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

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## ABSTRACT

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 impact 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 (Broinstein 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 favourable 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 behaviour 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 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

64  productivity (Stienen et al. 2006). Interspecific kleptoparasitism may also diminish feeding rates due
65  to a greater time spent airborne in order to evade kleptoparasites (Le Corre 1997; Stienen et al.
66  2001; Blackburn et al. 2009). Direct comparison of kleptoparasitism rates between breeding colonies
67  of puffins *Fratercula arctica*, with or without gulls, illustrated that chick feeding rates were higher in
68  gull-free colonies (Finney et al. 2001). To better understand the costs imposed by kleptoparasitism
69  (e.g. increased provisioning costs for adults), further comparisons are needed of colonies that differ
70  only in the presence of a kleptoparasitic species. For these studies, key factors to investigate include
71  the total amount of food stolen and the costs of attempting to feed offspring under the threat of
72  kleptoparasitism. In addition, detailed information on what is stolen and when, is necessary to
73  determine which factors make birds vulnerable to robbery and therefore more likely to be the
74  targets of kleptoparasitic attacks. Specifically, direct comparison of inter- versus intraspecific
75  kleptoparasitism is crucial to determine the relative costs they impose, how they differentially affect
76  behaviour and whether they interact to affect the outcome of kleptoparasitism (Ens et al. 1990). For
77  example, where provisioning adults are vulnerable to intra and interspecific kleptoparasitism in
78  different contexts, this has the potential to drive different behaviours in single-species versus mixed
79  colonies. Such investigations would help to elucidate the dynamics underlying interactions within
80  mixed-species aggregations and shed light on the evolution of these relationships, particularly when
81  there are potential shifts between mutualism and parasitism.
82
83  In southern Africa, greater crested terns *Thalasseus bergii* often breed in mixed-colonies with
84  Hartlaub's gulls *Chroicocephalus hartlaubii* (Uys 1978). Greater crested terns generally lay one egg,
85  and for the first 2–4 days after hatching parents feed their chick in the nest cup. Thereafter, feeding
86  occurs progressively away from the nest cup as the chicks become mobile. Mobile chicks gather in
87  crèches until they fledge and can accompany adults to feeding and roosting areas (Heydorn and
88  Williams 1993). Terns returning to provision offspring are often victims of kleptoparasitism by other
89  terns, but also by Hartlaub's gulls (Gaglio and Sherley 2014). However, the impact of
90  kleptoparasitism on the terns has not been explored. In this study, we investigate the direct costs of
91  kleptoparasitism by comparing the frequency of kleptoparasitic attempts, and the amount of food
92  stolen between a single-species tern colony, and a mixed-species colony where terns breed in
93  association with Hartlaub's gulls. We explore whether patterns of intraspecific kleptoparasitism vary
94  between these colonies, to better understand whether any differences are potentially driven by the
95  presence of gulls. We then investigate the relative costs of intra- versus interspecific
96  kleptoparasitism within a mixed colony, specifically considering the factors affecting when terns are
97  vulnerable to kleptoparasitism. Finally, we investigate the indirect costs borne by terns to prevent
98  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 three 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 7,500 pairs in 2013 and ca 8,000 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 south-east end of the island. The mixed colony totalled ca 2,500 tern and 1,000 gull breeding pairs in 2013 and ca 800 terns and 1,300 gulls in 2014 (Department of Environmental Affairs [DEA] unpublished data). In 2015, all terns bred in a single mixed colony of ca 8,000 pairs of terns and 1,400 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 $7.0 \pm 2.5$ nests m$^{-2}$; Gaglio et al. 2015). Being only 2 km apart, the two 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 hours 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 two deep-cycle 12V batteries and an AC/DC power

133 inverter. The camera system was placed 20–50 m from the colony edge and focussed on 6–8 nests;

134 the camera system was moved daily to record a different area of the colony with non-overlapping

135 nests and a total of 229 nests were monitored during 35 days of video-recording. As chicks became

136 mobile, video-recording was not possible; feeding frequencies and rates of kleptoparasitism were

137 gathered from a hide, using focal observations on individual chicks (distance 10–30 m) banded with

138 metal and engraved colour rings as part of routine ringing operations (carried out for the DEA). Each

139 chick was followed for at least two consecutive feeds. Data for mobile young were collected at the

140 mixed-colony only. Only mobile chicks were ringed, so analyses comparing nestling and mobile chick

141 data could potentially include individual chicks recorded both within the nest and when mobile.

