and 84% small; $\chi^2 = 0.81$, df = 1, $P = 0.36$). "Silver" fish dominated prey at both colonies, but were marginally more abundant at the single-species colony (99%) than the mixed-species colony (92%; $\chi^2 = 4.18$, df = 1, $P = 0.04$).

Impact of gulls on terns at mixed versus single-species colonies

While adults were incubating, their partners occasionally returned with prey ($n = 13$ out of 1150 return visits identified during 400 h of video-recording during the incubation period). As the number of prey recorded during this period was very low, (and only one attempt of intraspecific kleptoparasitic was recorded), kleptoparasitism of incubating birds was unlikely to be an important cost and was excluded from analyses. During chick provisioning, terns suffered increased kleptoparasitism pressure in the presence of gulls (Supplementary Table S1); overall, the likelihood that a prey item returned to the colony was subject to a kleptoparasitic attempt was greater (44.1 ± 4.4 %, mean ± SE) at the mixed-species colony than at the single-species colony (7.5 ± 1.9%; $Z = -5.05$, $P \leq 0.001$, $n = 682$, Figure 1a, Supplementary Table S2). Similarly, significantly more prey returned were stolen or lost at the mixed- species colony (22.6 ± 2.7 %) than at the single-species colony (4.1 ± 1.1%; $Z = -6.13$, $P \leq 0.001$, $n = 682$, Figure 1b, Supplementary Table S2). When considering kleptoparasitism by terns, there was no significant difference between the 2 colonies in the likelihood of a kleptoparasitism attempt by a tern, but prey returned were more often lost or stolen as a result of tern kleptoparasitism at the mixed colony (mixed-species 8.0 ± 3.8%, single-species 3.1 ± 1.8%; attempts: $Z = -1.25$, $P = 0.21$, $n = 682$; stolen: $Z = -2.54$, $P = 0.010$; $n = 682$; Figure 1c and d; Supplementary Table S2).

Comparison of intraspecific and interspecific kleptoparasitism at the mixed colony

Gulls and terns were equally likely to attempt kleptoparasitism on nestlings, though there was a nonsignificant trend for gulls to attempt more kleptoparasitism than terns ($Z = -1.89$, $P = 0.058$, $n = 578$). However, significantly more prey were stolen from or lost by mobile chicks as a result of gull kleptoparasitism (6.5 ± 1.3 %) than tern kleptoparasitism attempts (1.1 ± 0.52%), (interaction: $Z = 2.59$, $P = 0.009$, $n = 578$; Figure 2, Supplementary Table S3).

Prey size was an important determinant of kleptoparasitism by terns at the mixed-species colony; they were more likely to attempt to steal larger prey (large = 36.5 ± 11.1%, small = 23.2 ± 7.9%) and more large prey were stolen or lost as a result of tern kleptoparasitism (large = 9.5 ± 3.8%, small = 3.1 ± 1.4%; attempted: $Z = -2.56$, $P = 0.010$, $n = 582$; stolen or lost: $Z = -3.03$, $P = 0.002$, $n = 582$; Figure 3a and c; Supplementary Table S3). Conversely, prey size did not affect the likelihood of gulls attempting kleptoparasitism (large = 41.7 ± 7.0%, small = 31.1 ± 4.8%; $Z = -1.84$, $P = 0.064$, $n = 582$), nor whether prey were stolen or lost following such attempts (large = 14.4 ± 4.0%, small = 8.5 ± 2.0%; $Z = -1.82$, $P = 0.068$, $n = 582$), but there was a nonsignificant trend in the same direction as for terns. However, there was a greater likelihood (2-fold for gulls [nestlings = 10.0 ± 2.6%, mobile chicks = 5.1 ± 1.6%], and 5-fold for terns [nestlings = 6.7 ± 1.5%, mobile chicks = 1.2 ± 0.6%]), that provisioning attempts to nestlings resulted in prey being stolen or lost, than provisioning attempts to mobile chicks, following either tern ($Z = 4.13$, $P < 0.001$, $n = 1158$) or gull kleptoparasitism ($Z = 2.49$, $P = 0.012$, $n = 1158$; Figure 3b and d; Supplementary Table S4).

