Biocontrol of western flower thrips by heteropteran bugs
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Density-dependent survival and reproduction of the predatory bug *Orius insidiosus* and its consequences for mass rearing

Survival and reproduction of the predatory bug *Orius insidiosus* (Say) (Heteroptera: Anthocoridae) were determined at low and high predator densities to assess the consequences for mass rearing. Nymphal survival in groups of 15 individuals, which hatched during 3 h, 2 days or 4 days, was compared with nymphal survival of isolated nymphs. Eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) were supplied *ad libitum*. When the variation in hatching age was 3 h or 2 days, survival until adult eclosion in groups was not lower than of single nymphs. However, when the variation in hatching age was 4 days, survival was lower during the second part of nymphal development. Thus, for mass-rearing purposes, eggs should be collected at least every second day to synchronize age. Providing only 1 prey egg per day per individual during the first 3 days after hatching, did not result in a higher mortality of nymphs kept in groups. The presence of a gravid female in a group of nymphs increased mortality, and thus it is important to keep adults away from rearing jars with young nymphs. Adult survival and reproduction in groups of 8 females and 8 males were compared with survival and reproduction of single pairs (female and male). Food supply was proportional to the number of surviving individuals. Three weeks after adult eclosion, adult survival was not significantly lower in groups, but fecundity was 18% lower. Adult survival and egg production were also recorded in a laboratory colony of *O. insidiosus*. Mortality of newly-eclosed adults was three times higher in females than in males. In rearing jars with predatory bugs of less than 1 month old (since oviposition) female adult survival was 0.73-0.83. When all females had commenced oviposition, the daily ovipositional rate varied from 3.23 to 3.66, which is 50% lower than in single pairs. Possible explanations and remedies for the reduction in oviposition are discussed.

Within a few years *Orius* predatory bugs have become commonly used biological control agents in European greenhouses. Many commercial insectaries mass produce this predator. To improve mass-rearing efficiency of *Orius insidiosus* (Say), Van den Meiracker studied the influence of the amount of food on survival, developmental rate, adult size and reproduction (Chapter 2). In this paper the effects of the predator density on its rearing efficiency are investigated.

High predator densities in mass-rearing systems may promote cannibalism and mutual interference. Cannibalism has been observed in the laboratory in several *Orius* species, e.g. *O. insidiosus* (Barber, 1936), *Orius tristicolor* (White) (Askari & Stern, 1972), and *Orius tantillus* (Motschulsky) (Mituda & Calilung, 1989). Cannibalism has also been observed in the field in *O. insidiosus* in corn (Dicke & Jarvis, 1962) and sweet pepper (P.M.J. Ramakers, pers. comm.), and in *Orius suteri* (Poppius) in potato (Nakata, 1994). Rearing difficulties due to cannibalism have been
reported for *Xylocoris flavipes* (Reuter) (Arbogast, 1979), and *Anthocoris nemorum* (L.) (Jacobson, 1991). Mass production of *O. tristicolor* was hampered by cannibalism (Gilkeson *et al.*, 1990) and for the same reason Oetting & Beshear (1991) expected mass-rearing problems with *O. insidiosus*. Although it became evident that cannibalism is no serious impediment for rearing *Orius*, it may cause losses that affect mass-rearing efficiency. Less is known about mutual interference. Evans (1976) found that mutual interference between adult *Anthocoris confusus* Reuter lead to a density-dependent decrease in egg production, and may thus affect rearing efficiency.

The objective of this paper is to study whether cannibalism and mutual interference affect rearing efficiency of *O. insidiosus* when food supply is adequate. Not all individuals in a culture develop at the same rate, which results in variation in size. Variation in size may promote cannibalism, since cannibalism often involves large individuals preying on smaller ones (Polis, 1981). In an *Orius* culture a substrate for oviposition is provided, e.g. bean pods. Variation in size will be increased when the collection frequency of bean pods with eggs is decreased. Experiments were done to find out if cannibalism occurs during nymphal development. The effect of variation in egg-collection frequency was tested, using nymphs which hatched during different time intervals. Food requirements of developing nymphs change continuously. Therefore, the first experiment was done under the condition of ample food supply. The experiment was repeated in first instars, provided a much lower but sufficient food supply. When *Orius* eggs are collected females may accidentally be transferred, when they still have their ovipositor in the bean pods. The influence of such stowaways on nymphal survival was also studied, to find out if extra effort is necessary to avoid accidental transfer.

