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Egg Mass Destroying Behaviour of the Female Giant Water Bug *Lethocerus deyrollei* Vuillefroy (Heteroptera : Belostomatidae)

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Abstract — After being laid on emergent aquatic vegetation, the egg masses of *Lethocerus deyrollei* are brooded by the male. In laboratory studies, females were observed to destroy egg masses and ingest the fluid of eggs. Brooding males fought with these attackers at first, but then gave up the defense and mated with them. After destroying the egg masses, females laid new ones at the same sites on the same night or the following one, and males brooded the new offspring. The population density of this species is very low. Most males engage in brooding and cease to become acceptable mates after most of the females lay the first egg masses. It is costly for females to search out free males in the aquatic vegetation. By destroying egg masses, however, individual females can gain new mates with little exertion and can make them brood their own offspring. Furthermore, the survival of their own offspring increases with the elimination of their competitors.

Eliminating the young of other individuals of the same sex sometimes increases the killers' own fitness. Termed as sexually selected infanticide (Hrdy 1979), this phenomenon is known to occur among mammals (especially in primate; review in Hiraiwa-Hasegawa 1988), and birds (e.g. Stephens 1982; Freed 1986). Among vertebrate individuals, the main benefit of killing young is an increased probability of obtaining a mating opportunity and thereby producing their own offspring.

In invertebrates, even parents may not recognize their own progeny, many species may not recognize immature conspecifics (Polis 1984), and cannibalism and infanticide are therefore more likely to be indiscriminate. The killing of young in invertebrates occurs primarily for obtaining nutrients; in some cases the offspring of killers enjoy a resultant increase in fitness.

In scorpions and probably many other cannibalistic species, mothers decrease potential predation on their own offspring by eating conspecifics in the territory (Polis 1984). Foundress queens of the paper wasp *Roparidia fasciata* eat eggs in colonies both for obtaining nutrients and for feeding their own larvae (Iwahashi 1989). They also kill larvae and pupae both to obtain nutrients and to gain nests to lay their own eggs.

However, no insect species have previously been observed to kill young or eggs to increase the probability of obtaining a mating opportunity (as vertebrates do). In this study, we observed this phenomenon occurring in *Lethocerus deyrollei.*

Lethocerus deyrollei is a large predatory insect (body length 48 ~ 65 mm) inhabiting still waters such as rice fields and densely vegetated ponds. It is nocturnal and moves little in the daytime. Breeding season in the field starts in late May and finishes in August. In the laboratory, a female laid 6 egg masses - a total of 431 eggs - in one breeding season (Ichikawa 1985). Monogamy has not been observed. Egg masses are laid on emergent vegetation above the water surface. In the process of laying an egg mass, the sequence of copulation and oviposition are repeated more than 10 times with the same mate (Ichikawa 1989).

Females leave their egg masses, and males then brood them (Ichikawa 1988). Males cannot descriminate their own progeny from others', but ordinarily brood only their own egg masses. Their eggs fail to hatch and desiccate without brooding. At night, brooding males ascend vegetation to their egg masses and supply them with the water attached to their bodies (Ichikawa 1988).

Under laboratory conditions it was noted that egg mass destruction occasionally occurred at night when some females were introduced to aquaria with a brooding male, and that it never occurred when isolated males were brooding. Experiments were conducted to investigate which individuals destroyed egg masses.

Materials and methods

Experiment 1 - 1

We wanted to observe how individuals destroyed egg masses and identify the individuals doing so. Four males and 11 females were used, of which 3 females (Nos. 8923, 8925, 8926) were col-

lected in western Hyogo Prefecture in the spring of 1989. All other individuals were born in aquaria in the summer of 1988. Their parents had been collected at the same site in early summer, 1988. This group was kept in an aquarium at room temperature until the start of experiments. Kin relationship within the group was not clear. Egg masses used in experiments were laid in aquaria on sticks 25 cm long 2 cm dia.