142 However, the probability that individuals were sampled at both chick stages was low due to the large

143 number of chicks monitored (229 nestlings monitored out of a total of ca 26,700 nestlings at both

144 colonies and 149 mobile chicks monitored out of a total of ca 11,200 mobile chicks [1,250 banded] at

145 the mixed colony). Hence, age classes were compared directly in the same analysis within the mixed

146 colony. Breeding by greater crested terns is highly synchronous within the same colony (Crawford et

147 al. 2005), and most chicks were already out of their nest-cup when visual observations of mobile

148 chicks took place (25 days of observations), so there was little temporal overlap in data collected for

149 nestlings and mobile chicks.

150

151 A kleptoparasitism attempt was defined as a movement by an individual bird toward a tern holding a

152 prey item (either an adult or chick), and aiming to seize the item, or the aerial pursuit of an adult

153 tern carrying prey (following Finney et al. 2001). No aerial chases were observed on terns not

154 carrying prey and we did not observe chicks stealing food from one another. Intraspecific

155 kleptoparasitism typically occurred on the ground between neighbours at the nest, usually when

156 chicks were handling prey items, which often fell to the ground. These attempts were differentiated

157 from attacks that did not target prey. For example, attacks over territory were observed largely by

158 incubating terns, which use their beaks to chase away intruders and defend their nest. By

159 comparison, interspecific kleptoparasitism by gulls occurred in the air as well as on the ground, and

160 adults with prey were targeted as they approached their nest or while transferring prey to chicks.

161 We also recorded the number of feeding passes per food item by adults attempting to deliver prey.

162 A feeding pass occurred when an adult approached its chick with a food item at a distance of ≤ 1 m,

163 but then flew away. Finally, for a subset of successful food deliveries, irrespective of whether there

164 was a kleptoparasitism attempt, we recorded 'delivery + handling time' as the time elapsed (in

165 seconds) from when a tern landed near the nest (≤ 1 m) with a prey item in its bill until the prey was

166 swallowed by its chick.

167

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

181

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

189

190 **Statistical analyses**

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

196

197 To further investigate the outcome and consequences of kleptoparasitism, generalised linear mixed
198 models (GLMMs) were performed using the package lme4 (Bates and Maechler 2009), allowing for
199 the inclusion of both fixed and random terms. ID code (nestling or mobile chick identity) nested
200 within year, was used to fit random intercepts in all models to account for repeated measures. We
201 used a hypothetico-deductive approach and created maximal models from which terms were
202 sequentially dropped in order of significance and retained in the model only when log-likelihood

203  ratio tests indicated that their removal significantly reduced the model's explanatory power. The
204  residuals for each model were checked for over-dispersion and visually for homogeneity of variance.
205

206  *The impact of gulls at mixed versus single-species breeding colonies*
207  To investigate whether terns suffered increased kleptoparasitism pressure in the presence of gulls,
208  we first used a GLMM (binomial error, logit link) to determine: (i) the overall likelihood of a
209  kleptoparasitism attempt and (ii) whether food was stolen or lost following kleptoparasitism (tern
210  and gull kleptoparasitism combined), at the two colonies. We then used a GLMM (binomial error,
211  logit link) to determine the likelihood of (iii) a tern kleptoparasitism attempt only and (iv) whether
212  food was stolen following the attempt at the two colonies. It was not possible to investigate colony
213  differences in gull kleptoparasitism alone, because this was not observed at the single-species site.
214  Explanatory variables were colony (single-species, mixed) and prey item size (small, large). We first
215  undertook an analysis with the subset of feeding attempts where prey size was known, to determine
216  whether prey size affected kleptoparasitism. Where this did not significantly improve model fit
217  (likelihood-ratio test), we removed prey size and then analysed the full dataset. Similar methods
218  were used in all subsequent analyses where prey size was included as an explanatory variable.
219

