

FACTORS AFFECTING CANNIBALISM AMONG NEWLY HATCHED WOLF SPIDERS (LYCOSIDAE, *PARDOSA AMENTATA*)

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ABSTRACT. Cannibalism is a common phenomenon among young wolf spiders (Lycosidae). The purpose of this study was to investigate how various factors influence cannibalistic tendencies in hatchlings of *Pardosa amentata* (Clerk 1757). The basic experimental approach was to place pairs of unfed hatchlings of similar body mass in small containers without prey and to measure if and when cannibalism happened. From the data, we identified three different cannibalistic strategies. One large group of hatchlings never cannibalized and thus died from starvation. Another group cannibalized shortly before the time at which they were predicted to die from starvation. In these spiders, there was a strong positive relationship between average body mass of the contestants and their latency to cannibalize. A third group cannibalized quickly and the latency to cannibalize in these spiders was independent of body mass. We also tested if cannibalistic tendencies were higher among unrelated pairs than among pairs of siblings, but we did not find any support for this hypothesis. In another experiment we tested if maternal effects influenced cannibalism, i.e. if siblings from certain mothers were more cannibalistic than siblings from others. We did not find any evidence that maternal effects influenced whether or not cannibalism occurred. However, when cannibalism did occur, the latency to cannibalize varied significantly among siblings from different mothers beyond what would have been predicted solely from hatchling body mass.

Keywords: Lycosidae, intraspecific predation, spiderlings, kin recognition, maternal effects

Cannibalism among wolf spiders is often observed in the field. One example is *Pardosa lugubris* (Walckenaer 1802) which seems to be the most important predator of its own species (Edgar 1969), and it was estimated that juveniles of this species included conspecifics as 29% of their total diet (Hallander 1970). Other examples are *Schizocosa ocreata* (Hentz 1844) and *Pardosa milvina* (Hentz 1844) in which cannibalism is assumed to be an important regulating factor on population density (Wagner & Wise 1996; Buddle et al. 2003).

A variety of factors has been suggested as potential selective forces, promoting or inhibiting cannibalistic behavior. The most obvious advantage connected with cannibalism is that the cannibal gains a meal in addition to the normal diet and cannibals often show higher growth and survival rates than their non-cannibalistic conspecifics (Polis 1981). As can-

nibals are facing prey with similar predatory abilities, an obvious cost of cannibalism is the risk of retaliation. Another intriguing cost of cannibalism is the potential loss of inclusive fitness when a cannibal kills a genetically related individual (Elgar & Crespi 1992; Pfennig & Sherman 1995). If this cost is large, we would predict spiders to be able to distinguish between kin and non-kin and to treat kin and non-kin differently (Pfennig & Sherman 1995). Kin recognition has been shown to occur in many cannibalistic animals (see references in Pfennig 1997) and also some spiders seem to be able to identify and subsequently avoid eating a close relative (Evans 1999; Bilde & Lubin 2001; Anthony 2003; Roberts et al. 2003). Wolf spider females carry their young on the abdomen for about a week. Thus, hatchlings have a good opportunity to learn chemical or visual cues, which could later be used to recognize siblings from non-siblings.

Adult wolf spiders can survive starvation

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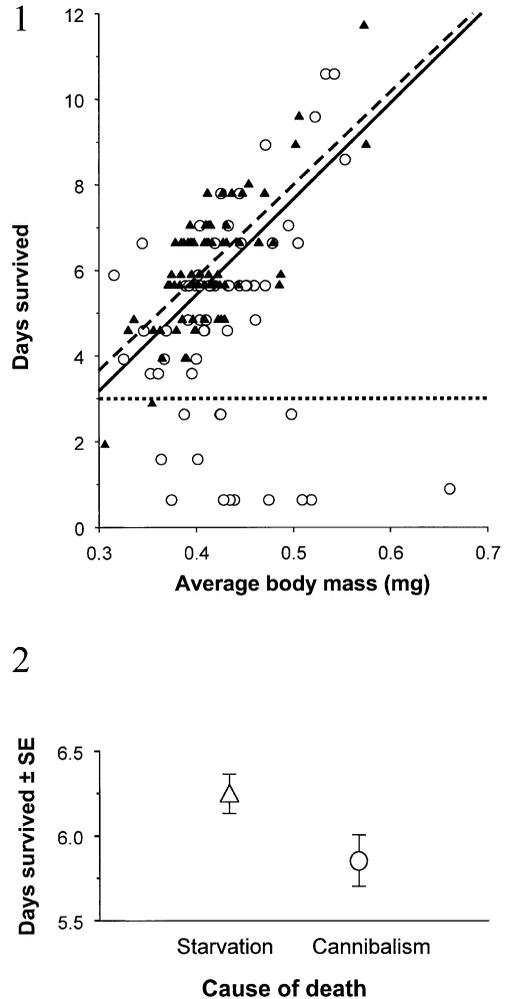
for several months (Anderson 1974). Newly hatched spiderlings on the other hand can only survive a few days or weeks before their nutrient reserves are depleted (Wagner & Wise 1996; Toft & Wise 1999). This means that the first meal is of utmost importance for spiderlings and cannibalism can therefore be important for juvenile survival.