An aquarium (L 90 × H 45 × W 45 cm) containing 10 cm of water was placed in the open air under a roof. On the day preceding each experiment, an egg mass laid on a stick, a male bug which had been brooding the egg mass, and 1 ~ 3 sticks without egg masses were placed into the aquarium. One to 4 females were introduced onto the sticks without egg masses during the daytime. Observations of behaviour began after sunset. Six replicates were made. Females with large abdomen (undetermined maturity) were used in 5 replicates. Females with small abdomen (determined immaturity) were specifically selected for an experiment. Some of the behaviour was recorded by video camera and analyzed. A 10 W white bulb (30 lux) was used for observation after sunset. A 20 W white bulb was added (total 80 lux) for the video portions filmed after bugs started moving.

Experiment 1 - 2

On the day preceding an experiment, 2 egg masses on 2 sticks with 2 brooding males were placed in the aquarium used in Exp.1-1. A female was introduced during the daytime and was observed as in Exp.1-1.

Experiment 2

We investigated the minimum egg mass size which males brooded by gradually removing eggs from the masses. Three egg masses with 3 brooding males were used. Males had been collected from the Exp.1 site in the preceding year and egg masses were laid on sticks in the laboratory. We removed eggs with tweezers every morning. The behaviour of males was observed every night.

Results

Experiment 1 - 1

Egg masses were destroyed by females 5 times out of 6 (Table 1). In all instances males fought with females at first, but soon came to mate with them (Fig.1-a,b). Their behaviour is summarized below. We noted that females with small abdomen did not destroy egg masses. They were dissected after the experiment; there were 0, 0 and 6 mature eggs in their ovaries, respectively.

Female behaviour

1. In the daytime, females stayed on the sticks without egg masses.
2. After sunset, females came to the sticks on

Table 1. Eggmass destruction by females

Date	Brooding males no.	No. of Eggs	Attacking females no.	Destruction	Oviposition after destruction	No. of Eggs
May 29	8968	105	8906	+	same night	88
			8923	+	same night	96
July 14	8975	68	8912[a]	−	none	0
			8916	−	none	0
July 27	8968	96	8923	+	next night	102
			8926	−	none	0
August 2	8961	74	8925	+	next night	80
			8911	−	none	0
			8902	−	none	0
August 6 − 7	8965	80	8904	−	none	0
			8911	−	none	0
			8926[b]	−	none	0
August 11	8965	80	8923	+	6 days later	80
			8926[c]	−	none	0
July 10	8968	105	8912	+	next night	68
	8975	94		+		

a, b and c are mothers of respective egg masses.
[ ] : Bugs were put into the same aquarium.
All females which destroyed egg masses also sucked the fluid of eggs.

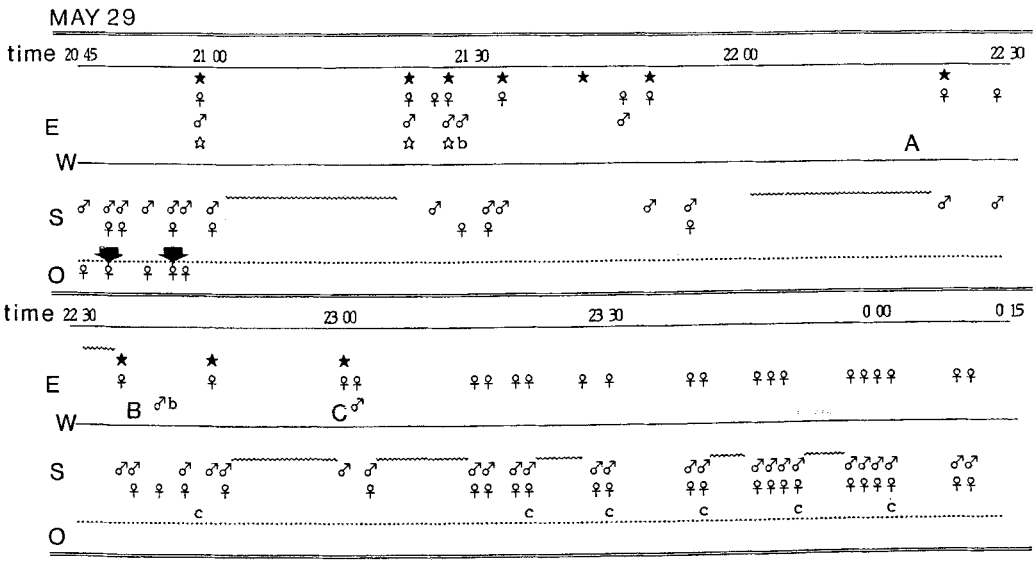

Fig. 1-a. Egg mass destroying behaviour (1).