Large prey items were nearly twice as likely to be stolen as small prey ($Z = -2.89$, $P = 0.003$, $n = 289$, Figure 3e, Supplementary Table S5), and kleptoparasitism attempts were more often successful when targeted at nestlings than mobile chicks. However, the success of gull attacks was independent of chick age, whereas the success of attempts by terns on their own, or in conjunction with gulls (both species) was lower on mobile chicks (Nestlings: gulls = 22.4 ± 7.9%, terns = 38.7 ± 7.9%, both = 55.8 ± 12.2%; Mobile chicks: gulls = 21.0 ± 7.8%, terns = 5.1 ± 3.7%, both = 6.3 ± 4.6%; $Z = 2.44$, $P = 0.014$, $n = 468$; Figure 3f, Supplementary Table S5).

Parental costs due to kleptoparasitism avoidance tactics

Adults performed more feeding passes per prey item returned to a chick at the mixed-species (1.8 ± 0.14) than at the single-species colony (1.5 ± 0.13; $Z = -2.10$, $P = 0.035$, $n = 682$; Figure 4a, Supplementary Table S6) and when under a kleptoparasitic attack (attack: 2.1 ± 0.19, no attack: 1.2 ± 0.10; $Z = -7.18$, $P < 0.001$, $n = 682$; Figure 4b, Supplementary Table S6). Investigation of feeding passes at the mixed colony only revealed a similar pattern with more feeding passes when adults were under attack (attack: 2.4 ± 0.11, no attack: 1.2 ± 0.06; $Z = 14.9$, $P < 0.001$, $n = 582$; Figure 4b, Supplementary Table S6), and also showed that more feeding passes were made when provisioning nestlings versus mobile chicks ($Z = 3.15$, $P = 0.001$, $n = 582$; Supplementary Table S6). Typically, adults fed their chicks on the first attempt when not under attack but needed 2 or more passes when there was a kleptoparasitism attempt.

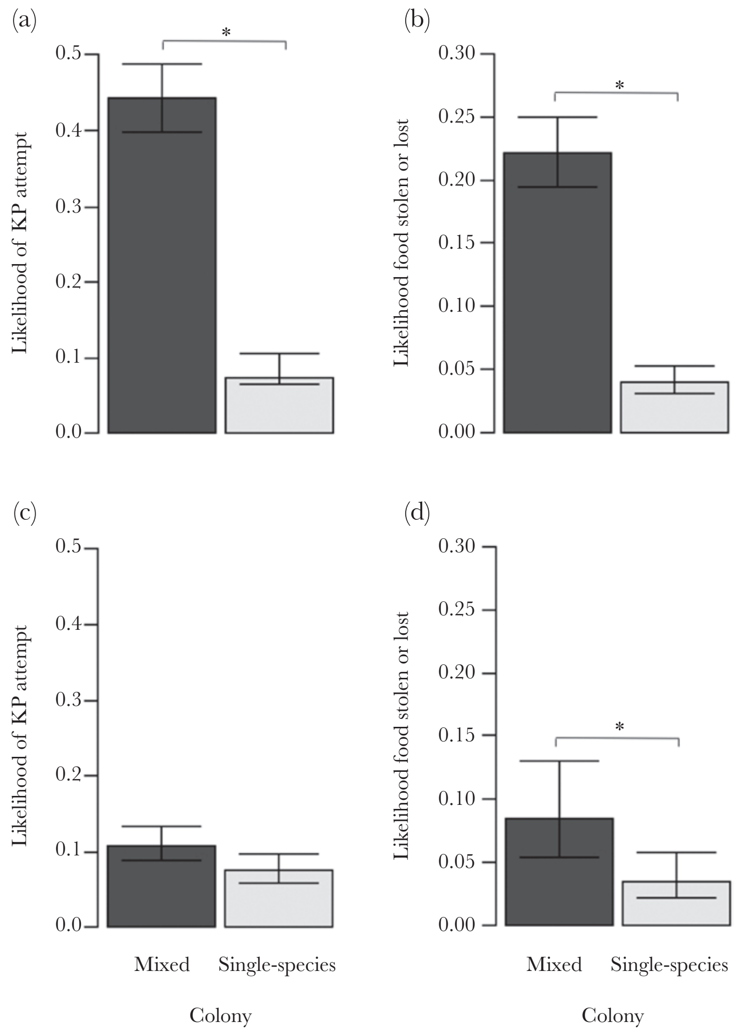

Figure 1

Overall likelihood (a) that a kleptoparasitism attempt was made on greater crested terns returning prey to chicks, (b) that a returned prey item was lost or stolen, (c) that a kleptoparasitism attempt was made by terns only, and (d) that a returned prey item was lost or stolen as a result of kleptoparasitism by a tern only, comparison between mixed- and single-species colony. Predicted means from models ± 1 SE are shown for all panels.