The possible effect of cannibalism and mutual interference on adult survival and reproduction was examined, comparing a group of 8 females and 8 males with a pair of a female and a male. The actual effect of high rearing densities in cultures was also studied. Adult survival and ovipositional rates of cohorts of different ages were determined in a laboratory colony of *O. insidiosus*.

**MATERIALS AND METHODS**

**Rearing method**

The laboratory colony of *O. insidiosus* was initiated in June 1989 with a strain from Georgia (U.S.A.). Predatory bugs were kept in plastic one-litre jars with four ventilation holes covered with fine nylon gauze. The jars were lined with crumpled paper tissues (Kleenex®) to provide hiding places and reduce cannibalism. Eggs of the flour moth, *Ephestia kuehniella* Zeiler, supplied by Koppert Biological Systems (The Netherlands), were provided as food twice a week. These eggs have been used successfully in cultures of other anthocorids (e.g. Daumal, 1968; Samsøe-Petersen *et al.*, 1989). The weekly supply amounted approximately 15,000 eggs per jar. Bean pods (*Phaseolus vulgaris* L.) were used as oviposition sites (Isenhour & Yeargan, 1981). Beans with *Orius* eggs were collected from jars with adult bugs and placed in fresh jars twice a week. After hatching, nymphs were provided with a fresh bean pod.
to ensure a regular supply of moisture. After adult eclosion fresh beans were provided twice a week for oviposition, as described above. In this way a synchronized rearing system could be maintained, with each jar containing insects varying 3-4 days in age. See Table 3 for the number of adults per jar. This number was not determined by the number of predator eggs, which was usually several times higher, but rather by food supply and probably cannibalism. Jars were usually discarded after 4 weeks. This is approximately 2 weeks after adult eclosion, but well before the end of the oviposition period. In one aspect the rearing method is essentially different from other methods described for rearing anthocorids, e.g. *O. insidiosus* (Isenhour & Yeargan, 1981), *O. majusculus* (Alauzet et al., 1992; Fischer et al., 1992), and *Anthocoris nemoralis* (F.) (Samsøe-Petersen et al., 1989). These authors used two transfers per cycle: (1) eggs were transferred from oviposition containers to separate containers for nymphal development, from which (2) adults were transferred to oviposition containers. Rearing and experimental conditions were 25°C, 75% r.h., and L16:D8.

**Effect of predator density on nymphal survival**

Nymphs were collected 0-3 h after hatching and divided over three experimental treatments. Each treatment consisted of eight 25 ml glass pots with 15 nymphs each. The glass pots were lined with filter paper, and were closed with snap caps. Nymphs were given ample supply of *E. kuehniella* eggs (on paper sheets of 40 × 18 mm) and a piece of bean pod twice a week. In the first treatment all nymphs were put in the pots simultaneously. In the second treatment newly-hatched nymphs were added to the pots in three groups of five nymphs with intervals of 24 h, thus creating a hatching range of 2 days. In the third treatment newly-hatched nymphs were added to the pots in five groups of three nymphs with intervals of 24 h, creating a hatching range of 4 days. A control was done with 1 nymph per glass pot (*n* = 40). Survival until adult eclosion was determined.

To determine the effect of predator density when food supply just satisfies demands (rather than exceeding it), 15 newly-hatched nymphs were put in a glass pot (*n* = 8) with a piece of bean pod. The daily supply of *E. kuehniella* eggs (on paper sheets of 25 × 7 mm) per pot matched the number of surviving nymphs. This should provide a sufficient amount of food, since consumption during the first days after hatching is about 1 egg per day (Chapter 1). For comparison 40 nymphs were treated separately with 1 egg/day. Survival was determined after 3 days, which is at the time of the first moult. Net consumption was determined daily by estimating the extent of collapse of each egg (see Chapter 1).