A female was put into an aquarium in which a male had been brooding an egg mass. E, W, S, O show egg mass, water surface, on the stick in the water, and other place in the water respectively. ♂ and ♀ show the location of the male (No. 8968) and the female (No. 8906) in the aquarium at respective times. From 23:15 to 0:15 the male stayed in the water and the female ascended the stick many times. ★ : egg mass destroying by the female. ☆ : struggle. b: egg mass brooding by the male. c: courtship behaviour of the male. : copulation.

⬇ : the male drove away the female. A: one-third of the egg mass was destroyed. B: 10 eggs remained. C: 2 eggs remained.

Normal mating behaviour started from about 0:00. The female laid 88 eggs the same night.

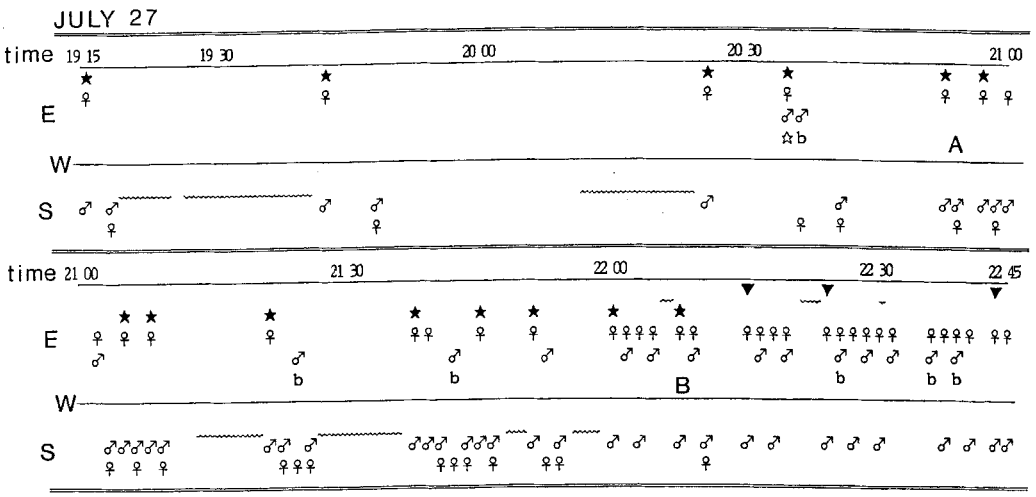

Fig. 1-b. Egg mass destroying behaviour (2).

Observation started at 19:15, when egg mass destroying had started. Two females were put into an aquarium in which a male had been brooding an egg mass. E, W, S show egg mass, water surface, on the stick in the water respectively. ♀ and ♂ show the location of the female (No. 8923) and the male (No. 8968) at respective times. ★ : egg mass destroying by the female. ☆ : struggle between the male and the female. ▼ : the female beat her ovipositor several times on the stick.

: copulation. A: a quarter of the egg mass was destroyed. B: half of the egg mass was destroyed and many of the remaining eggs were sucked and became flat. The female laid 102 eggs on the following night. Another female (No. 8926) was unconcerned with the egg mass.