In the present experiments we investigated cannibalistic tendencies among equally sized pairs of unfed hatchlings and provided them no choice other than to cannibalize or to die from starvation. Using this approach we evaluated different hypotheses about what influences cannibalistic tendencies in the hatchlings. In the first experiment, we paired sibling and non-sibling hatchlings in order to test if cannibalism was dependent on kinship. From these results we also describe three apparently different strategies among hatchlings. Potentially, a mother of a brood can affect the condition of her spiderlings and thus also their cannibalistic propensities, for example through her nutritional status before reproduction. The rates of cannibalism may also vary between closely related species or among and even within populations, due to genetic differences (Thibault 1974; Stevens & Mertz 1985; Tarpley et al. 1993). In a second experiment we therefore tested if there was variation in cannibalistic tendencies among hatchlings descending from different mothers.

METHODS

The wolf spider.—The wolf spider *Par-dosa amentata* is abundant in Europe in many open, humid habitats, especially grasslands and agricultural fields with a well-developed litter layer (Alderweireldt & Maelfait 1988). Reproduction takes place in May–July. Females carry the eggsac for 2–3 weeks and hatchlings spend about one week on their mother's abdomen before they disperse (Roberts 1995).

Experiment 1.—The purpose of this experiment was to test if kinship affected cannibalism and to describe the cannibalistic tendency of hatchlings in general. Subadult male and female *P. amentata* spiders were collected in spring in a meadow at Stjær, Denmark (56°07'N, 9°91'E), and brought to the laboratory. They were housed individually in plastic containers (diameter 35 mm, height 80 mm) with a plaster bottom, which was wetted



Figures 1–2.—1. Effects of body mass and cause of death on the survival time of wolf spider hatchlings (Experiment 1). Survival time was measured from the time spiderlings were paired. Each point represents the time passed until one of the two spiders in a pair died from starvation (black triangles) or from cannibalism (open circles). Body mass is the average mass of the two hatchlings in a pair. Regression lines are based on spiders that died after day 3, i.e. > 7 days old (above horizontal dotted line); death from starvation = broken regression line, cannibalism = solid regression line. 2. Number of days survived adjusted for average body mass (least squares means, calculated on spiders dying after day 3 in the experiment, i.e. > 7 days old).

frequently to maintain a permanent high humidity in the container. The spiders were fed wild type *Drosophila melanogaster* (Meigen) in excess until maturity. Fruit flies were raised

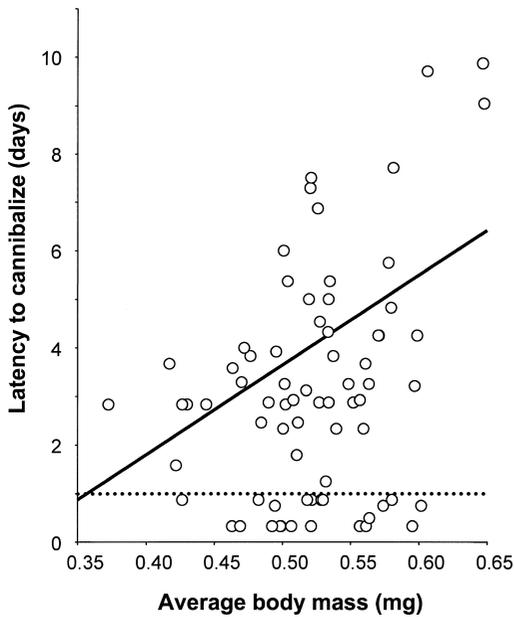


Figure 3.—Relationship between average body mass of hatchling pairs and their latency to cannibalize (Experiment 2). The two spiderlings always originated from the same eggsac. Each point represents the time passed until cannibalism occurred. The regression line is based on spiders cannibalizing after day 1 (above horizontal dotted line), i.e. > 7 days old. About 64% of the spiders did not cannibalize at all and are not shown in the figure.