220  *Comparison of intraspecific and interspecific kleptoparasitism at the mixed colony*
221  For the mixed colony only, we first used GLMMs (binomial error, logit link) to test whether terns or
222  gulls more frequently kleptoparasitise food. For this, we investigated the proportion of parental
223  feeding passes per nestling or mobile chick on which there were (i) kleptoparasitism attempts by
224  either terns or gulls and (ii) the proportion of occasions when food was stolen or lost. Explanatory
225  variables were kleptoparasitism type (tern, gull), chick stage (nestling, mobile) and their interaction.
226  We then used GLMMs (binomial error, logit link) to further investigate the factors affecting the
227  likelihood of (iii) a tern or (iv) gull kleptoparasitism attempt, and whether food was stolen or lost
228  following (v) a tern or (vi) gull kleptoparasitism attempt at the mixed-species colony. Explanatory
229  variables were prey size and chick stage.
230

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

238

*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 two 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 $P < 0.05$.

251

## 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; $\chi^2 = 0.81$, d.f. = 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%; $\chi^2 = 4.18$, d.f. = 1, p = 0.04).

259

### 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 hours 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 (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 = < 0.001, n = 682, Figure 1a, Table S2). Similarly, significantly more prey returned were stolen or lost at the mixed- (22.6 ± 2.7 %) than at the single-species colony (4.1 ± 1.1 %; $Z = -6.13$, p = < 0.001, n = 682, Figure 1b, Table S2). When considering kleptoparasitism by terns, there was no significant difference

272  between the two colonies in the likelihood of a kleptoparasitism attempt by a tern, but prey
273  returned were more often lost or stolen as a result of tern kleptoparasitism at the mixed colony
274  (mixed 8.0 ± 3.8 %, single-species 3.1 ± 1.8 %; attempts: $Z$ = −1.25, $p$ = 0.21, n = 682; stolen:  $Z$ =
275  −2.54, $P$ = 0.010; n = 682; Figure 1c,d; Table S2).

276

**Comparison of intraspecific and interspecific kleptoparasitism at the mixed colony**

278  Gulls and terns were equally likely to attempt kleptoparasitism on nestlings, though there was a non-
279  significant trend for gulls to attempt more kleptoparasitism than terns ($Z$ = −1.89, p = 0.058, n = 578).
280  However, significantly more prey were stolen from or lost by mobile chicks as a result of gull
281  kleptoparasitism (6.5 ± 1.3 %) than tern kleptoparasitism attempts (1.1 ± 0.52 %), (interaction: $Z$ =
282  2.59, p = 0.009, n = 578; Figure 2, Table S3).

283

284  Prey size was an important determinant of kleptoparasitism by terns at the mixed-species colony;
285  they were more likely to attempt to steal larger prey (large = 36.5 ± 11.1 %, small = 23.2 ± 7.9 %) and
286  more large prey were stolen or lost as a result of tern kleptoparasitism (large = 9.5 ± 3.8 %, small =
287  3.1 ± 1.4 %; attempted: $Z$ = −2.56, p = 0.010, n = 582; stolen or lost: $Z$ = −3.03, p = 0.002, n = 582;
288  Figure 3a,c; Table S3). Conversely, prey size did not affect the likelihood of gulls attempting
289  kleptoparasitism (large = 41.7 ± 7.0 %, small = 31.1 ± 4.8 %; $Z$ = −1.84, p = 0.064, n = 582), nor
290  whether prey were stolen or lost following such attempts (large = 14.4 ± 4.0 %, small = 8.5 ± 2.0 %; $Z$
291  = -1.82, p = 0.068, n = 582), but there was a non-significant trend in the same direction as for terns.
292  However, there was a greater likelihood (two-fold for gulls [nestlings = 10.0 ± 2.6 %, mobile chicks =
293  5.1 ± 1.6 %], and five-fold for terns [nestlings = 6.7 ± 1.5 %, mobile chicks = 1.2 ± 0.6 %]), that
294  provisioning attempts to nestlings resulted in prey being stolen or lost, than provisioning attempts to
295  mobile chicks, following either tern ($Z$ = 4.13, p < 0.001, n = 1,158) or gull kleptoparasitism ($Z$ = 2.49,
296  p = 0.012, n = 1,158; Figure 3b,d; Table S4) .