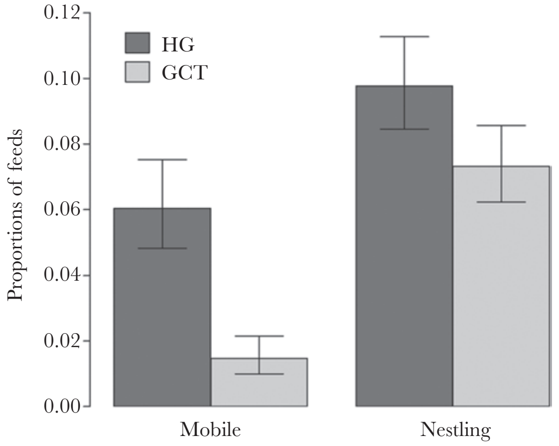

Figure 2

Overall proportion of parental feeds by greater crested terns that were stolen or lost resulting from attempted kleptoparasitic attacks by terns or Hartlaub's gulls. HG = Hartlaub's gull; GCT = greater crested tern. Predicted means from models ± 1 SE are shown.

Adult terns were approximately 3 times more likely to swallow prey when provisioning chicks (n = 560) at the mixed-species colony (14.2 ± 4.5 %) than the single-species colony (5.9 ± 2.1 %; $Z = 2.14$, $P = 0.031$, $n = 560$; Figure 4c, Supplementary Table S7). Adults were also more likely to swallow prey when attacked than when not under attack, both when considering data from the 2 colonies combined together (for colony comparison) (attack: 15.1 ± 4.9 %, no attack: 5.2 ± 1.6%, $P = 0.001$; Supplementary Table S7) and at only the mixed-species colony (for chick age and kleptoparasitic species comparison) in order to investigate the effect of chick age (attack: 3.3 ± 1.70%, no attack: 1.2 ± 0.7%, $Z = 2.6$, $P = 0.007$, $n = 560$; Figure 4d, Supplementary Table S7). Finally, data from both colonies combined show that handling time for successfully delivered prey without any interference was significantly shorter compared to when adults were subject to a kleptoparasitic attack (2-sample t-test: $t = -9.16$, df = 20, $P < 0.001$; Figure 5).

DISCUSSION

This study compares patterns of kleptoparasitism in a single-species breeding colony of greater crested terns and in a mixed-species colony of terns and Hartlaub's gulls, and indicates that breeding in association with gulls carries an extra cost for provisioning terns. Monitoring 2 colonies makes it impossible to entirely exclude the possibility that colony differences do not result from the presence versus absence of gulls. Nevertheless, acknowledging this practical constraint, our findings suggest that the association between gulls and terns conceivably increased the rate of kleptoparasitism and the amount of food that terns lost to parasitism fourfold compared