on instant *Drosophila* medium (formula 4–24 Plain, Carolina Biological Supply, Burlington NC), mixed with crushed dogfood (Techni-Cal ADULT®, Martin Pet Foods, Canada). Fully matured females were mated with a single male and different males were used for each female in order to avoid offspring from different females being half-siblings. The young descending from eight eggsacs were chosen for the experiment. These eggsacs hatched within a period of four days and when hatchlings were 4 ± 1 days old, they were weighed to the nearest μg . Pairs of hatchlings descending from the same eggsac ($n = 71$) or from different eggsacs ($n = 71$) were then placed in the same plastic tube (diameter 20 mm, height 60 mm). The tubes contained a plaster bottom, which was wetted frequently to maintain a permanent high humidity in the container. Body mass asymmetry was avoided by pairing spiders of almost equal body mass (mean body mass \pm SE = $421 \pm 4 \mu\text{g}$; mean weight difference \pm SE = $2.6 \pm 0.2 \mu\text{g}$; max.

weight difference = $14 \mu\text{g}$). Spiderling age (days since hatching) at the start of the experiment varied up to three days within a pair. Experimental conditions were set at 25 ± 0.1 °C; 16L:8D. The spiderlings never received any food but had constant access to water from the plaster. Spiders were checked for deaths twice daily. Cannibalism left clear marks of partly or fully digested body parts and a stereomicroscope was used in case of doubt. An outcome of the experiment was recorded when one of the two hatchlings was dead, due to starvation or cannibalism.

Experiment 2.—The purpose of this experiment was to test if the tendency to cannibalize varied among spiderlings from different eggsacs. Females of *P. amentata* with an eggsac were collected from the same location as in experiment 1, thus, we were only able to test for maternal effects on cannibalism and not for paternal effects. The spiders were taken to the laboratory and kept as in experiment 1. At 4 days of age, hatchlings from 19 eggsacs were weighed. At day 6, hatchlings of approximately the same body mass were paired (mean body mass \pm SE = $519 \pm 3 \mu\text{g}$; mean weight difference \pm SE = $2.7 \pm 0.2 \mu\text{g}$; max. weight difference = $13 \mu\text{g}$). In all pairs, the two hatchlings descended from the same eggsac ($n = 205$ pairs, 4–17 pairs from each eggsac). Experimental conditions and procedures were the same as in experiment 1.

Data analysis.—Differences in the cause of death between kin and non-kin hatchling pairs were analyzed using the Pearson statistic. The latency to cannibalize between kin and non-kin were analyzed using Student's *t*-test, after testing for equal variances (Bartlett's Test, $\alpha > 0.05$). Linear regression was used to test for correlation between mean body mass of pairs and the time spent before one of the two hatchlings died from either cannibalism or starvation. Regression lines were analyzed using Analysis of Covariance (ANCOVA), with body mass as the covariate. First, we tested for equal slopes and if they were not significantly different, we tested if intercepts were equal and calculated means adjusted for the covariate (least squares means). We used logistic regression to test if hatchlings from different eggsacs differed in their probability to cannibalize or to die from starvation. All statistical analyses were performed with JMP 5.0 for Windows (SAS Institute).

RESULTS

Experiment 1.—The proportion of pairs resulting in a cannibalistic event was not affected by kinship, i.e. whether or not the two spiders in a pair originated from the same eggsac (Pearson $\chi^2 = 0.26$, $P = 0.61$; siblings 41 %, non-siblings 45 %, $n = 142$). Furthermore, the time passing until a cannibalistic act occurred did not differ between sibling and non-sibling pairs (t-test, $DF = 59$, $P > 0.80$; siblings = 8.82 ± 0.40 days \pm SE, non-siblings = 8.99 ± 0.49 days \pm SE). Thus, we found no evidence that relatedness affected the cannibalistic tendency in hatchlings. In our description of general patterns of cannibalism below, we therefore pool data from siblings and non-siblings.