297

298  Large prey items were nearly twice as likely to be stolen as small prey ($Z$ = −2.89, p = 0.003, n = 289,
299  Figure 3e, Table S5), and kleptoparasitism attempts were more often successful when targeted at
300  nestlings than mobile chicks. However, the success of gull attacks was independent of chick age,
301  while the success of attempts by terns on their own, or in conjunction with gulls (both species) was
302  lower on mobile chicks (Nestlings: gulls = 22.4 ± 7.9 %, terns = 38.7 ± 7.9 %, both = 55.8 ± 12.2 %;
303  Mobile chicks: gulls = 21.0 ± 7.8 %, terns = 5.1 ± 3.7 %, both = 6.3 ± 4.6 %; $Z$ = 2.44, p = 0.014, n =
304  468; Figure 3f, Table S5).

305

**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, 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, Table S–6). 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, 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; Table S6). Typically, adults fed their chicks on the first attempt when not under attack but needed two or more passes when there was a kleptoparasitism attempt.

Adult terns were approximately three times more likely to swallow prey when provisioning chicks (n = 560) at the mixed- (14.2 ± 4.5 %) than the single-species colony (5.9 ± 2.1 %; Z = 2.14, p = 0.031, n = 560; Figure 4c, Table S7). Adults were also more likely to swallow prey when attacked than when not under attack, both when considering data from the two colonies combined together (for colony comparison) (attack: 15.1 ± 4.9 %, no attack: 5.2 ± 1.6 %, p = 0.001; 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, 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 (two-sample t-test: t = -9.16 d.f. = 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 two 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 to the single-species colony. This increase could not be accounted for by the small difference in intraspecific kleptoparasitism rates between the two 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

340    type is favoured and relatively large, which may be predicted to increase kleptoparasitism at the

341    single species colony contrary to the observed results. The presence of gulls also increased the time

342    – and likely energy expenditure – required to deliver prey to chicks, and further reduced chick

343    provisioning rates when parents resorted to swallowing prey themselves to avoid parasitism. Adult

344    terns feeding small nestlings bring approximately 36 g of anchovies to the nest each day, but only ca

345    58% of this food is delivered successfully (Gaglio 2017). Results from this study showed that

346    approximately 1.7 $g \cdot d^{-1}$ (8.3%) of food is lost due to gull kleptoparasitism. The presence of gulls also

347    extended the period when chicks were at risk from kleptoparasitism, because gulls were better able

348    to steal food from mobile chicks than terns were. At this stage, parents deliver approximately 47 $g \cdot d^{-}$

349    $^1$ of anchovies to the colony (Gaglio 2017), of which about 6.7% (3.1 $g \cdot d^{-1}$) is stolen by gulls. These

350    estimates are conservative, because gulls tend to steal larger prey. As a result, our findings indicate

351    that terns suffer both direct and indirect costs of gull kleptoparasitism in a mixed-species colony that

352    reduce chick provisioning rates, potentially impacting reproductive success. Consequently, breeding

353    assemblages could reflect overall parasitic, and not mutualistic relationships, shifting towards

354    parasitism when food theft is common and the costs of associating with other species outweigh the

355    benefits.

356

357    Breeding stage proved to be an important determinant of chick susceptibility to kleptoparasitism,

358    suggesting a function for precocial chick behaviour in kleptoparasitism avoidance. Mobile chicks that

359    had left the nest to join crèches suffered less kleptoparasitism than nestling chicks, mainly as a result

360    of reduced intraspecific kleptoparasitism, likely because terns were less successful when they

361    targeted mobile chicks. Nestlings may be particularly vulnerable to other terns because they are

362    restricted to the nest cup in close proximity to neighboring adults. Their predictable location may

363    also allow kleptoparasitic individuals to accurately predict where the prey will be returned,

364    increasing their probability of success (Stienen 2006; pers. obs.). However, the high rate of prey loss

365    by nestlings to both terns and gulls results in part because inexperienced adults may attempt to

366    deliver prey that are too large for their nestlings, which struggle to swallow such large prey items.

367    This increases handling time and consequentially the time available for kleptoparasitism (*sensu*

368    García et al. 2014). The movement of mobile chicks away from other nesting adults, combined with

369    the improved ability of mobile chicks to receive and swallow prey (reduction in delivery + handling

370    time), likely explains the lower success of kleptoparasitism during this stage. Precocial behaviour by

371    chicks has been proposed to be an anti-kleptoparasitism tactic in sandwich terns breeding in mixed-

372    species colonies (Stienen and Brenninkmeijer 1999), and the same strategy seemingly is employed

373    by greater crested terns.

374

375 The size of prey returned to the colony affected kleptoparasitism risk differentially between gulls

376 and other terns. Both species were more successful when trying to steal larger prey, but only terns

377 targeted larger prey more often. Similar increases in kleptoparasitism on larger food items have

378 been observed in other studies (Steele and Hockey 1995; Ratcliffe et al. 1997 García et al. 2010).

379 Selection for large prey items by terns may be driven by the fact that large prey items are more

380 conspicuous and easier to steal, especially due to the inability of nestlings to handle them. The fact

381 that gulls did not target larger prey items more often, despite being more successful when they did

382 so, could result from gulls adopting an opportunistic kleptoparasitic strategy. Furthermore, small

383 prey may offer insufficient benefits to counter competition costs for terns, but not gulls (Morand-

384 Ferron et al. 2006; Stienen 2006; García et al. 2010).

385

386 Provisioning terns likely suffer indirect costs from kleptoparasitism through energy invested in

387 evading food theft attempts (Hulsman 1984; Stienen and Brenninkmeijer 1999; Stienen et al. 2001).

388 Adults typically required one attempt to deliver prey to their nestlings, but when pursued by other

389 terns or gulls, adults flew off and made subsequent delivery attempts, or swallowed prey

390 themselves. The increased delivery passes (32%) and longer handling times (85%) to deliver prey to

391 nestlings when under a kleptoparasitic attack illustrate how terns expend considerable time and

392 energy avoiding kleptoparasitism. Furthermore, adults increase the proportion of prey swallowed

393 (particularly at the mixed-species colony) in response to kleptoparasitism. Although swallowing prey

394 themselves redeems some of the adult's investment in provisioning attempts, offspring provisioning

395 rate decreases and adults still pay a cost for the time and energy expended in the round trip to

396 capture and return with prey. Nevertheless, these behavioural tactics likely mitigate the overall

397 impact of kleptoparasitism. In addition to evasive behaviours during kleptoparasitic attacks,

398 individuals may reduce kleptoparasitism costs by adjusting provisioning, by, for example, providing

399 prey less vulnerable to kleptoparasitism (Finney et al. 2001), or modifying prey choice (García et al.

400 2008). Recently, there has been extensive consideration of how breeders adjust provisioning in

401 response to predation pressure (Zanette et al. 2011) and future work exploring adjustments in

402 response to kleptoparasitism could further illustrate the counter tactics employed by breeders and

403 their associated indirect costs. Such trait-mediated indirect effects may have significant impacts at

404 the population level (Werner and Peacor 2003), emphasising the need to understand the broader

405 behavioural impact of kleptoparasitism.

