



Variation in Guiana dolphin parental care according to calf age class

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Abstract

An extended period of parental care is fundamental for survival of cetacean offspring. Although qualitative descriptions of parental care and mother-calf spatial relationships are available for several species, studies using a quantitative approach throughout development of offspring are scarce. Here, we analyzed how strategies of parental care occur during the ontogeny of the Guiana dolphin, *Sotalia guianensis*, in the Cananéia estuarine system, São Paulo, Brazil. We tested the hypothesis that both the strategy and frequency of parental care vary according to the development of the offspring and assessed whether such changes are associated with the life stage of the calves. The frequency of parental care did not decrease according to the age of the calves. However, parental care strategies directed at infants were more diversified than those directed at neonates and juveniles. Increasing maternal-calf separation can expose older calves to new and risky situations and may demand different strategies of care. We conclude that there is a shift in the strategy adopted by the *S. guianensis* mothers according to the requirements of each age class, with parental care being dispensed until calves become fully independent.

Keywords Animal behavior · Calves · Cananéia estuarine system · Mother-calf relationship · Ontogeny · *Sotalia guianensis*

Introduction

Parental care is a fundamental feature of life history of many animal taxa and can be defined as any behavior that increases survival of offspring (Trivers 1972). Considered a key innovation, the emergence of parental care is responsible for shaping the evolution of a wide range of behavioral, physiological,

morphological, and social traits in many vertebrate groups (Kleiman and Malcom 1981; Farmer 2000). In mammals, patterns of care can be highly variable, ranging from minimal care to prolonged supplying of nutrients and resources provided by parents and group members (Clutton-Brock 1991).

As many other mammals, cetaceans exhibit a general pattern in which mothers provide protection to offspring until they become independent (Mann and Smuts 1999; Whitehead and Mann 2000). However, the ocean poses a challenging environment which does not offer shelter where parents can leave their offspring while foraging or avoiding predators. Thus, dolphin calves must be efficient swimmers at birth (Dearolf et al. 2000) with the ability to join and leave their mothers in different contexts (Mann and Smuts 1998, 1999; Mann and Watson-Capps 2005). These periods of separation can increase the vulnerability of calves to potential threats such as predation, entanglements in fishing gear, and boat collisions in populated coastal areas. Given that newborn cetaceans exhibit high rates of mortality (Whitehead and Mann 2000), one might expect adults to provide specific strategies of care to maximize offspring survival during this critical period. On the other hand, the increasing independence of the calves might also demand different strategies of care.

According to parent-offspring conflict theory, the mother and calf relationship will experience age-related changes as the calf gains independence (Trivers 1974).

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Consequently, parental care of the youngest calves would be more intense than in older calves, given that parents would be investing more energy in future offspring as their calves develop. Studies of mother-calf proximity in cetaceans show support to Trivers' theory (Mann and Smuts 1999; Krasnova et al. 2006). For instance, mothers of bottlenose dolphins seem to decrease their role in maintaining proximity, while infants spend more time socializing or traveling independently over time (Mann and Smuts 1999).

Most studies addressing parental care investment in dolphins focus on mother-calf proximity maintenance for both captive (e.g., Cockcroft and Ross 1990) and wild dolphins (e.g., Gubbins et al. 1999; Mann and Smuts 1999; Sardi et al. 2005; Tardin et al. 2013). Interestingly, less attention has been given to the relationship between strategies of care and the ontogeny of calves, which may reveal valuable information regarding social structure of a given species and animal breeding systems (e.g., Mann and Smuts 1999; Krasnova et al. 2006).

The Guiana dolphin, *Sotalia guianensis* (van Bénédén 1864), is a small delphinid endemic to coastal waters of western Central and South America (da Silva and Best 1996). The species reproduces and gives birth throughout the year with a peak between December and February (Rosas and Monteiro-Filho 2002; Rosas and Barreto 2008). Like other cetaceans, *S. guianensis* is characterized by extensive maternal investment with a set of parental care strategies varying according to social traits such as

size and group composition (Rautenberg and Monteiro-Filho 2008; Tardin et al. 2013).

In this study, we tested the hypothesis that the frequency of parental care exhibited by *S. guianensis* varies with offspring development. Our prediction is that parental care would be more frequent in the early stage of development (neonate phase) and then decrease as the calf matures. Specifically, we aim to analyze (1) how parental care changes throughout the offspring developmental period and (2) how changes in the nature of parental care reflect the life stage of the calves.

Material and methods

Study area

Cananéia estuarine system is located in the southeastern Brazilian coast, São Paulo State (Fig. 1). This estuary consists of a complex of channels and lagoons connected to each other, comprising an area of approximately 115 km² (Miyao et al. 1986). Field surveys were conducted in four stations. Three land-based stations were located in different beaches: Trincheira Beach (located in a cliff about 3 m high), Ponta da Trincheira, and Itacuruçá Beach (Fig. 1). Ponta da Trincheira and Itacuruçá Beach are sloping beaches where dolphins are frequently observed. Observations from the three land-stations were obtained within a radius of approximately 100 m from the shoreline. The fourth sampling station was along a bay, Baía de Trapandé, which was surveyed by boat.

Fig. 1 Cananéia estuarine system and its three islands: Ilha de Cananéia (a), Ilha Comprida (b), and Ilha do Cardoso (c). The shaded area represents field surveys conducted by boat. Symbols correspond to the land-based stations: Itacuruçá Beach (square), Ponta da Trincheira (triangle), and Trincheira Beach (circle)



Data collection

We carried out 81 field surveys from July 2011 to June 2012, totaling 326 h of sampling effort, 175 h with land-based surveys and 151 h with boat-based surveys. We classified calf age classes based primarily on ontogenetic variation in color patterns and body length (Randi et al. 2008; Rosas and Barreto 2008; Table 1). Color pattern is a reliable character to assess age classes of *S. guianensis* dolphins given that it varies as the calf matures. Young calves have little body mass, making the blood vessels more evident and characterizing the immature individuals by a pinkish coloration. As the animal matures, the blood vessels become less evident, reducing the pinkish coloration in both ventral and dorsal region. Individual behavioral patterns (Monteiro-Filho et al. 2008, Table 1) were only used to validate individual age classes when morphological features were not evident (e.g., adjacent age classes with similar sizes and/or coloration). Following these criteria, we recognized individuals as neonates, infants, juveniles, and adults (cf. Randi et al. 2008). Six months of ad libitum observations

Table 1 Morphological features of *S. guianensis* (Randi et al. 2008; Rosas and Barreto 2008) used to recognize the age classes. The behavioral patterns (Monteiro-Filho et al. 2008) were used to validate age classes when necessary

Age class	Morphological features	Behavioral description
Neo-nate	Body length ranging from 88 and 98 cm (< ½ of adult length). Pinkish pigmentation on both ventral and dorsal region. Pronounced fetal folds or lumpiness	Individuals rarely separate from their mothers
Infant	Body length of approximately 120 cm (larger than ½ of adult length). Pinkish pigmentation on the ventral region and grayish pigmentation on the dorsal region	As individuals become more proficient swimmers, separations from the mother become more frequent Individuals start to briefly interact with other adults and calves
Juvenile	Body length ranging from 120 and 160 cm. Dorsal region predominantly grayish and a light-colored ventral region. Differ from adult individuals by a pinkish spot on dorsal fin	Individuals are frequently observed interacting with other adults and calves. Juveniles are also seen in solitary swims practicing skills such as those associated with foraging
Adult	Body length ranging from 160 to 220 cm. Dorsal region predominantly grayish and a light-colored ventral region	Individuals are predominantly seen in foraging activities or taking care of calves. Adults are usually seen in solitary swims and/or interacting with calves and adults in largest associations

were made before behavioral data collection to ensure the ability of the single observer to correctly assign the age classes. Data from individuals whose age classes could not be estimated accurately were excluded from the analyses. In Cananéia estuary, the basic social structure is composed by an adult and its calf (Monteiro-Filho et al. 2018). We defined groups composed of one (or two) adults and one calf as “small associations,” whereas “large associations” are groups composed of more than three individuals (including adults and calves) performing any activity together during the observation period. Groups composed only of adults and solitary adults are frequently encountered in the Cananéia region, but they were not recorded in this study.

We recorded parental care behaviors using focal sampling and sequential sampling methods (Altmann 1974; Lehner 1996). Behavioral categories of parental care were quantified based on a previous description (Rautenberg and Monteiro-Filho 2008; Table 2). When we had one adult accompanying the calf, we considered this adult as the mother. When we had more than one adult (i.e., small and large associations), we rely on behavioral patterns to identify the mother. We recognize that alloparental care might have been quantified as parental care behavior. However, provision of care of other individuals were also considered a strategy of care toward the calf. When a group of dolphins was sighted, we selected an individual (focal individual) and recorded all parental care behaviors dispensed to this calf. To minimize potential sample biases and to ensure independence between samples, we restricted the sampling to a maximum of six consecutive 5-min sections for the same individual. After this period, even if the same group remained in the area, we started to record another group of dolphins. During boat surveys, once dolphins were sighted, we reduced boat speed and maintained a 100 m distance from the group.

As other delphinids (e.g., *Tursiops truncatus*), *S. guianensis* displays a fluid, fission-fusion social system (e.g., Santos and Rosso 2008). In addition, the density of individuals estimated in the Cananéia estuary was 12.41 individuals/km² with an abundance of 195 animals (Havukainen et al. 2011). Although we cannot assure that a given group was not sampled twice, the probability of pseudoreplication was presumably low and outweighed by (1) fission-fusion dynamics, (2) size of the population, and (3) individuals moving constantly throughout the Cananéia estuary. In many cases, we were able to track individuals during the sampling section by distinguishing features such as natural marks and scars.

Statistical analysis

We used a Kruskal-Wallis test to compare data obtained during boat expeditions and land-based stations to detect possible bias. No effect was detected ($H = 3.4286$; $df = 2$; $P = 0.1801$), and the data were then combined into a single dataset.

Table 2 Description of parental care behaviors of *S. guianensis* at the Cananéia estuarine system (cf. Rautenberg and Monteiro-Filho 2008)

Behavior	Description
Echelon swimming	Calf swims close and roughly parallel, touching mother's flank above midline
Escort	In order to move the calf away from a source of risk (e.g., boats, beaches, and mud banks), the calf is positioned between two adults and driven to a safe area
Meeting among small associations	Occurs when several small associations (adults with calf) get together. Adults leave their calf interacting with other individuals so that they can forage near dangerous areas. Also occurs when dolphins get together to travel between areas
Alternation	One adult accompanies the calf, while the other adult moves away to forage. Then, the one who was feeding returns to accompany the calf, so the other adult can forage too
Crèche	This behavior is derived from meeting among small associations, when several groups get together for different activities. Some adults of the group—probably mothers—forage in further distant places, while other individuals assist in offspring care accompanied by a larger number of calves

We performed a canonical discriminant analysis (CDA) to investigate how different strategies of care contribute to the discrimination of calf age classes, as well as how much overlap in received care there may be between the calf age classes. The dataset was organized in a unit-by-variable matrix (calves are units grouped by the age class and the frequency of occurrence of parental care behavior classes are the variables; Cruz-Castillo et al. 1994). Here, we aimed to identify which of the five parental care behaviors would be responsible for maximizing the separation of individuals observed in different age classes.

To evaluate specific differences in frequencies of parental care in each age class, we performed a series of chi-square goodness-of-fit test (Zar 1999), comparing all age classes within each behavioral category. We adopted a significance level of 0.05. All analyses were carried out in R software using the CANDISC (Friendly and Fox 2015) and STATS packages (R Development Core Team 2014).

Results

Out of the 326 h of sampling effort, 61 h (18.7%) was of direct observation of dolphins in which 698 parental care behaviors were quantified in 685 5-min sampling sections. Of the 495 groups observed, 415 (84%) had calves present. The remaining groups either had no calves or age classes could not be identified and were excluded from the analyses. Observed group sizes varied from solitary individual (6%), small associations (63%), and large associations (31%).

Although both canonical discrimination functions explain 100% of the variation in the data, we did not observe any segregation of individuals in three age classes in different groupings (Fig. 2). The first canonical discrimination explained 67% of the variation (eigenvalue = 0.2522), while the second function explained the remaining variation (33%; eigenvalue = 0.1234). The first axis was strongly associated

with echelon swimming, whereas the second axis was more associated with crèche (Fig. 2). Even though some behaviors may be more frequent in determined age class, it was not possible to differentiate these classes based on the set of behaviors of parental care received.

When we analyzed how frequencies of each behavior were distributed among age classes, we observed that behaviors directed at infants were more diversified than those directed at neonates and juveniles. Except for echelon swimming, all behavioral categories were more frequent in the infant class (Fig. 3).

Echelon swimming was the predominant behavior in mother-neonate dyads ($\chi^2 = 75.36$; $df = 2$, $P < 0.001$), showing an abrupt decrease in older age classes (Fig. 3). In infants and juveniles, echelon swimming was observed mostly during specific activities, such as foraging. Alternation was performed exclusively for infants and juveniles ($\chi^2 = 53.16$, $df = 2$, $P < 0.001$; Fig. 3). In these age classes, alternation represented the predominant behavior.

The meeting among small associations was equally distributed among all *S. guianensis* age classes ($\chi^2 = 4.07$, $df = 2$, $P = 0.1305$; Fig. 3). During this behavior, we generally observed the occurrence of crèche ($\chi^2 = 83.7$, $df = 2$, $P < 0.001$), when juveniles were also observed providing care to the youngest individuals. Thus, crèche was not observed between mothers and juveniles (Fig. 3). Escort behavior was also observed in all classes but showed higher frequencies in neonates and infants ($\chi^2 = 37.54$, $df = 2$, $P < 0.001$; Fig. 3).

Discussion

Infancy is the most vulnerable period in the life of a mammal in which survival and development of offspring depend on the quality of mother-calf relationships. We expected our data to conform to the patterns commonly found in studies of mammalian development. In this study, it was not possible to

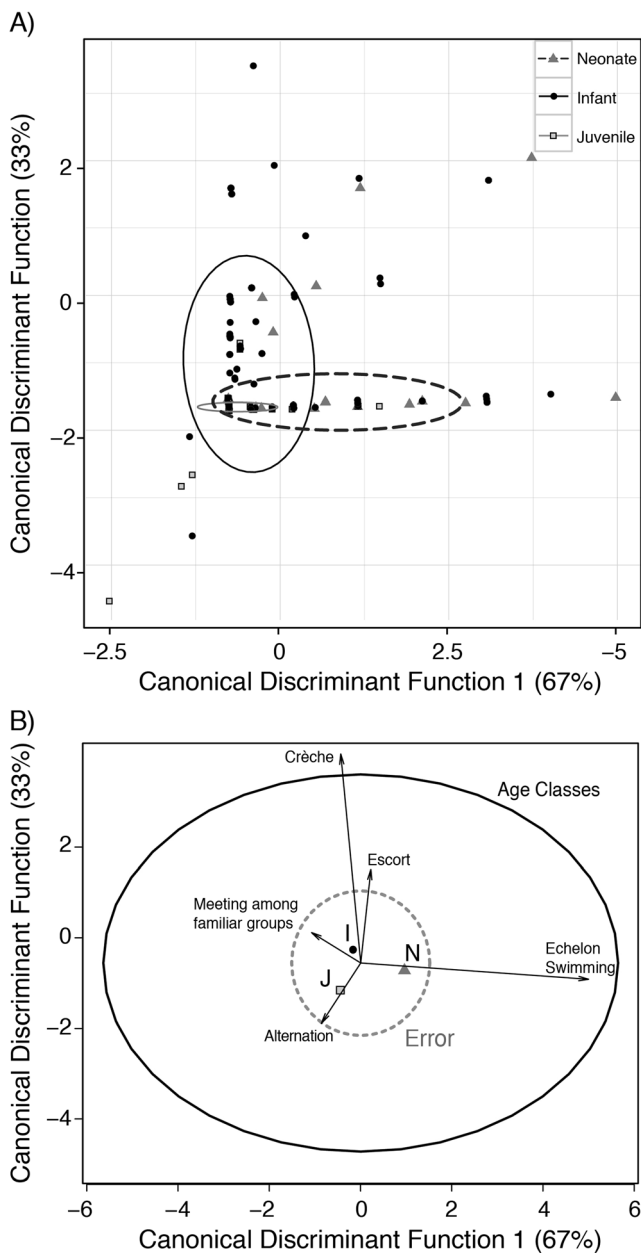


Fig. 2 **a** Ordination of the three age classes of *Sotalia guianensis* calves receiving five parental care behaviors according to the first two canonical discrimination functions. **b** Hypothesis-error plot showing the influence of parental care behaviors in ordination of the three age classes of *Sotalia guianensis* calves: Neonate (N), Infant (I), and Juvenile (J)

differentiate age classes based on the frequency of parental care received. However, our results show that the variation lies in the strategy of care, which seems to be specifically dispensed according to *S. guianensis* calf age class.

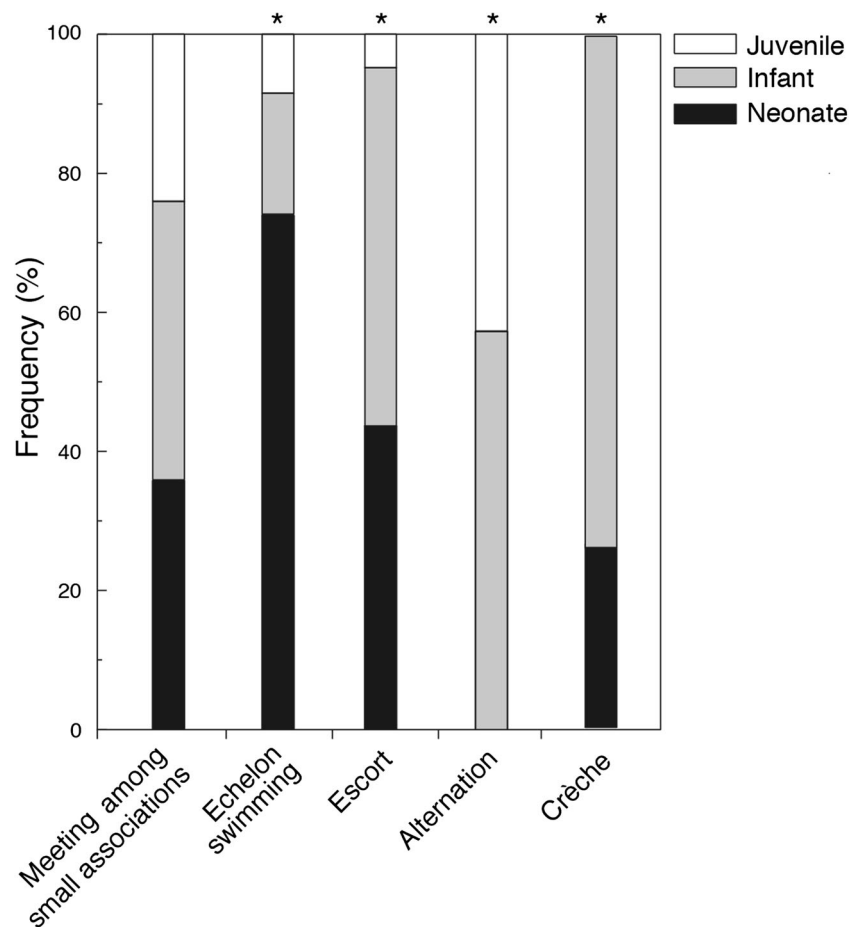
A period of high nutritional dependence is a universal feature of mammalian development (Nicolson 1987), so we expected higher care provision for *S. guianensis* neonates. Although infants and juveniles are more independent than neonates, our findings suggest that individuals in these age classes can also benefit from adult care. These benefits may

not be limited to protection from threats; the extended social relationships provide opportunities for juveniles to observe and learn foraging, social and communication skills from adults. We also observed developmental shifts in patterns of mother-calf contact in *S. guianensis*, similarly to captive (e.g., Gubbins et al. 1999) and wild *T. truncatus* (e.g., Mann and Smuts 1999). Thus, while the increasing separations from mother could indicate the juveniles’ growing capability to live in a marine environment, we hypothesize that this may also demand a wider repertoire of care. At this stage, calves start to venture into situations not experienced when they were continuously accompanied by their mothers. In addition to independent foraging and establishing social relationships with other conspecifics, juveniles need now to avoid predators and anthropogenic threats (e.g., boat collision, entanglement in fishing gear) by themselves. Therefore, our results suggest that there is not a unique phase in the life of *S. guianensis* calves in which parental care is most frequent. Rather, there is a shift in the strategy of care according to the requirements of each age class.

Meeting among small associations was equally distributed among all age classes. During this behavior, different groups gather around large schools of fish. While group members forage, calves establish social relations mainly through playing, as observed by Monteiro-Filho et al. (2008). Social behaviors like these are essential during the early stages of life, allowing calves to develop and improve motor and cognitive skills (Bekoff 1972; Monteiro-Filho et al. 2008). After the first week of calf life, mothers start to engage in meetings among small associations. This might be an advantageous situation, given that mothers may benefit from the foraging behaviors performed by other group members (e.g., crossing fishery, herding, and circle formation—see Monteiro-Filho 1995). These foraging strategies aim to surround or direct schools of fish to facilitate the capture. As a result, mothers can feed from these fish without leaving the young calf, even though they did not actively participate in the strategy.

Alloparental care, i.e., provision of calf care by individuals other than the mother, is widely recorded among long-lived social mammals such as primates (Nicolson 1987; Fairbanks 1990), elephants (Lee 1987; Schulte 2000), and cetaceans (*Physeter macrocephalus*: Whitehead 1996; *Stenella longirostris*: Johnson and Norris 1994; *Orcinus orca*: Haenal 1986). We observed potential alloparental care in crèche, escort, and alternation behaviors. Limitations encountered by offspring (i.e., lower agility and maneuverability) can affect individual foraging strategies of the adult. The crèche and alternation represent alloparental strategies that allow mothers to trap their prey in shallow areas, while the calf stay in safer areas in the presence of a nearby adult. The escort behavior is usually used by the mother and a second adult in order to keep the offspring away from boats, preventing possible collisions between the inexperienced dolphins and the boat.

Fig. 3 Frequencies (%) representing the parental care behaviors dispensed to each age class of *Sotalia guianensis* over the observation time. Asterisk denotes a significant difference in frequency of age classes for each behavior category through the chi-square test



Shortly after birth and during the improvement of motor skills, dolphin calves swim almost exclusively in synchrony with their mothers (Gubbins et al. 1999; Mann and Smuts 1999; Noren and Edwards 2007; Rautenberg and Monteiro-Filho 2008; Chechina 2009). Among all categories of parental care behaviors observed in the Cananéia region, echelon swimming was significantly more frequent in mother-neonate dyads. In addition to maternal protection, echelon swimming theoretically provides hydrodynamic benefits, pushing calves forward and enabling them to keep up with the moving group (Weihs 2004). However, this behavior may also increase energy expenditure of adults (Noren et al. 2008), as well as reduce foraging efficiency (Monteiro-Filho 1995; Noren 2007). These factors may contribute to the observed decrease in echelon swimming frequencies and the increase of other parental care strategies in older age classes. We primarily observed juveniles engaged in echelon swimming during foraging activities, which may suggest that in addition to protection, juveniles can also have the opportunity to observe and improve foraging skills by swimming in synchrony with the adults (Hoppitt and Laland 2008).

We observed escort behavior mainly in neonates and infants, especially when they approached boats. Boat traffic is a

known threat to coastal dolphins, and collisions, injuries, and behavioral changes are documented in several species (Stone and Yoshinaga 2000; Laist et al. 2001; Nowacek et al. 2001; Valle and Melo 2006; Waerebeek et al. 2007). Therefore, given the high frequency of this particular behavior, we hypothesized that both infants and neonates are still unaware of these potential threats. On the other hand, adults do not seem to have an apparent reaction when juveniles approach boats. We believe that escort behavior could be an anticipation of the adult to avoid direct contact between calves and boats. Since juveniles already actively participate in foraging activities in the same areas as adults (Monteiro-Filho et al. 2008), they apparently have reached enough maturity and motor skills to avoid direct contact with boats.

In summary, the long period of care observed in this study may reflect the effort required by calves to learn behavioral and social skills necessary to survive in the complex and dynamic ocean environment. We believe that our findings shed new light on important aspects of *S. guianensis* behavior (e.g., mother-calf relationships under natural environmental conditions), providing the basis for future intra and interspecific comparisons. Much remains to be learned about *S. guianensis* parental care behaviors, and further systematic

investigation on intraspecific variation throughout the species distribution and the influence of social structure and environmental variables are interesting venues of research.

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