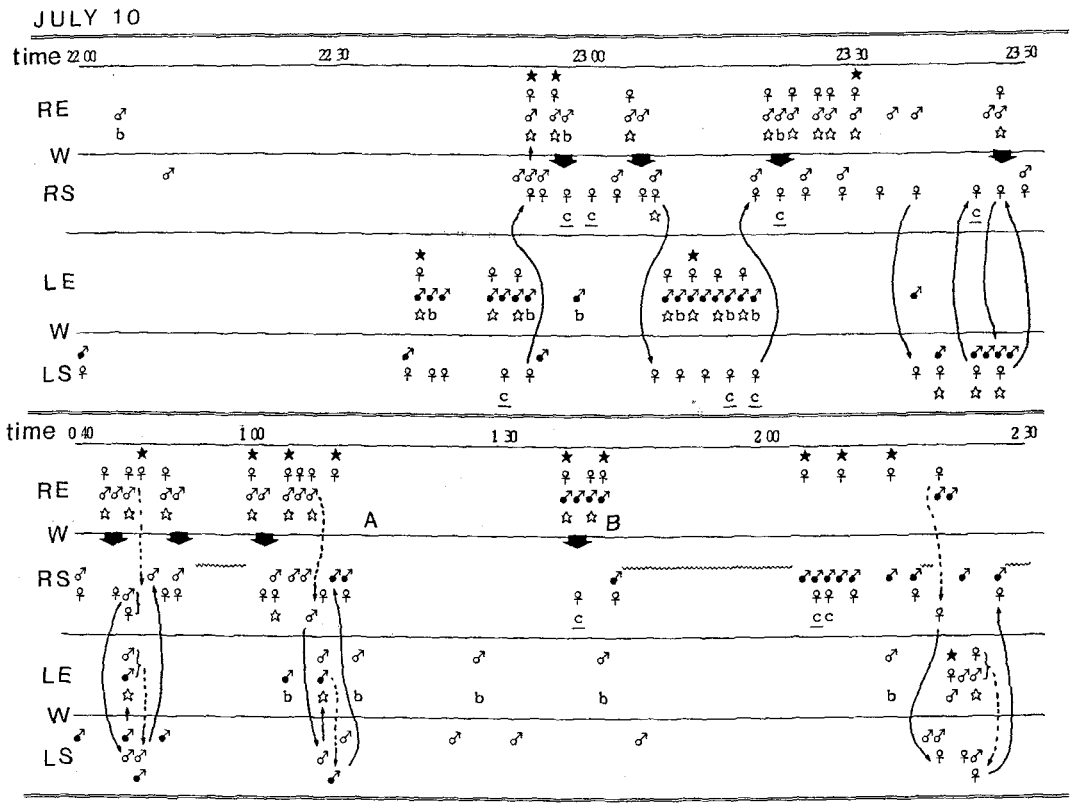

Fig. 1-c. Egg mass destroying behaviour (3).

A female (No.8912 ♀) was put into an aquarium in which 2 males (No.8968 ♂ , No.8975 ♂) had brooded several egg masses. RE, W, RS, LE, LS show the right egg mass, water surface, on the right stick in the water, left egg mass and on the left stick in the water respectively. ♀ , ♂ , ♂show the locations of the female and males at respective times.

ww: copulation. ★ : egg mass destroying by the female. ☆ : struggle. b : egg mass brooding c : courtship behaviour of a male. c : courtship behaviour of the female. ⇣ : falling from the egg mass into the water. ↺: moving from one stick to another and successive moving.

⬇ : the female was driven away by a male, the result of a struggle near the egg mass. A : about 25 eggs remained. B : only 5 eggs remained. Both egg masses were destroyed by the next morning. The female mated male No. 8975 and laid 68 eggs on the following night.

which egg masses were being brooded. Males fiercely tried to drive them away and were initially successful. Nevertheless, the females successfully ascended the sticks by dodging the males.

3. Upon ascending the sticks, females started destroying egg masses. They fastened their claws to the eggs and moved their forelegs back and forth. Eggs were torn off from sticks and dropped into the water (Fig.2). Females did not take careful aim with their forelegs, but moved them at random, often striking air as the egg masses became smaller. Females performed this destroying motion in short bouts of 15 ~ 25 s, and then rested for 30 s to several min. During the resting time they thrust stylets into eggs and sucked the fluid of eggs (Fig.3). This sequence of sucking and destruction was repeated 1 ~ 3 times per ascent.

4. Females descended to the water after 1 ~ 3 min of destruction and sucking. They repeated this ascent/descent sequence until the egg masses became very small (0 or several eggs).

5. When males mounted them, females stopped destroying and copulated.

6. After almost all of eggs had been destroyed, females engaged in further copulation. In 2 instances, females started to lay eggs at the same site on the same night. In 2 other instances, females laid eggs on a stick the next night after copulating with the same mate. In one case, a female copulated many times while destroying an egg mass. Nevertheless she laid no egg that night or the following night. She copulated again with the same mate 6 days later and thereafter laid an egg mass.