The effect of the presence of a gravid female was tested in a 25 ml glass pot with 15 newly-hatched nymphs. Ample supply of *E. kuehniella* eggs was given (on paper sheets of 40 × 18 mm). Survival of these nymphs was compared with the treatment described above, where 15 nymphs of the same age were given ample food supply.

**Effect of predator density on adult survival and reproduction**

Eight 25 ml glass pots were provided with 8 females and 8 males, collected from the stock colony, 0-24 h after adult eclosion. *E. kuehniella* eggs were supplied every day (on paper sheets of 40 × 18 mm). Van den Meiracker found that moth 8 eggs/day per
female was adequate for optimal oviposition, and that net consumption by males was approximately 3 prey eggs/day (Chapter 2). Therefore, daily food supply amounted 8 prey eggs per female and 3 eggs per male, and was adjusted to the number of surviving individuals. A fresh piece of bean pod was provided every day for oviposition. The control treatment consisted of 16 pots with a single pair of a female and a male. Net consumption, oviposition and survival were recorded daily for 3 weeks.

Adult survival and reproduction in the laboratory colony

In June 1991 beans from five successive rearing jars were collected 3 days after their introduction into the jars, and the numbers of \textit{Orius} eggs in them were counted. This was repeated after 3 days. At that moment all dead and live predatory bugs in the five jars were counted. When newly-eclosed adults die before the pigmentation is complete they remain pale. Pale dead adults were counted to assess mortality shortly after adult eclosion. The proportion of females, adult survival, and ovipositional rate were also determined for each jar. The adults in the rearing jars originated from eggs laid during 3-4 days. Since oviposition was determined over 3-day intervals, the variation in age in the two oviposition samples was 6-7 days.

Statistical analysis

The Fisher exact test was used to compare survival at high and low predator densities. Differences in fecundity were tested using the Wilcoxon two-sample test. In all tests $\alpha$ was taken 0.05. In the case of multiple comparisons $\alpha$ was corrected to $\alpha' = 1 - (1-\alpha)^{1/n}$ ($n$ denotes the number of comparisons). Tests were one-tailed with alternative hypotheses that survival and fecundity were higher at low than at high predator density.

RESULTS

Effect of predator density on nymphal survival

Six days after hatching survival in the treatments with 15 nymphs per pot was not significantly lower than in the control (Table 1). However, during the period from 6 days after hatching until adult eclosion, survival in the treatment with a hatching range of 4 days was significantly lower than in the control treatment (Table 1). This also applies to the whole period from hatching to adult eclosion (Table 1).

When food supply was 1 \textit{E. kuehniella} egg per nymph on average, survival of nymphs in groups of 15 was 0.92 after 3 days. During this period net consumption was 95-100% of food supply. In nymphs treated separately nymphal survival (0.33) was significantly lower, while only 17-30% of the amount of food was consumed.

The presence of a gravid female in a pot with 15 nymphs resulted in a nymphal survival of 0.66, 0.65 and 0.63, 5, 6 and 9 days after hatching. Survival was significantly lower than in the absence of a female.
Table 1. Survival of nymphs of *O. insidiosus* at different densities and different ranges of hatching.

<table>
<thead>
<tr>
<th>Predator density</th>
<th>hatching range</th>
<th>Survival from hatching to 6 days old(^1)</th>
<th>Survival from 6 days old(^1) to adult eclosion</th>
<th>Survival from hatching to adult eclosion</th>
</tr>
</thead>
<tbody>
<tr>
<td>1/pot</td>
<td>3 h</td>
<td>0.93</td>
<td>1.00</td>
<td>0.93</td>
</tr>
<tr>
<td>15/pot</td>
<td>3 h</td>
<td>0.90</td>
<td>0.97</td>
<td>0.88</td>
</tr>
<tr>
<td>15/pot</td>
<td>2 days</td>
<td>0.95</td>
<td>0.98</td>
<td>0.93</td>
</tr>
<tr>
<td>15/pot</td>
<td>4 days</td>
<td>0.87</td>
<td>0.88(^2)</td>
<td>0.76(^2)</td>
</tr>
</tbody>
</table>

\(^{1}\) 5-7 days old and 4-8 days old in the series with a hatching range of 2 or 4 days respectively; \(^{2}\) Significantly different from the control (1/pot).