Fig. 1 shows the relationship between average body weight of hatchling pairs and the time until one of the two hatchlings died. The data indicate a presence of three different cannibalistic strategies. One group of hatchlings never cannibalized (57%) and consequently died from other reasons than cannibalism. In this non-cannibalistic group, there was a positive correlation between mean body mass and survival time of the first dying hatchling (linear regression, $t = 8.45$, $n = 79$, $P < 0.0001$; $R^2 = 0.48$). A similar type of positive correlation was found in pairs where cannibalism happened after 3 days of the experiment (33% of all pairs; linear regression, $t = 6.95$, $n = 47$, $P < 0.0001$; $R^2 = 0.52$). The regression line of spiders cannibalizing after day 3 of the experiment (i.e. > 7 days old) and the regression line of spiders dying from other reasons than cannibalism did not have significantly different slopes (ANCOVA, $SS = 0.04$, $F = 0.03$, $P = 0.85$, Fig. 1), but the intercepts of the two regression lines differed significantly (ANCOVA, $SS = 4.53$, $F = 4.20$, $P = 0.04$). The least squares means of survival days adjusted for body mass showed that spiders cannibalizing after day 3 (> 7 days old), did so on average 0.4 days (i.e. less than 10 h) before equal sized spiders would die from other reasons than cannibalism (Fig. 2). Besides the two strategies where spiders either died or cannibalized in a size dependent way, 10% of the pairs cannibalized early, within the first 3 days of the experiment. Among these pairs, there was no correlation between mean body mass and the time passing until cannibalism

occurred (linear regression, $t = 0.93$, $n = 14$, $P = 0.37$, $R^2 = 0.07$).

Experiment 2.—We found the same three cannibalistic patterns in this experiment as described from experiment 1 (Fig. 3). Either spiders did not cannibalize at all (64.4%); they cannibalized in a body mass dependent way (25.4%, linear regression, $n = 52$, $t = 4.57$, $P < 0.0001$, $R^2 = 0.29$); or they cannibalized within the first day of the experiment (i.e. before being 7 days old) regardless of body mass (10.2%, linear regression, $n = 21$, $t = 0.18$, $P = 0.86$, $R^2 = 0.002$).

Mother identity did not affect whether or not cannibalism occurred within a pair of hatchlings (logistic regression, Wald $\chi^2 = 23.05$, $DF = 18$, $P = 0.19$). However, when cannibalism did occur, the latency to do so varied significantly among hatchlings from different eggsacs, after correcting for the effect of body mass (ANCOVA on the latency to cannibalize with mean body mass as covariate, $DF = 13$, $SS = 186.5$, $F = 5.20$, $P < 0.0001$, Fig. 4); five eggsacs in which fewer than three pairs cannibalized were omitted from this analysis, thus, 14 eggsacs were included with a total of 65 pairs.

DISCUSSION

The results of this study indicate that three different cannibalistic strategies exist in the wolf spider hatchlings. Either we observed no cannibalism, late and size dependent cannibalism, or early and size-independent cannibalism. This pattern appeared in two separate experiments, which suggests that it is a general pattern of this wolf spider species.

More than half of the spiderlings belonged to the group that never cannibalized and consequently died from other causes than cannibalism. As all spiderlings were deprived of food we expect that the main part of these non-cannibalizing spiders died from starvation. The body mass of an animal probably correlates positively with the amount of nutrient reserves that are stored in the body. Furthermore, light animals are often found to have proportionally higher specific metabolic rate than heavier animals (Edwards 1946; Phillipson 1963). Together, these two factors may explain the observed pattern of lighter spiders dying from starvation sooner than heavier spiders.