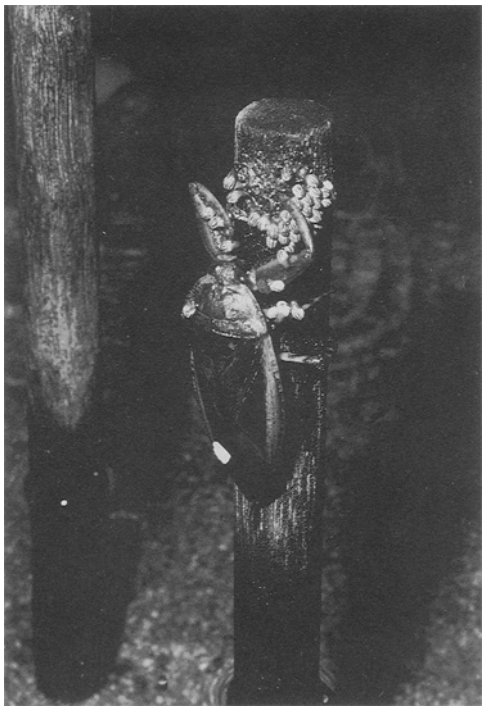

Fig.2. A female destroying an egg mass by hooking her claws on it and moving forelegs back and forth. Eggs are torn off from the stick and drop into the water.

Fig.3. A female thrusting her stylets into eggs and sucking the egg fluid.

Male behaviour

1. At first, males aggressively drove away females.
2. When females dodged the males and ascended the sticks, males chased them and tried to drive them away, thereafter covering the egg masses with their bodies. In this posture, stylets were often positioned below the eggs. When brooding, stylets were above or on egg masses.
3. Males initially succeeded in driving away females (the first 2 or 3 times). Nevertheless, females soon reached the egg masses, and the males gave up dirving them away. Males descended to the water or tried to mount the females.
4. When males descended into the water, they tried to copulate with the attacking females when the latter also descended.
5. When males ascended to partially destroyed egg masses, they either brooded them or copulated with the female invaders.
6. When egg masses were reduced to less than 10 eggs, males stopped brooding.
7. After females laid new egg masses, males brooded them until hatching.

Experiment 1 - 2

After struggles with males female No.8912 was driven away 14 times by males (⬇ in Fig.1-c). She also slipped down into the water twice with a male in the course of struggle, and struggled in the water. After attempted ascents, she moved to another stick 7 times (↑ ↓ in Fig.1-c), changing her target.

Male No.8968 fell into the water while defending his egg mass (1:08) moved to another male's stick by mistake and then struggled with that stick's male. Male No.8975 was defeated and driven away, and moved to the vacant stick. These individuals thereafter brooded each other's egg masses.

Male No.8975 guarded his egg mass until 1:38. He gave up guarding at 1:41, when only 5 eggs remained in the egg mass. Thereafter he copulated with the invading female in the water.

Next morning, both egg masses had been destroyed. The next night, the female mated male No.8975 and laid 68 eggs. No.8975 then brooded his new egg mass.

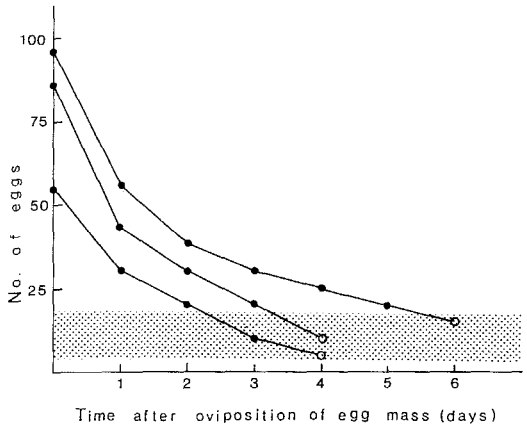

Fig.4. Relationship of males' brooding and size of egg mass. Males brood their egg masses at night. They are usually in water in the daytime. Eggs were removed by tweezers every morning and observations conducted after sunset. We difined that males had "given up" when they stopped ascending after 1 or 2 ascents.
Shaded area is the range of egg number when males gave up brooding.

Experiment 2

All males continued to brood their egg masses until 20 eggs remained. They stopped brooding when egg masses were reduced to 5 ~ 15 eggs (Fig.4).

Discussion

Which individuals destroyed egg masses ?