Table 2. Survival and fecundity of adult *O. insidiosus* 3 weeks after adult eclosion, kept at two different densities.

<table>
<thead>
<tr>
<th>Initial predator density</th>
<th>Survival Females(^1)</th>
<th>Survival Males(^1)</th>
<th>Fecundity (mean ± s.d.)(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 pair/pot</td>
<td>0.81</td>
<td>0.73</td>
<td>128.8 ± 43.0</td>
</tr>
<tr>
<td>8 pairs/pot</td>
<td>0.59</td>
<td>0.63</td>
<td>105.3 ± 14.4</td>
</tr>
</tbody>
</table>

\(^{1}\) No significant difference between the two predator densities; \(^{2}\) Significant difference between the two predator densities.

**Effect of predator density on adult survival and reproduction**

After the first day survival of adult females was always lower at a density of 8 pairs per pot than at 1 pair per pot (Fig. 1A). However, neither in females nor in males the difference in survival was significant after 3 weeks (Table 2). Average net consumption of *E. kuehniella* eggs was 95% of supply in pots with 1 pair, whereas only 0.1% was left in pots with 8 pairs. The ovipositional rate was usually lower at the highest predator density (Fig. 1B). On average the ovipositional rate was 12% lower at 8 pairs/pot than at 1 pair/pot. The mean ovipositional rate of females from single pairs was significantly higher than that of females from groups. The mean fecundity after 21 days was significantly lower in females kept at the high density (Table 2).

**Adult survival and reproduction in the laboratory colony**

The number of predatory bugs that became adult varied from 339 to 501 per jar (Table 3). The proportion of females at the time of adult eclosion was always about 0.5. Mortality before pigmentation was complete, was higher in females (12% on average) than in males (4% on average) (Table 3). From 17 to 30 days after oviposition, adult survival was relatively constant in females (Table 3). In males more variation was found. After pigmentation was completed, mortality was about
two to three times higher in males than in females. Thirty days after oviposition survival was relatively low in both sexes.

No oviposition occurred when females were younger than 17 days, but in jars with 14-21 day-old females many eggs were laid. In jars with older females the net ovipositional rate was higher and relatively constant, except in the second sample of the oldest jar (Table 4). However, the ovipositional rate per live female had not decreased in this oldest jar. The ovipositional rate per live female varied from 3.23 to 3.66.

Table 3. Proportion of females and proportion with complete pigmentation (alive and dead), and survival in rearing jars of O. insidiosus of different ages.

<table>
<thead>
<tr>
<th>Jar nr.</th>
<th>Days since Oviposition</th>
<th>n</th>
<th>Proportion of females</th>
<th>Proportion complete pigmentation</th>
<th>Survival after adult eclosion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Females</td>
<td>Males</td>
</tr>
<tr>
<td>1</td>
<td>17-20</td>
<td>423</td>
<td>0.54</td>
<td>0.81</td>
<td>0.94</td>
</tr>
<tr>
<td>2</td>
<td>20-24</td>
<td>410</td>
<td>0.52</td>
<td>0.92</td>
<td>0.96</td>
</tr>
<tr>
<td>3</td>
<td>24-27</td>
<td>366</td>
<td>0.56</td>
<td>0.87</td>
<td>0.98</td>
</tr>
<tr>
<td>4</td>
<td>27-30</td>
<td>339</td>
<td>0.48</td>
<td>0.90</td>
<td>0.97</td>
</tr>
<tr>
<td>5</td>
<td>30-34</td>
<td>501</td>
<td>0.51</td>
<td>0.88</td>
<td>0.97</td>
</tr>
</tbody>
</table>

Figure 1. Adult survival of females (A) and ovipositional rate (B) of O. insidiosus kept at two different (initial) densities.
DENSITY-DEPENDENT SURVIVAL AND REPRODUCTION OF ORIUS INSIDIOSUS

Table 4. Daily ovipositional rates of *O. insidiosus* of different ages in rearing jars.

