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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.

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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 pu ns *Fratercula arctica*

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 di erentiated 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 com-

link) to determine (vii) what factors a ect 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 terms and gulls.

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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 e ect 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 a ecting 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 di erence 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 %)

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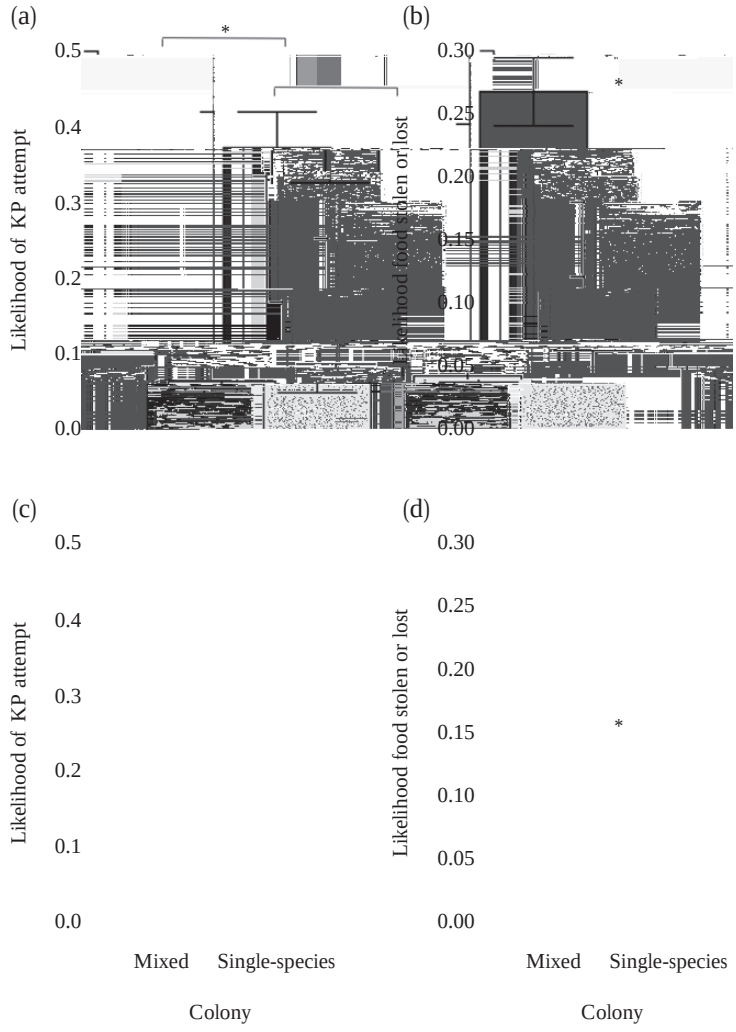

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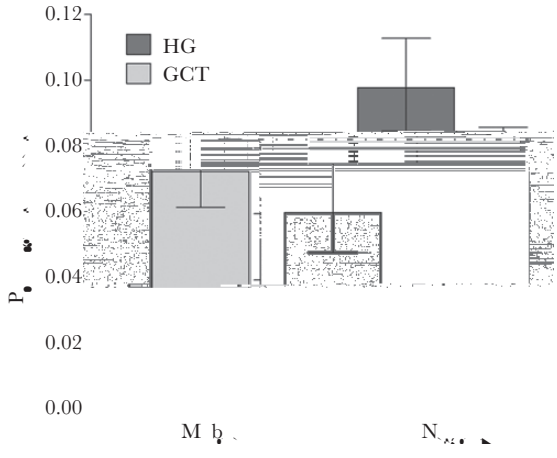
Overall likelihood (a) that a kleptoparasitism attempt was made on greater crested terns returning prey to chicks, (b) that a returned prey item was lost or stolen, (c) that a kleptoparasitism attempt was made by terns only, and (d) that a returned prey item was lost or stolen as a result of kleptoparasitism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



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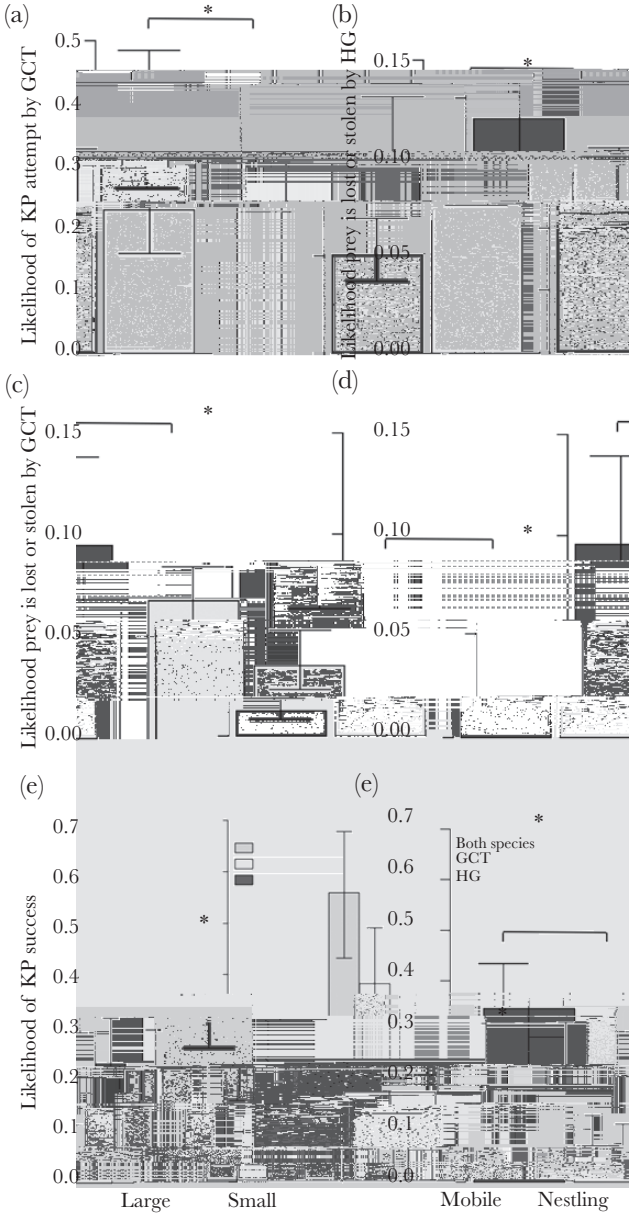
Overall proportion of parental feeds by greater crested terns that were stolen or lost resulting from attempted kleptoparasitic attacks by terns or Hartlaub's gulls. HG = Hartlaub's gull; GCT = greater crested tern. si0 -1.307 / a

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 e ect 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 di erences 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



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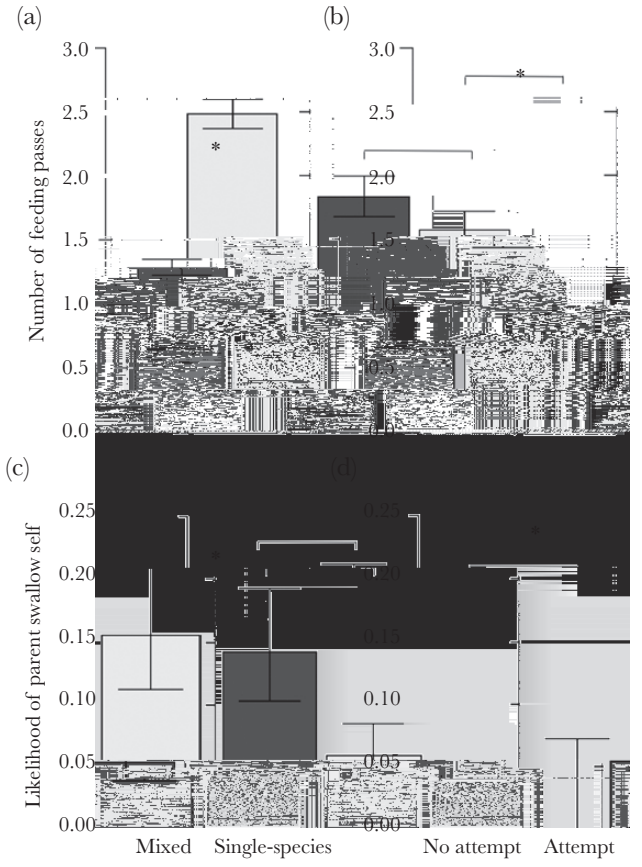
(a) The likelihood that greater crested terns attempted to kleptoparasitise prey from terns according to prey size. (b) The likelihood that prey were stolen or lost following a gull kleptoparasitism attempt according to chick stage. The likelihood that a prey item 8 Tw (ptTJ0 0 0fle)yen kleptoparasitic attempt aTJ(y ter) a-27 (ns ani ding to prey sizewhick stage. The iskerelihood t



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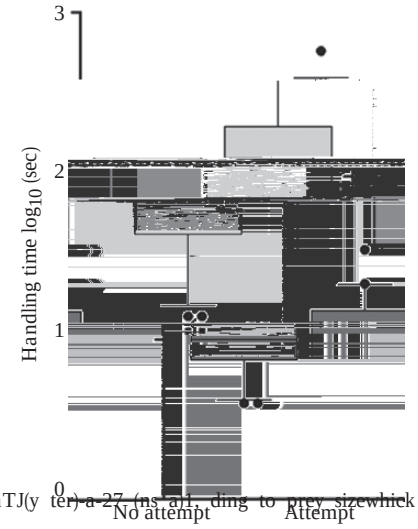
Overall number of feeding passes performed by adult greater crested terns (a) at the single-species and mixed colonies and (b) when a kleptoparasitism attempt was observed (Attempt) or not (No Attempt). Likelihood that adults swallowed a prey item returned to the nest (c) at the mixed or single-species 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.



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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 di erence in intraspecific kleptoparasitism rates between the 2 colonies. Nor does this seem to result from inherent di erences 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 su er 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 su ered 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 a ected kleptoparasitism risk di erentially 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 (
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(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 kleptoparasit-

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