Female No.8912 destroyed an egg mass and laid her own egg mass on July 10. However she was unconcerned with the appearance of another egg mass on July 14. *L. deyrollei* females lay most of the eggs in their ovaries into egg masses. The subsequent clutches mature by the next oviposition. On July 14, the eggs in the ovary of female No.8912 may not have been sufficiently mature. Four females, with nearly empty ovaries, also did not destroy nearby egg masses. Therefore, presumably only sufficiently mature females destroy egg masses.

Why do females destroy egg masses ?

When a mature female wants to mate a free male to make him brood her own egg mass after other females have laid their first egg masses, most males are already brooding and unavailable. Population density of *L. deyrollei* is relatively low in the field. Free males must be scarce. Females, which have laid their first egg masses and become mature again, similarly have the same difficulty. It must be costly for them to search for free males.

In aquaria a female laid 6 egg masses. If females gain mates as a result of egg mass destruction, they save time and increase their fitness. Destroyers will lay more eggs than females which lose time searching for free males in a limited breeding season.

Why hasn't monogamy evolved ?

Sex ratio of this species is nearly equal (among adults emerging our laboratory over 6 years, no significant sex ratio differences was observed, ♂ 105 : ♀ 111, $P > 0.5$). Egg production and development rates are also nearly equal (e.g. at 27 ~ 29 ℃ , it takes 7 days for eggs to hatch, and a female laid 90 eggs 8 days after laying 78 eggs). Males can start brooding the day after previous eggs have hatched. Operational sex ratio, therefore, is nearly equal. If an individual female stayed near the same male, she would not need to expend any energy to find another male. When she would reach maturity, her previous egg mass would have hatched and her mate would be free from brooding. However, monogamy has not been observed in this species.

Nymphs of this species are very cannibalistic (unpub. data). Cannibalism also occurs among siblings. In cases in which 1st and 2nd instars are mixed and reared in an aquarium, the smaller individuals always disappear first, though cannibalism also occurs among littermates. If an individual female mated the same male and laid the next egg mass after the hatching of her previous egg mass, many of the younger nymphs would be eaten by the older group. When the later eggs would hatch, previously hatched nymphs would be 2nd or 3rd instars, and the larger ones would eat their siblings. Waiting near the same mates therefore, is disadvantageous for females. On the other hand, when an individual female succeeds to find another male brooding another's egg mass, she can destroy it and lay her own egg mass. The survival rate for her progeny will increase as the result of the death of their competitors.

In some Arthoropods, dispersal of mothers decreases the probability of cannibalism on close relatives. It occurs in those species that are apparently unable to discriminate their own progeny (Polis 1984). The behaviour of *L. deyrollei* females after oviposition has not been investigated in the field. However, we expect they move well away from their own egg masses. Males of this species are unable to discriminate their own egg masses from others' (Ichikawa 1988).

Male behaviour

Males initially resisted destroying behaviour, but soon gave up and mated the destroying females. Males are much smaller than females (student t-test $P < 0.001$, $N = 30$, ♂ / ♀ ≒ 0.87), so it must be difficult for them to defend their eggs (Exp.1-1). One female, however, was driven away 14 times and moved to another stick 7 times (Exp.1-2). In the aquarium, the female could not move far away, and returned to the same sticks. In the field, there might be some males which succeed in completely driving away females.

Copulation and brooding behaviour occurred at random after females started destroying (Exp.1-1). After destruction started, males wanted to brood remaining egg masses, but also wanted to mate to gain new offspring without losing time.

Male No.8968 gave up brooding when almost all eggs were killed (C in Fig.1-a). In Exp.1-2, male No.8975 resisted the destroyer when about 25 eggs remained, and gave up when only 5 eggs remained. It was also certified in Exp.2 that males gave up brooding when their egg masses were reduced to small sizes. Females, therefore, had to destroy egg masses thoroughly to make males give up brooding.

It might be possible for males to brood 2 egg masses at the same time. If they could do so, they could avoid losing "older" egg masses. However, this would not be advantageous for females, as the survival rate of their own offspring would decrease from the cannibalism among the nymphs of varying ages. Rankin (1935) showed photographs of *L. americanus* egg masses. One of them is composed from 2 parts and appears to be laid by 2 females. He collected them in the field. However, male brooding behaviour of *L. americanus* has not been reported, and egg masses shaped similarly to that in Rankin's photo have not been reported in *L. deyrollei*.

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