<table>
<thead>
<tr>
<th>Jar nr.</th>
<th>Sample 1 Days since oviposition</th>
<th>Net ovipositional rate¹</th>
<th>Sample 2 Days since oviposition</th>
<th>Net ovipositional rate¹</th>
<th>Oviposition rate²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11-17</td>
<td>-</td>
<td>14-20</td>
<td>1.41</td>
<td>1.84</td>
</tr>
<tr>
<td>2</td>
<td>14-21</td>
<td>1.15</td>
<td>17-24</td>
<td>2.67</td>
<td>3.23</td>
</tr>
<tr>
<td>3</td>
<td>18-24</td>
<td>2.83</td>
<td>21-27</td>
<td>2.72</td>
<td>3.66</td>
</tr>
<tr>
<td>4</td>
<td>21-27</td>
<td>2.57</td>
<td>24-30</td>
<td>2.44</td>
<td>3.25</td>
</tr>
<tr>
<td>5</td>
<td>24-31</td>
<td>2.74</td>
<td>27-34</td>
<td>1.89</td>
<td>3.43</td>
</tr>
</tbody>
</table>

¹ per female that became adult; ² per female still alive at the end of the 3-day interval

**DISCUSSION**

Cannibalism usually involves larger or older individuals preying on smaller or younger individuals (Polis, 1981). Such asymmetric interactions have been observed in several anthocorids, e.g. *O. insidiosus* (Barber, 1936), *A. nemorum* (Hill, 1957), *Nidicola marginata* Harris & Drake (Peet, 1973), *Scoloposcelis mississippensis* Drake & Harris and *Lycocoris elongatus* (Reuter) (Schmitt & Goyer, 1983). In arthropods younger mobile stages may eat older stages during the vulnerable period of moulting (Polis, 1981). Hill (1957) found late instars of *A. nemorum* feeding on an adult, and Peet (1973) observed adult *N. marginata* feeding on other adults, but neither of these authors mentioned whether it concerned feeding on moulting individuals. In the present study rearing nymphs of *O. insidiosus* in groups did not influence survival as long as the age difference of the nymphs was 2 days or less. When the hatching range was 4 days, survival was lower, especially among older instars. In the laboratory colony, where eggs were collected after 3-4 days, predation on newly-moulted nymphs was frequently observed, but apparently this phenomenon is not important when ages are approximately the same and food supply is in excess of demand. These results indicate (1) that age synchronization of a mass-rearing system will reduce cannibalism, as suggested by Waage et al. (1985), and (2) that eggs should be collected at least every second day. Providing hiding places in rearing containers (e.g. using crumpled wiping tissues) may further reduce cannibalism.

Low food quality or quantity may also enhance cannibalism (Polis, 1981). Evans (1976) found no cannibalism among *Anthocoris confusus* nymphs when food supply was adequate, but cannibalism occurred at lower prey densities. Cannibalism among nymphs of *Xylocoris flavipes* increased when food supply was reduced (Arbogast, 1979). In the present study nymphal survival of *O. insidiosus*, 3 days after hatching, did not increase when food supply was reduced from excessive to just meeting demands. The fact that consumption, as well as survival were very low in the control experiment with 1 nymph per pot, indicates that finding a single *E. kuehniella* egg is difficult for a newly-hatched nymph, but essential for survival (cf. Chapter 2). Thus rearing newly-hatched nymphs in groups is the best strategy to keep survival high,
when food supply should not exceed demands. It should be investigated whether cannibalism increases in older instars when food supply adjusted to demands instead of provided ad libitum. Askari and Stern (1972) investigated cannibalism in *O. insidiosus* provided many spider mites. When the density of nymphs was increased from 1 to 6 per cage, survival to the adult stage was reduced from nearly 1 to 0.5. The difference with the present study does not necessarily reflect a difference between the strains that were used, since it is difficult to compare food quantity, food quality, space and hiding places in both experiments.

Cannibalism on eggs and newborn animals is widespread (Polis, 1981). Even when food was supplied ad libitum, the presence of a gravid female clearly reduced survival of *O. insidiosus* nymphs, especially during the first days after hatching. