ORIGINAL ARTICLE

Alloparental feeding in Adélie penguins: why is it uncommon?

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Abstract We investigated alloparental interactions and conditions which could facilitate or prevent the expression of alloparental behaviours in Adélie penguins (*Pygoscelis adeliae*), a long-lived seabird which nests in high-density colonies around Antarctica. Observation sessions were carried out during the crèche stage on 48 identified pairs and 50 identified chicks in a 217-nest subcolony. As the season progressed, young were fed less often by their own parents because these were increasingly absent from the breeding site and less responsive to their offspring's solicitations. As a consequence, young and particularly those with a low body mass, coming from a two-chick brood, opted for gradually soliciting more from other adults to obtain food, preferentially those nesting in their direct vicinity. Unsuccessful breeders represented a low and constant part of the adult population and were not specifically solicited by unrelated young. Despite the increasing chick demand, only 4.1% (3 out of 73) of alloparental solicitations resulted in feeding, which is negligible compared to parental feeding. To investigate factors that could trigger the appearance of alloparental care, we carried out comparisons with king (*Aptenodytes patagonicus*) and emperor penguins (*Aptenodytes forsteri*) which represent the closest species for which data on alloparental behaviour were available. Our results show different trends to those observed in these species and three factors may explain the low occurrence of alloparental behaviour in Adélie penguins: (1) the low and constant proportion of unsuccessful breeders, (2) the absence of chick selectivity towards unsuccessful breeders, and (3) the late period of chick accessibility for potential alloparents.

Keywords Alloparental care · Intergenerational conflict · Penguins

Introduction

Alloparental care (i.e. care of young by an unrelated adult) is inconsistent with life history theory: it is likely to incur fitness costs such as a decrease in adult survival (Rabenold 1990) or that of their offspring (Brown et al. 1995). An intergenerational conflict between unrelated young and adults is therefore predictable (Pierotti and Murphy 1987; Oro and Genovart 1999): young are expected to stimulate alloparental care while adults tend to restrain this behaviour (Brown 1998).

To explain this apparently paradoxical behaviour, several proximate facilitating factors can be proposed: (1) parental misrecognition (Brown et al. 1995), (2) high nest density (Saino et al. 1994) and proximity (Lecomte et al. 2006), (3) young accessibility, (4) young age and condition (Brown et al. 1995), and (5) breeding failure (Brown and Vleck 1998).

If alloparents can ultimately benefit from caring for unrelated young, alloparental care is likely to occur. In this context, several evolutionary hypotheses have been proposed: (1) kin selection when alloparental care is directed to closely related young, this can apply particularly in philopatric species (Riedman 1982), (2) reciprocal altruism when alloparents benefit from alloparental care for their

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offspring within one breeding season or over subsequent years (Pierotti 1982), and (3) acquisition of parental experience if parental care requires specific skills (Riedman 1982).

Alloparental behaviour has been described in many birds (Riedman 1982) and more specifically in long-lived birds (Arnold and Owens 1998) like seabirds (Birkhead and Nettleship 1984; Hebert 1988; Morris et al. 1991; Brown 1998). In penguins, alloparental care has been reported in three species: in little penguins (*Eudyptula minor*), 1.0–3.5% of chicks are fed by alloparents (Wienecke 1995); in emperor penguins (*Aptenodytes forsteri*), 7–15% of chicks are fed by alloparents (Jouventin et al. 1995); and in king penguins (*Aptenodytes patagonicus*), more than 65% of all chicks are fed by alloparents (Lecomte et al. 2006). These observations suggest that alloparental behaviour may exist in other species belonging to this order.

In penguins, the breeding period is divided into a guard stage and a crèche stage (Spurr 1975). Semi-altricial chicks are first constantly guarded at least by one parent while the other forages at sea to bring food back to its offspring. Alloparental care may occur during the guard stage in some species like emperor penguins where chicks are stolen from parents (Jouventin et al. 1995). In contrast, Adélie penguin (*Pygoscelis adeliae*) parents vigorously defend their nest during the guard stage and intruders are violently repelled. The only time when alloparents can have access to the chicks is when chicks are left unguarded during the subsequent crèche stage, when their demand for food requires both parents to forage simultaneously. During this period, adults return progressively less frequently to the subcolony until the end of the crèche stage when they permanently leave their breeding site. During the crèche stage, chicks get mobile and can walk away from their nest and consequently become accessible to potential alloparents. At that time, they have the option of waiting for irregular parent returns or seeking alloparental care and food from other adults.