406

407 Terns often breed in association with gulls because gulls are more aggressive and effective at

408 deterring predators, thereby providing protection to terns (Fuchs 1977; Veen 1977; Urban et al.

409 1986; Stienen 2006). At Robben Island, Hartlaub's gull may help to repel predators such as kelp gulls

410     *Larus dominicanus*, which steal tern eggs or chicks, thereby compensating for kleptoparasitism costs

411     when such nest predation risk is high. However, Hartlaub's gulls choose to associate with tern

412     colonies, since gulls occupy sites only once terns start breeding, as also observed in other gull-tern

413     associations (Stienen and Brenninkmeijer 1999; Stienen et al. 2001; García et al. 2010). Hartlaub's

414     gulls generally target different prey from terns (Ryan 1987) and therefore may benefit by exploiting

415     terns when the payoffs from self-foraging decline (Brockmann and Barnard 1979; Ens et al. 1990;

416     Flower *et al.* 2013). Associating with gulls may entail greater costs when the ratio of kleptoparasitic

417     individuals to hosts increases (Wood et al. 2015). Consistent with this prediction, data in Table S1 suggest that

418     Hartlaub's gull may steal a larger proportion of tern prey when relative tern numbers decline, though this

419     pattern is unclear and is confounded by between year effects. Nevertheless, such changes in the costs of

420     associating with gulls could potentially switch the relationship from being mutualistic to parasitic, as described

421     in other systems (e.g. Groom 1992; Baigrie et al. 2014). Increasing nest failure, or nest abandonment by terns

422     under such circumstances might aggravate per capita kleptoparasitism on remaining breeders, potentially

423     threatening colony persistence (Oro et al. 1996; St. Clair et al. 2001; Blackburn et al.2009, Wood et al. 2015),

424     with profound consequences at the population level. However, this appears to be an unlikely threat to greater

425     crested terns on Robben Island at present, as the species' breeding numbers have increased over the last few

426     decades in this region (Crawford 2009).

427

428     Further studies that explore components of fitness (e.g. fledging success, survival and chick growth

429     rates) with or without kleptoparasitism are needed to better determine the mutualistic or parasitic

430     nature of mixed-species associations (Finney et al. 2001). In addition, it is important to monitor food

431     availability and the ratio of gulls to terns breeding together, and to assess how kleptoparasitism

432     varies in response to changing environmental conditions (especially in an exploited environment

433     such as the Benguela ecosystem). Ideally, more long-term data on variation in kleptoparasitism and

434     nest predation rates are required to explore the costs and benefits from associating with other

435     species and effects on breeding behaviour and population viability.

436

437     To conclude, greater crested terns breeding in association with Hartlaub's gulls they most likely

438     suffer increased kleptoparasitism risk compared with when they only breed with conspecifics. This

439     association correlated with a larger proportion of prey stolen, lost or swallowed by the adult,

440     resulting in adult terns spending more time and energy avoiding attack by gulls. These impacts likely

441     reduce the amount of food delivered to chicks and increased energetic costs of prey provisioning,

442     with potential negative effects on tern reproductive success. Our findings highlight the importance

443     of assessing the indirect costs incurred by individuals that alter their behaviour in response to

444     interactions with other species. Additionally, our study indicates a potential role for intraspecific

445     kleptoparasitism in the evolution of precocial chick behaviour. 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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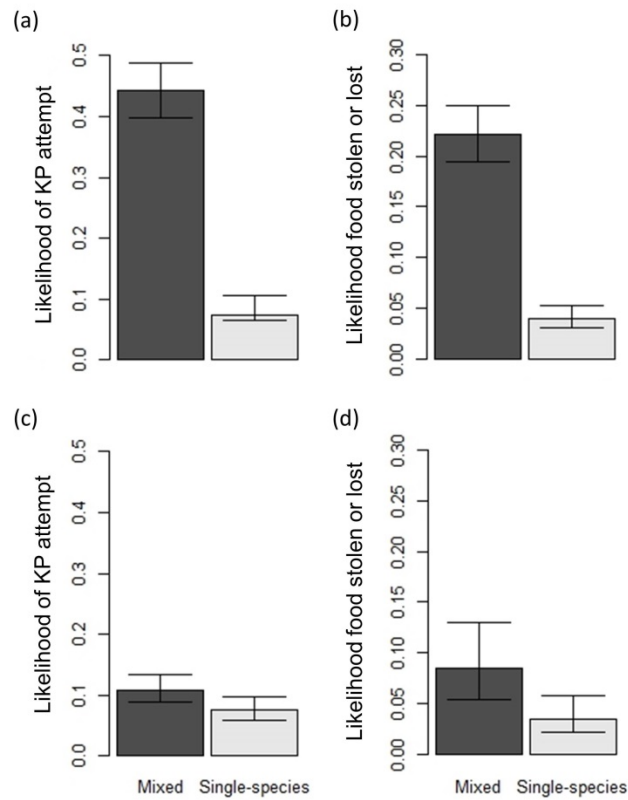
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567    Figure 1. Overall likelihood (a) that a kleptoparasitism attempt was made on greater crested terns returning

568    prey to chicks, (b) that a returned prey item was lost or stolen, (c) that a kleptoparasitism attempt was made

569    by terns only, and (d) that a returned prey item was lost or stolen as a result of kleptoparasitism by a tern only,

570    comparison between mixed and single-species colony. Predicted means from models ± 1 SE are shown for all
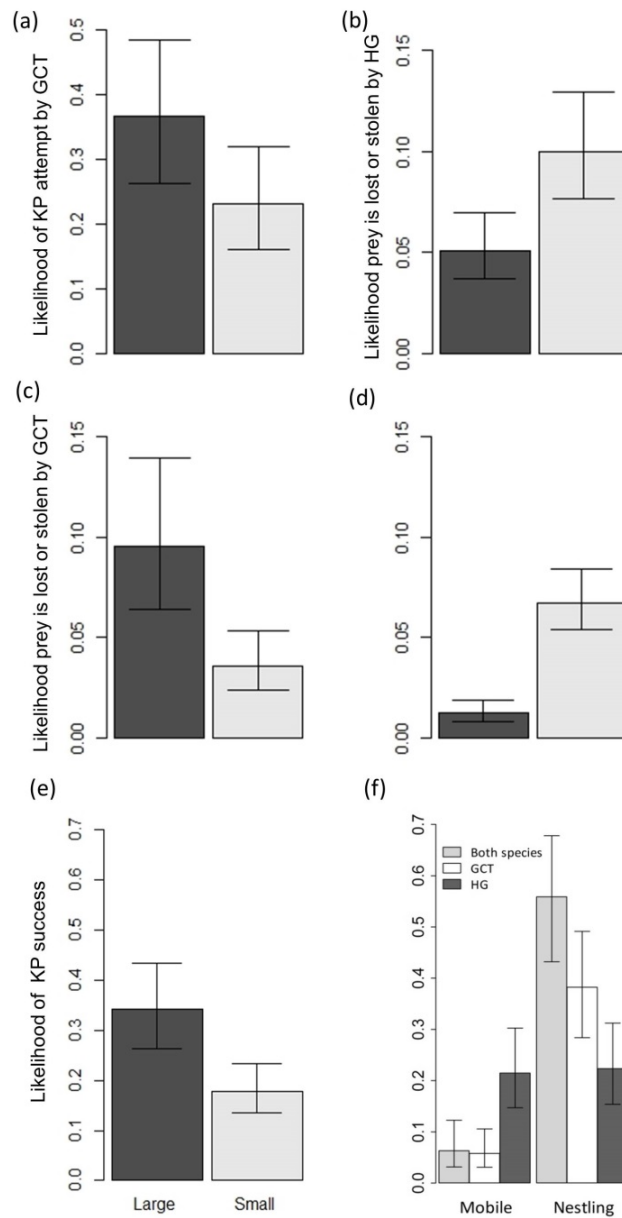
571    panels.

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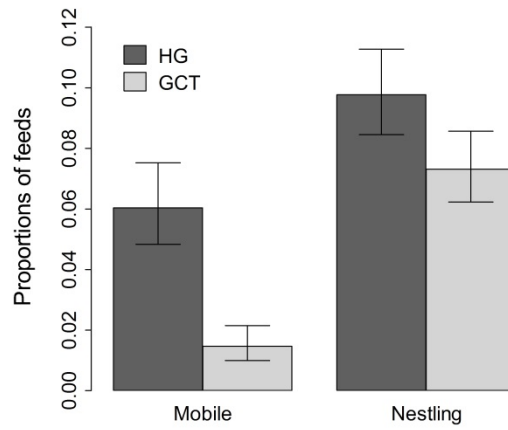
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575   Figure 2. Overall proportion of parental feeds by greater crested terns that were stolen or lost resulting from

576   attempted kleptoparasitic attacks by terns or Hartlaub's gulls. HG = Hartlaub's gull; GCT = greater crested tern.

577   Predicted means from models ± 1 SE are shown.

578

579

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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.
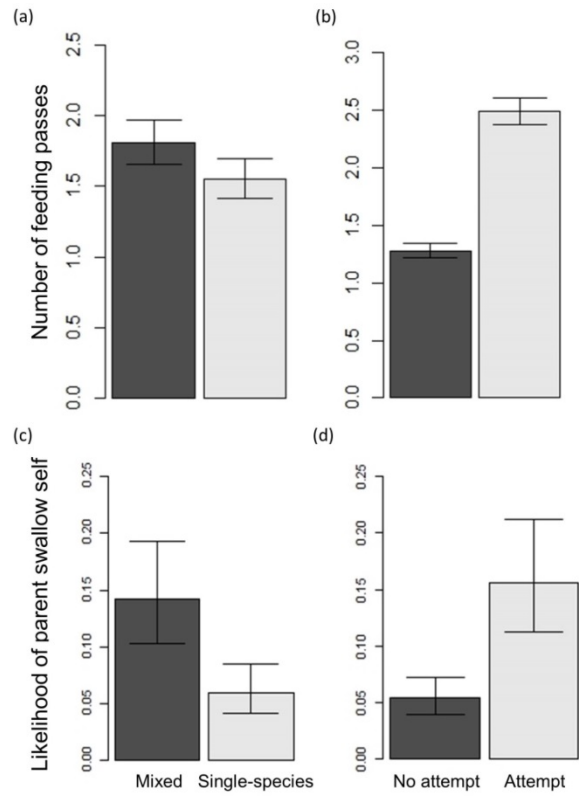
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593    Figure 4. Overall number of feeding passes performed by adult greater crested terns (a) at the single-species

594    and mixed colonies and (b) when a kleptoparasitism attempt was observed (Attempt) or not (No Attempt).

595    Likelihood that adults swallowed a prey item returned to the nest (c) at the mixed or single-species colony, and

596    (d) when a kleptoparasitic attempt occurred (Attempt) or not (No Attempt) for data from mixed colony only.

597    Predicted means from models ± 1 SE are shown for all panels.

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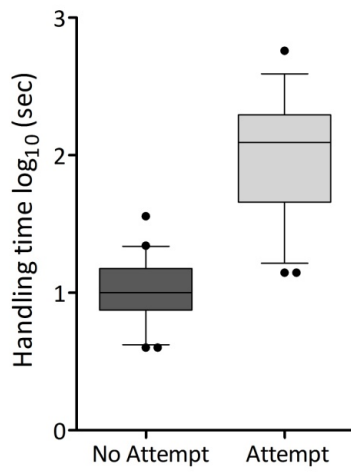
Figure 5. Comparison of time taken to deliver a prey item (handling time, $\log_{10}$ seconds; box-plot whiskers $10^{th}$ and $90^{th}$ percentile) when no kleptoparasitism was observed (No attempt) and when at least one kleptoparasitic attempt was performed by terns and/or gulls (Attempt).

605