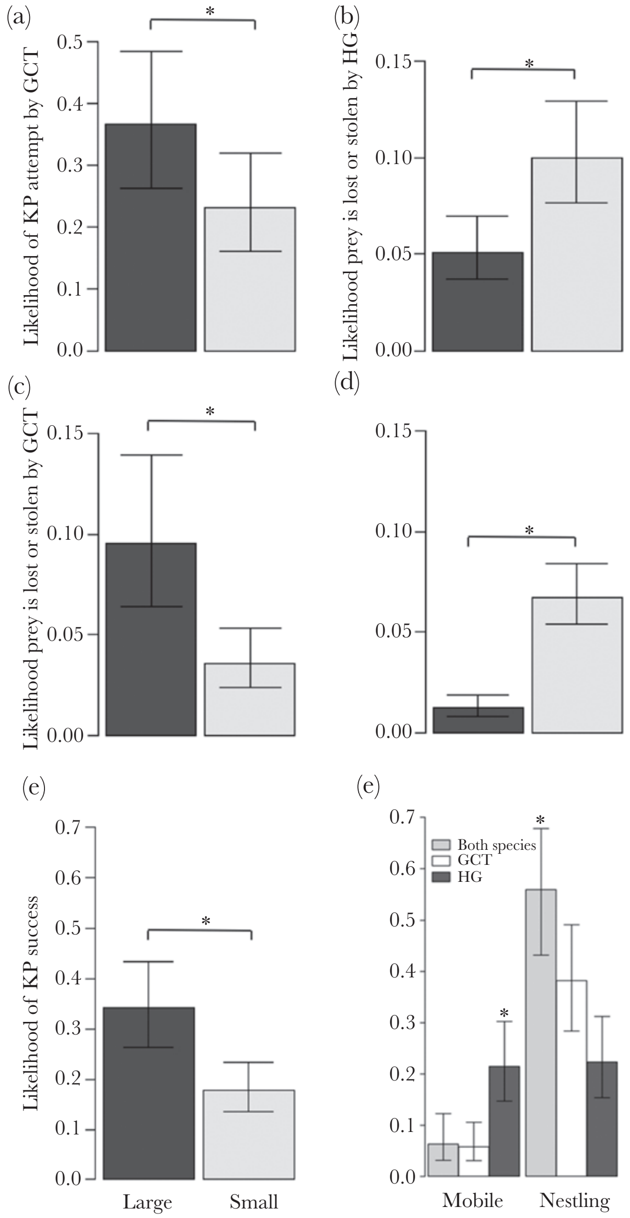

Figure 3

(a) The likelihood that greater crested terns attempted to kleptoparasitise prey from terns according to prey size. (b) The likelihood that prey were stolen or lost following a gull kleptoparasitism attempt according to chick stage. The likelihood that a prey item was successfully stolen during a kleptoparasitic attack by a tern, (c) according to prey size and (d) chick stage. (e) The likelihood that a prey item was successfully stolen during a kleptoparasitic attack according to prey size. (f) The likelihood of successful kleptoparasitism by species (GCT = greater crested tern; HG = Hartlaub's gull; or both) when an attack was performed, according to chick stage. Predicted means from models ± 1 SE are shown for all panels.

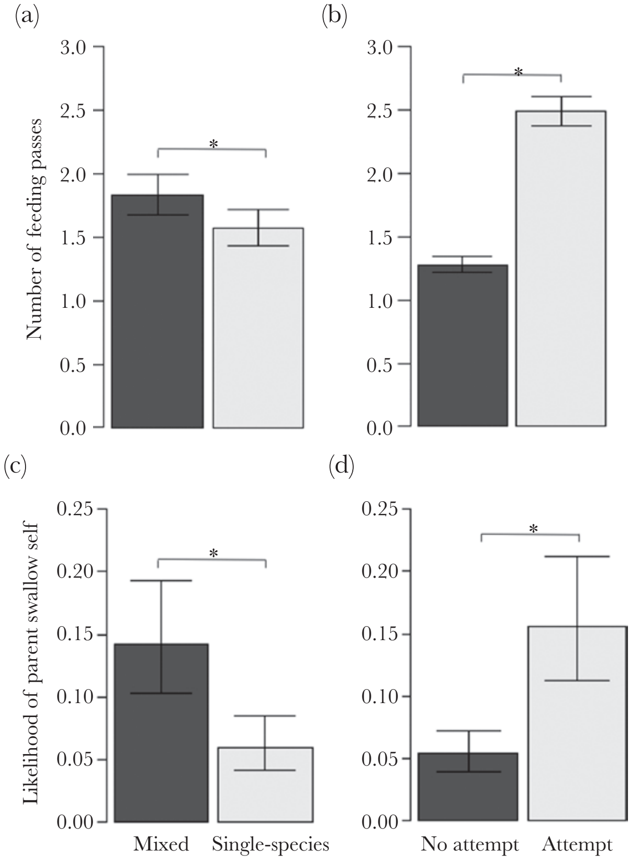

Figure 4

Overall number of feeding passes performed by adult greater crested terns (a) at the single-species and mixed colonies and (b) when a kleptoparasitism attempt was observed (Attempt) or not (No Attempt). Likelihood that adults swallowed a prey item returned to the nest (c) at the mixed or single-species colony, and (d) when a kleptoparasitic attempt occurred (Attempt) or not (No Attempt) for data from mixed colony only. Predicted means from models ± 1 SE are shown for all panels.

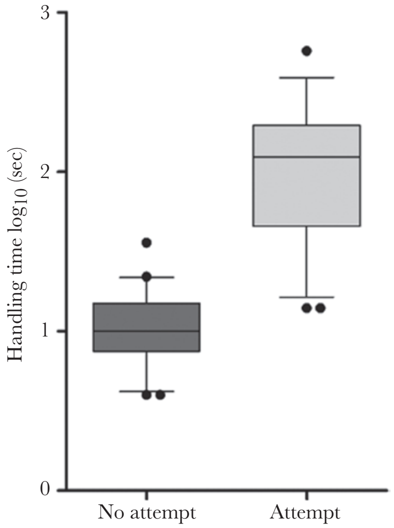

Figure 5

Comparison of time taken to deliver a prey item (handling time, $\log_{10}$ seconds; box-plot whiskers 10th and 90th percentile) when no kleptoparasitism was observed (No attempt) and when at least one kleptoparasitic attempt was performed by terns and/or gulls (Attempt).

to the single-species colony. This increase could not be accounted for by the small difference in intraspecific kleptoparasitism rates between the 2 colonies. Nor does this seem to result from inherent differences between the colonies, which were only 2 km apart; the sizes of prey delivered at each colony were similar, as were nest densities. Marginally more silver fish were delivered to the single species colony, but this prey type is favored and relatively large, which may be predicted to increase kleptoparasitism at the single species colony contrary to the observed results. The presence of gulls also increased the time—and likely energy expenditure—required to deliver prey to chicks, and further reduced chick provisioning rates when parents resorted to swallowing prey themselves to avoid parasitism. Adult terns feeding small nestlings bring approximately 36 g of anchovies to the nest each day, but only ca 58% of this food is delivered successfully (Gaglio 2017). Results from this study showed that approximately 1.7 $g \cdot d^{-1}$ (8.3%) of food is lost due to gull kleptoparasitism. The presence of gulls also extended the period when chicks were at risk from kleptoparasitism, because gulls were better able to steal food from mobile chicks than terns were. At this stage, parents deliver approximately 47 $g \cdot d^{-1}$ of anchovies to the colony (Gaglio 2017), of which about 6.7% (3.1 $g \cdot d^{-1}$) is stolen by gulls. These estimates are conservative, because gulls tend to steal larger prey. As a result, our findings indicate that terns suffer both direct and indirect costs of gull kleptoparasitism in a mixed-species colony that reduce chick provisioning rates, potentially impacting reproductive success. Consequently, breeding assemblages could reflect overall parasitic, and not mutualistic relationships, shifting towards parasitism when food theft is common and the costs of associating with other species outweigh the benefits.

Breeding stage proved to be an important determinant of chick susceptibility to kleptoparasitism, suggesting a function for precocial chick behavior in kleptoparasitism avoidance. Mobile chicks that had left the nest to join crèches suffered less kleptoparasitism than nestling chicks, mainly as a result of reduced intraspecific kleptoparasitism, probably because terns were less successful when they targeted mobile chicks. Nestlings may be particularly vulnerable to other terns because they are restricted to the nest cup in close proximity to neighboring adults. Their predictable location may also allow kleptoparasitic individuals to accurately predict where the prey will be returned, increasing their probability of success (Stienen 2006; personal observation). However, the high rate of prey loss by nestlings to both terns and gulls results in part because inexperienced adults may attempt to deliver prey that are too large for their nestlings, which struggle to swallow such large prey items. This increases handling time and consequentially the time available for kleptoparasitism (*sensu* García et al. 2014). The movement of mobile chicks away from other nesting adults, combined with the improved ability of mobile chicks to receive and swallow prey (reduction in delivery + handling time), likely explains the lower success of kleptoparasitism during this stage. Precocial behavior by chicks has been proposed to be an anti-kleptoparasitism tactic in sandwich terns breeding in mixed-species colonies (Stienen and Brenninkmeijer 1999), and the same strategy seemingly is employed by greater crested terns.

The size of prey returned to the colony affected kleptoparasitism risk differentially between gulls and other terns. Both species were more successful when trying to steal larger prey, but only terns targeted larger prey more often. Similar increases in kleptoparasitism on larger food items have been observed in other studies (Steele and Hockey 1995; Ratcliffe et al. 1997 García et al. 2010). Selection for large prey items by terns may be driven by the fact that large prey items are more conspicuous and easier to steal, especially due to the inability of nestlings to handle them. The fact that gulls did not target larger prey items more often, despite being more successful when they did so, could result from gulls adopting an opportunistic kleptoparasitic strategy. Furthermore, small prey may offer insufficient benefits to counter competition costs for terns, but not gulls (Morand-Ferron et al. 2006; Stienen 2006; García et al. 2010).

Provisioning terns likely suffer indirect costs from kleptoparasitism through energy invested in evading food theft attempts (Hulsman 1984; Stienen and Brenninkmeijer 1999; Stienen et al. 2001). Adults typically required one attempt to deliver prey to their nestlings, but when pursued by other terns or gulls, adults flew off and made subsequent delivery attempts, or swallowed prey themselves. The increased delivery passes (32%) and longer handling times (85%) to deliver prey to nestlings when under a kleptoparasitic attack illustrate how terns expend considerable time and energy avoiding kleptoparasitism. Furthermore, adults increase the proportion of prey swallowed (particularly at the mixed-species colony) in response to kleptoparasitism. Although swallowing prey themselves redeems some of the adult's investment in provisioning attempts, offspring provisioning rate decreases and adults still pay a cost for the time and energy expended in the round trip to capture and return with prey. Nevertheless, these behavioral tactics likely mitigate the overall impact of kleptoparasitism. In addition to evasive behaviors during kleptoparasitic attacks, individuals may reduce kleptoparasitism costs by adjusting provisioning, by, for example, providing prey less vulnerable to kleptoparasitism (Finney et al. 2001), or modifying prey choice (García et al. 2008). Recently, there has been extensive consideration of how breeders adjust provisioning in response to predation pressure (Zanette et al. 2011) and future work exploring adjustments in response to kleptoparasitism could further illustrate the counter tactics employed by breeders and their associated indirect costs. Such trait-mediated indirect effects may have significant impacts at the population level (Werner and Peacor 2003), emphasizing the need to understand the broader behavioral impact of kleptoparasitism.

Terns often breed in association with gulls because gulls are more aggressive and effective at deterring predators, thereby providing protection to terns (Fuchs 1977; Veen 1977; Urban et al. 1986; Stienen 2006). At Robben Island, Hartlaub's gull may help to repel predators such as kelp gulls *Larus dominicanus*, which steal tern eggs or chicks, thereby compensating for kleptoparasitism costs when such nest predation risk is high. However, Hartlaub's gulls choose to associate with tern colonies, since gulls occupy sites only once terns start breeding, as also observed in other gull-tern associations (Stienen and Brenninkmeijer 1999; Stienen et al. 2001; García et al. 2010). Hartlaub's gulls generally target different prey from terns (Ryan 1987) and therefore may benefit by exploiting terns when the payoffs from self-foraging decline (Brockmann and Barnard 1979; Ens et al. 1990; Flower et al. 2013). Associating with gulls may entail greater costs when the ratio of kleptoparasitic individuals to hosts increases (Wood et al. 2015). Consistent with this prediction, data in Supplementary Table S1 suggest that Hartlaub's gull may steal a larger proportion of tern prey when relative tern numbers decline, though this pattern is unclear and is confounded by between year effects. Nevertheless, such changes in the costs of associating with gulls could potentially switch the relationship from being mutualistic to parasitic, as described in other systems (e.g. Groom 1992; Baigrie et al. 2014). Increasing nest failure, or nest abandonment by terns under such circumstances might aggravate per capita kleptoparasitism on remaining breeders, potentially threatening colony persistence

(Oro et al. 1996; St. Clair et al. 2001; Blackburn et al. 2009, Wood et al. 2015), with profound consequences at the population level. However, this appears to be an unlikely threat to greater crested terns on Robben Island at present, as the species' breeding numbers have increased over the last few decades in this region (Crawford 2009).

Further studies that explore components of fitness (e.g. fledging success, survival and chick growth rates) with or without kleptoparasitism are needed to better determine the mutualistic or parasitic nature of mixed-species associations (Finney et al. 2001). In addition, it is important to monitor food availability and the ratio of gulls to terns breeding together and to assess how kleptoparasitism varies in response to changing environmental conditions (especially in an exploited environment such as the Benguela ecosystem). Ideally, more long-term data on variation in kleptoparasitism and nest predation rates are required to explore the costs and benefits from associating with other species and effects on breeding behaviour and population viability.

To conclude, greater crested terns breeding in association with Hartlaub's gulls they most likely suffer increased kleptoparasitism risk compared with when they only breed with conspecifics. This association correlated with a larger proportion of prey stolen, lost, or swallowed by the adult, resulting in adult terns spending more time and energy avoiding attack by gulls. These impacts likely reduce the amount of food delivered to chicks and increased energetic costs of prey provisioning, with potential negative effects on tern reproductive success. Our findings highlight the importance of assessing the indirect costs incurred by individuals that alter their behavior in response to interactions with other species. Additionally, our study indicates a potential role for intraspecific kleptoparasitism in the evolution of precocial chick behavior. It is not clear whether the costs of kleptoparasitism exceed the anti-predator benefits derived from associating with gulls, but the phenology of the mixed-species colonies (where gulls begin nesting after terns) suggest that the association of gulls with terns may represent parasitism rather than mutualism. Further studies are needed to assess variation in the costs and benefits of associating with other species and under what conditions kleptoparasitism may threaten population persistence.

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