The spiders that did cannibalize could be

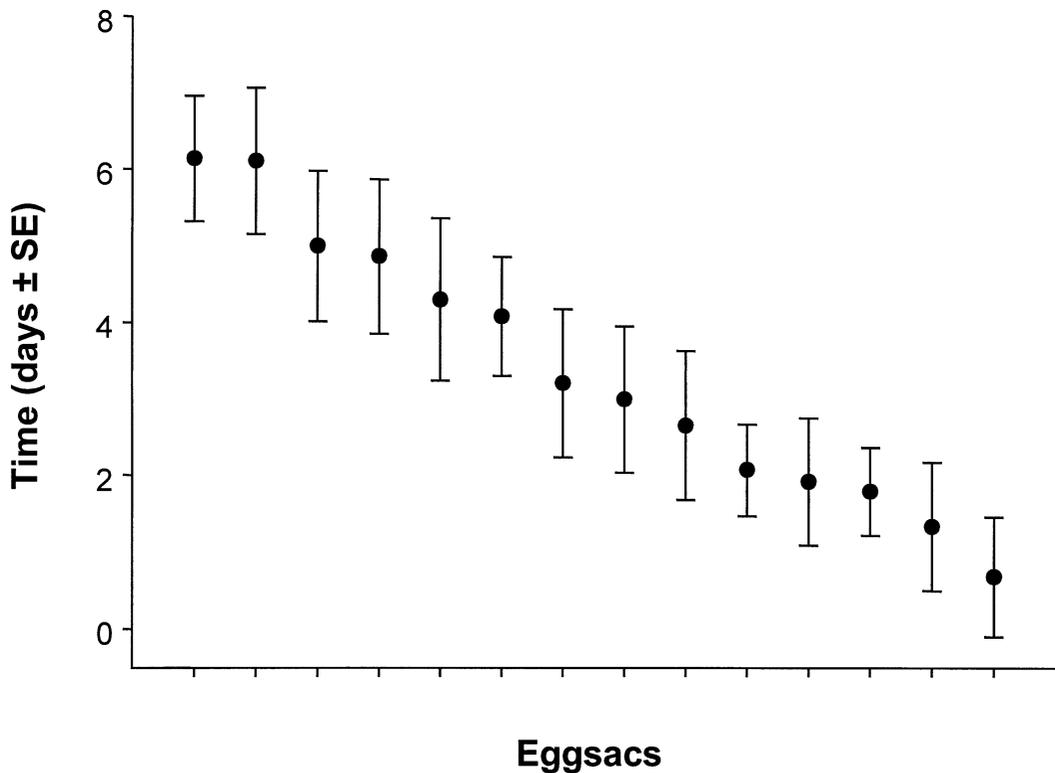


Figure 4.—Effect of eggsac origin on the latency to cannibalize in pairs of equal sized siblings (Experiment 2). Points show the time passing until cannibalism occurred adjusted for the effect of body mass ($n = 3$ – 9 pairs of siblings per eggsac, five eggsacs were not included because less than 3 pairs of spiderlings from these eggsacs cannibalized).

divided in two groups: a group where the onset of cannibalism was dependent on body mass, and a group, which cannibalized early. In the body mass dependent cannibalism lighter pairs cannibalized earlier than heavier pairs, which suggests that the latency to cannibalize depended on their level of nutrient reserves. In fact, this group of spiderlings generally waited to cannibalize almost until the time when they were predicted to die from starvation, which suggests that they chose to cannibalize as a very last option. In a relatively small proportion of spider pairs (ca. 10%) cannibalism appeared early in the experiment regardless of their body mass. This group of spiders did not seem to be under severe food stress when the cannibalism occurred, suggesting that these spiders had a higher keenness to cannibalize. Different cannibalistic strategies among individuals within a species have also been observed in other animals. In salamanders (Lannoo et al. 1989)

and spadefoot toad tadpoles (Pfennig et al. 1993) individuals can be divided into cannibalistic and non-cannibalistic forms and cannibalistic individuals are often characterized by actual morphological and physiological differences that enhance this feeding strategy.

Field studies have shown that conspecifics comprise a large part of the diet in juvenile and adult wolf spiders (Edgar 1969; Hallander 1970). However, in this experiment spiderlings were rather reluctant to cannibalize, even though they were kept in the same container with no escape possibilities. Why did the majority of hatchlings refuse to cannibalize when the consequence of such a decision is death from starvation? Our experimental setup does not provide a clear answer to that question. One likely explanation is that they fear the cost of retaliation.

The risk associated with attacking decreases as the asymmetry in body mass/size increases. Samu et al. (1999) found that the body mass

ratio between two juvenile spiders was the most important factor influencing cannibalism, and cannibalism was not observed within 24 hours if the body mass ratio was less than 2:1 (predator:prey). Here we paired spiderlings of equal body mass, which in principle have similar predatory abilities and therefore provide roughly 50/50 chance of dying, unless there are different risks associated with being an attacker or a defender. The fact that a large proportion of the spiders postponed cannibalism almost until they died from starvation indicates that risk of retaliation or other factors inhibit cannibalism. It is possible that cannibalism occurred when the risk of dying from starvation had outweighed these risks. We cannot exclude the possibility that some of the cannibalistic events happened after one of the spiders was dead or almost dead from starvation. If so, then cannibalistic acts should only confer little or no risk of retaliation. Another potential cost of cannibalism is the risk of receiving pathogens from conspecific prey (Pfennig et al. 1998). If this is a real cost in the field, it would explain the general reluctance to cannibalize in the majority of the spiders. However, we are not aware of any pathogens that might cause such a risk in wolf spiders, especially not among young hatchlings.

A general inhibition of cannibalism can be an indirect method to avoid eating relatives. Where such an inhibition has been demonstrated, it is often expressed in certain life stages. Filial cannibalism, for example, is inhibited in reproductively active females of the wolf spider *Scizocosa ocreata* (Wagner 1995). Moreover, cannibalism was less frequent in the 2nd instar of the wolf spider *Hogna helluo* (Walckenaer 1837), compared to 3rd instar spiderlings (Roberts et al. 2003). Avoidance of related prey can also be direct through kin recognition where relatives are recognized and disregarded as prey (Pfennig 1997). There is one study that supports kin discrimination among young spiderlings in a wolf spider (Roberts et al. 2003). In this species a higher frequency of cannibalism was observed in pairs of non-siblings compared to pairs of siblings. In the present experiment, we did not find any evidence supporting the hypothesis that siblings cannibalized each other less frequently than non-siblings. Thus, either *Pardosa amentata* hatchlings cannot recognize a

sibling from a non-sibling, or they do not care and cannibalize nevertheless. These results are also in contrast to data on social (*Diaea ergandros* Evans 1995) and sub-social (*Stegodyphus lineatus* Latreille 1817) spiders (Evans 1999; Bilde & Lubin 2001), in which the studies showed kin recognition and kin discriminating cannibalistic behavior. Compared to solitary spiders, social spiders and sub-social spiderlings spend long periods of time close to relatives and it is possible that such frequent encounters with relatives are a requirement for the evolution of kin recognition (Bilde & Lubin 2001). Spiderlings of a clutch do not leave their mother's abdomen at the same time but dispersal is distributed over several days and over a relatively large area (D. Mayntz, pers. obs.). Thus, the only time wolf spiders have a high chance of meeting siblings is when the spiderlings are gathered on their mother's abdomen. Avoiding cannibalism of kin may possibly be accomplished during other routes than actual kin recognition. For example, intra-brood cannibalism in *Pardosa pseudoannulata* (Bösenberg & Strand, 1906) rarely occurred due to the small size difference within the brood (Iida 2003). Moreover, *P. pseudoannulata* did not seem to cannibalize siblings less frequently than non-siblings (i.e. no evidence for kin recognition).

When we tested for variation in cannibalistic tendencies among hatchlings from different eggsacs, we did not find any evidence that maternal effects influenced whether or not cannibalism happened. However, when cannibalism did occur, hatchlings from different eggsacs showed variable latencies to do so (Fig. 4). We collected the eggsacs in the field. This made it impossible for us to assess the genetic influence from the fathers, and prevented us from separating genetic effects from other maternal effects that might have affected the hatchlings' tendency to cannibalize. Beyond pure genetic factors, possible maternal factors affecting cannibalistic tendency may include the nutritional history of the mother, the age of mother, or size of the brood. Heritability of cannibalistic behavior has been shown in fish, flour beetles, corn borers and ladybird beetles (Thibault 1974; Stevens & Mertz 1985; Tarpley et al. 1993; Wagner et al. 1999) but so far not in spiders. Half-sib experiments or actual selection experiments are needed before we can clarify how much ge-

netic effects contribute to the observed variation in the latency to cannibalize.

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