All reported alloparental interactions in Adélie penguins were based on occasional observations (Crawford 1974; Spurr 1975). Nevertheless, proximate factors such as high density of colonies (suggesting close neighbour proximity), chick mobility and irregular parental returns during the crèche stage may favour alloparental care. In addition, ultimate factors mentioned above (kin selection, reciprocal altruism and acquisition of parental experience) may be supported by high natal philopatry (Ainley et al. 1995) and nest site fidelity (Williams 1995) in this long-lived species. Because of these features that may favour the occurrence of alloparental behaviour, we hypothesised that alloparental interactions should exist in Adélie penguins.

In this study, we investigated alloparental care and feeding in Adélie penguins and examined factors influencing the expression of this behaviour at the sub-colony scale and from the perspective of both the chick and the adult.

Methods

The study took place in Pétrel Island (66°40′S, 140°00′E), Pointe Géologie Archipelago, Adélie Land, Antarctica, during the austral summer 2007–2008. The island holds about 15,000 pairs of Adélie penguins. In a 217-pair sub-colony, 48 pairs were identified with a Nyanzol-D mark painted on the breast feathers during the courtship period.

The dimension of the subcolony, the number of nests and distances between nests were measured from an aerial photography taken vertically at the beginning of the season.

Breeding phenology for each pair was established by daily observations. A pair was considered as "unsuccessful" if parents lost their egg(s) during incubation or their chick(s) during the guard stage. At the end of the guard stage, all the chicks of identified adults were quickly sprinkled with paint (Raidex®) for recognition when they would be left unguarded for the first time. At this moment, they were weighed with a spring balance (Salter, ±20 g) and individually identified with coloured fish tags (Floy-Tag, Seattle, USA) subcutaneously anchored in the neck. Each fish tag had a unique colour code easily distinguishable from a distance. Chicks were weighed a second time when they reached their maximum weight at 43–45 days (Ainley and Schlatter 1972) and the fish tags were removed before fledging.

As soon as almost all the chicks were unguarded (mean date: 20 January 2008 ± 6.4 days, mean chick age: 28.1 ± 5.9 days), the subcolony was observed ad libitum, continuously with 8 × 20 binoculars from a blind overhanging the subcolony, about 20 m apart, during 3-h sessions every morning (0800–1100 hours) and every afternoon (1500–1800 hours) from 26 January to 8 February. First chicks fledged on February 10 so that our observations covered the major part of the crèche stage.

Before each session, photography of the subcolony was taken to evaluate demographic parameters: number of chicks, unknown adults, identified successful and unsuccessful breeders. Every behavioural interaction implicating at least one identified individual was noted. Three alloparental situations happened: "identified adult/identified chick", "identified adult/unknown chick" and "unknown adult/identified chick". We distinguished several interactions: (1) parental solicitation: when a chick begs for food to its own parent, (2) alloparental solicitation: when a chick begs for food to an unrelated adult, (3) parental feeding: when an adult regurgitates food to its own chick, and (4) alloparental feeding: when an adult regurgitates

food to an unrelated chick. Feeding comprised several regurgitations and was scored as complete when no interaction between the adult and the chick occurred for at least 5 min (Dee Boersma and Davis 1997). A solicitation was considered as successful if it resulted at least in one regurgitation. Alloparental interactions unrelated to solicitations or feeding were also noted.

Demographic and behavioural trends during the study period were assessed with Spearman Rank correlations. The number of individuals was calculated for each session whereas behavioural rates were calculated on a daily basis (morning + afternoon). Student's t test was used to compare means and χ^2 or Fisher's exact tests to compare frequencies. Results are expressed as mean $\pm$ SD. Statistical analyses were performed on SPSS 14.0. All tests were two tailed with significance level set at $\alpha = 0.05$.

Results

Subcolony features and demographic parameters

The studied subcolony was 153 m^2 and contained 217 nesting pairs, resulting in a density of 1.42 nest/m^2. Its longest length was 18 m and its longest width was 13 m.

At the beginning of the crèche stage, among the 48 identified pairs, 10 (20.8%) had 2 chicks, 30 (62.5%) had 1 chick and 8 (16.6%) were unsuccessful (5 pairs lost their eggs during incubation and 3 pairs lost their chicks during the guard stage). Along the crèche stage, the total number of identified adults decreased (Fig. 1a) but the ratio between unsuccessful and successful breeders present in the subcolony remained unchanged (18.9 $\pm$ 5.5%; Spearman correlation, $r = 0.93$, $P < 0.01$). Only one chick

Fig. 1 Changes in the number of successful and unsuccessful Adélie penguin (*Pygoscelis adeliae*) parents observed in the subcolony (**a**) and in the number of parental/alloparental solicitations (**b**) during the crèche stage
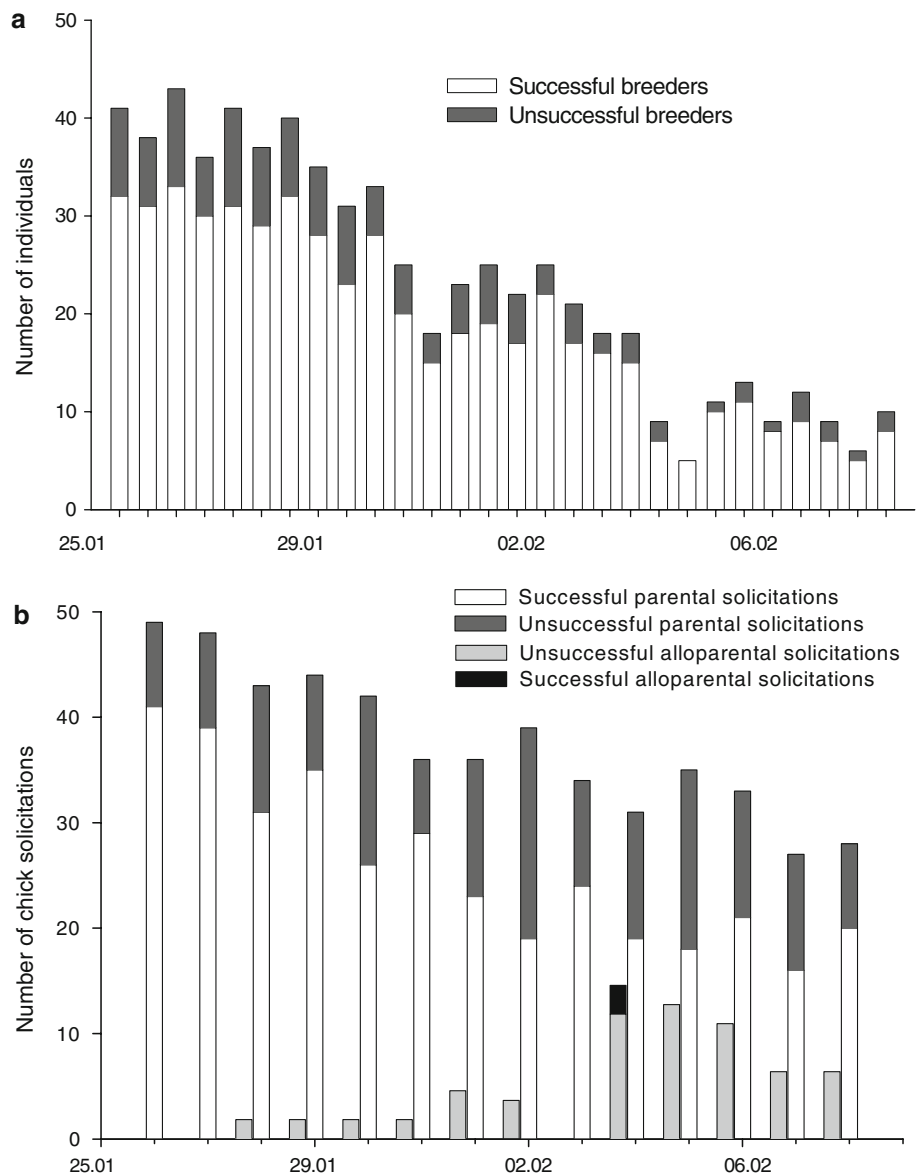
coming from a 2-chick brood died by skua predation and no pair became unsuccessful during the crèche stage.

The 50 identified chicks belonging to the 48 identified pairs represented 30.3% of the 165 chicks present in the subcolony.

Solicitations and feedings

During the crèche stage, parental solicitations and feedings decreased by half (Fig. 1b). As the number of successful parental solicitations decreased, the number of unsuccessful parental solicitations increased (Spearman correlation, $r = -0.52$, $P = 0.05$). As a result, the proportion of unsuccessful parental solicitations progressively increased (Spearman correlation, $r = 0.65$, $P = 0.01$; Fig. 1b).

At the same time, as parental solicitations decreased, alloparental solicitations became gradually more important (Spearman correlation, $r = -0.72$, $P < 0.01$; Fig. 1b). However, over the whole study period, only 3 out of the 73 alloparental solicitations (4.1%) resulted in feedings (Fig. 1b), accounting for 0.8% of total feedings. One chick was fed by an alloparent twice and the other chick only once. The resulting proportion of chicks fed by alloparents was 4% (2 out of 50).

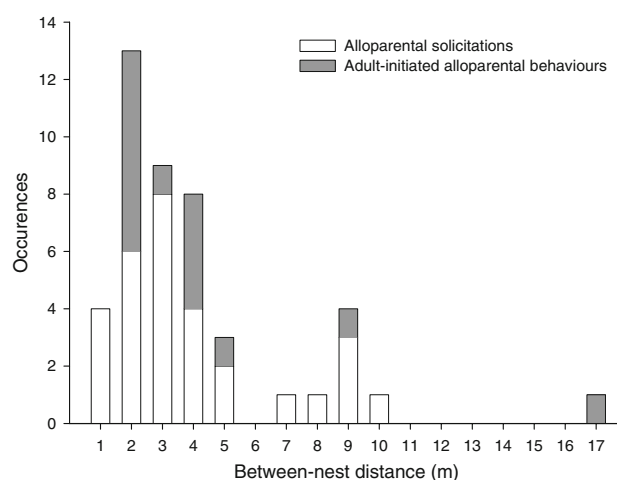### Young implicated in alloparental interactions

Sixty-four alloparental solicitations from identified chicks were observed; 46 (71.9%) implicated chicks coming from a two-chick brood. A significantly higher proportion of young coming from a two-chick brood (80.0%) solicited unrelated adults compared to single chicks (26.6%; Fischer exact test: $P = 0.007$). The three observed alloparental feedings occurred between unknown adults and two different identified chicks, each coming from a 2-chick brood. Only three cases of siblings competing while soliciting an unrelated adult were observed.

Young coming from a 2-chick brood had a significantly lower body mass than single chicks at the end of the guard stage ($1{,}579 \pm 156$ g vs. $2{,}639 \pm 141$ g, respectively; Student's t test, $t_{48} = 4.935$, $P < 0.001$) and at the end of the crèche stage ($3{,}525 \pm 116$ g vs. $4{,}120 \pm 99$ g, respectively; Student's t test, $t_{46} = 3.795$, $P < 0.001$).

Of the 30 alloparental solicitations observed between identified chicks and identified adults, 80% happened between individuals whose nests were less than 5 m apart (Fig. 2).

Adults implicated in alloparental interactions

Of the 39 alloparental solicitations, 15.4% observed between a chick and an identified adult were directed towards unsuccessful breeders, a proportion equivalent to

Fig. 2 Distribution of distances (m) between nests where identified chicks and identified adults implicated in alloparental interactions came from

the proportion of unsuccessful breeders in the subcolony (16.6%, $\chi^2 = 0.02$, $P = 0.88$).

Five types of adult-initiated alloparental behaviours were observed: (1) vocal displays ($n = 43$), (2) chick nibbling ($n = 21$), (3) chick pursuing ($n = 19$), (4) brooding attempts ($n = 16$), and (5) chick defending ($n = 6$). Among these adult-initiated alloparental behaviours, 15 occurred between identified chicks and identified adults. Thirteen (86.6%) happened between individuals whose nests were less than 5 m apart (Fig. 2).

Discussion

In Adélie penguins, as the crèche stage progressed, adult–young interactions partly shifted from the "parent–young" level to the "alloparent–young" level. These interactions resulted mainly from chick-initiated solicitations which were generally unsuccessful; allofeeding was highly uncommon and young clearly lost the intergenerational "arms race" (Brown et al. 1995).

Our results show different trends to those observed in the other penguin species in which alloparental care has been investigated. To explain such a discrepancy and investigate factors that could trigger the appearance of alloparental care in a long-lived species, a comparison of the situation between Adélie penguins and other penguin species seems worthwhile.

Subcolony features and demographic parameters

Our subcolony density (1.42 nest/m^2) was comparable to that of king penguins (1.6 incubating bird/m^2; Bauer 1967)

in Crozet Archipelago where alloparental feeding was described (Lecomte et al. 2006). Consequently, even if high density facilitates contacts between unrelated individuals, it cannot be considered as determinative for alloparental feedings.

Alloparental feeding was described as most common among unsuccessful breeders (Jouventin et al. 1995; Lecomte et al. 2006). In our study, the proportion of unsuccessful breeders (16.6%) was comparable to the proportion in emperor penguins (11–20%; Jouventin et al. 1995) but was very low compared to that of king penguins: Lecomte et al. (2006) counted 76% of unsuccessful breeders during the crèche stage. Moreover, in king penguins, parents that had lost their chick during the crèche stage allofed more after the death of their chick than before. Lecomte et al. (2006) report that 43% of pairs failed during this period. In Adélie penguins, most failures occur during the incubation period or during the guard stage (Davis and McCaffrey 1986; Clarke et al. 2002; this study) and very few pairs become unsuccessful during the crèche stage. Consequently, this low and constant proportion of unsuccessful breeders in the subcolony resulted in a low and constant probability for a chick to ask for food to an unsuccessful adult along the crèche stage.

Comparing the number of chicks per pair and chick body mass in our study with data available in the literature (Marchant and Higgins 1990; Culik 1994; Watanuki et al. 1992; Watanuki et al. 1994; Janes 1997; Ainley 2002), we can assume that the year when observations for alloparental behaviour were carried out was similar to a classic year in terms of reproductive success (0.96 chick per pair in this study vs. 0.97 ± 0.31 chick per pair in the literature) and chick body mass ($2,215 \pm 904$ g in this study vs. $2,458 \pm 236$ g in the literature; single chicks and chicks coming from two-chick broods, weighed at the same age or period). Therefore, it would be worthwhile conducting similar observations in years when breeding conditions differ and may modulate the frequency of occurrence of alloparental behaviours in Adélie penguins.

Young implication

The higher solicitation rate of young from two-chick broods towards unrelated adults cannot be due to sibling competition since siblings rarely solicited unrelated adults simultaneously. Chick condition is more likely the cause since young from two-chick broods presented a lower body mass which is known to increase begging (Iacovides and Evans 1998): Adélie chicks with a low body mass may present increased levels of baseline corticosterone (Walker et al. 2005) which facilitates begging towards adults (Kitaysky et al. 2000). This and the simultaneous decrease in parental feeding suggest that chick solicitations were driven by hunger and can, therefore, be considered as an honest signal from the chick to the adult.

Young actively solicited unrelated adults and their selectivity was oriented towards neighbours rather than unsuccessful breeders, which suggests that they waited near their nest and solicited any adult passing nearby.

Adult implication

As voice recognition is very effective in penguins (Spurr 1975; Davis and Mc Caffrey 1988; Jouventin and Aubin 2002), misrecognition is improbable and unrelated chicks are effectively recognized by adults. Nevertheless, as shown by adult-initiated alloparental interactions, adult Adélie penguins are interested in unrelated young. Since these alloparental behaviours were preferentially directed towards neighbour chicks, our findings are not opposed to reciprocal altruism and kin selection hypotheses, but data showing that offspring tend to breed near their parents in this species are still lacking.

Lecomte et al. (2006) report that allofeedings are more important at the beginning of the crèche stage in king penguins: adults seem to accept more easily feeding unrelated young chicks. As described for parental care (Varpe et al. 2004), alloparents may adjust their behaviour to the age of unrelated chicks as for emperor chicks who are adopted when they are 1–2 months, but not later, while they are still accessible (Jouventin et al. 1995, Fig. 3). Compared to king and emperor penguins, Adélie penguin
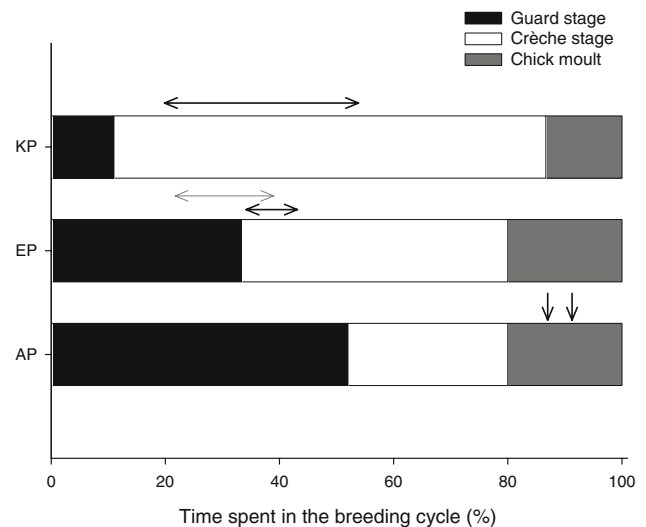
Fig. 3 Breeding phenology of king (*KP*) (*Aptenodytes patagonicus*), emperor (*EP*) (*Aptenodytes forsteri*), and Adélie (*AP*) penguins on a same time scale (breeding cycles were adapted according to data provided by Marchant and Higgins 1990). *Horizontal black arrows* indicate periods when allofeeding was described. *Horizontal grey arrow* corresponds to adoption period in emperor penguins. *Vertical arrows* indicate allofeeding occurence in our study

chicks are left unguarded and are accessible when they are older (Fig. 3), when they are probably less stimulating for unrelated adults. The stimulation that the chicks produce on the adult may also depend on the hormonal status of the adult. In emperor penguins, alloparental behaviour has been associated with persistent high levels of prolactin in failed breeders (Angelier et al. 2006). In contrast, at least in male Adélie penguins, prolactin levels were lower in unsuccessful parents than in parents still tending nests (Vleck et al. 2000). These low levels of prolactin might therefore partly explain the low occurrence of alloparental care in unsuccessful Adélie penguins.

To our knowledge, this article constitutes the first comprehensive study investigating alloparental feeding in Pygoscelids and provides the first data available in Pygoscelid species (Adélie, chinstrap *Pygoscelis antarctica* and gentoo penguins *Pygoscelis papua*). However, in the absence of data available in this genus, we were obliged to limit our comparison to king and emperor penguins. To improve our comparative approach, we invite other research teams to conduct similar studies and to publish their results even though alloparental behaviours are rare or absent in the studied species.

Zusammenfassung

Füttern durch Pflegeeltern bei Adeliepinguinen: Weshalb ist es selten?

Wir haben Pflegeeltern-Interaktionen und die Bedingungen, welche die Äußerung von Pflegeelternverhalten ermöglichen oder verhindern könnten, bei Adeliepinguinen (*Pygoscelis adeliae*) untersucht, einem langlebigen Seevogel, der in dichten Kolonien um die Antarktis herum brütet. Beobachtungen wurden während des „Kindergarten"-Stadiums an 48 identifizierten Paaren und 50 identifizierten Küken in einer Subkolonie mit 217 Nestern durchgeführt. Mit fortschreitender Brutsaison wurden die Jungvögel weniger häufig von ihren eigenen Eltern gefüttert, da diese zunehmend vom Nistplatz abwesend waren und weniger auf das Betteln ihrer Nachkommen reagierten. Folglich bettelten die Jungvögel, und besonders solche mit geringer Körpermasse, die aus einer Brut mit zwei Küken stammten, mehr und mehr andere Altvögel an, um Futter zu erhalten, vorzugsweise solche, die in unmittelbarer Nähe brüteten. Erfolglose Brüter stellten einen kleinen und beständigen Teil der Altvogelpopulation dar und wurden nicht ausdrücklich von unverwandten Jungvögeln angebettelt. Trotz des steigenden Bedarfs der Küken führten lediglich 4,1% (3 von 73) der Bettelversuche bei Pflegeeltern zur Fütterung, was verglichen mit dem Füttern durch die Eltern unbedeutend ist.

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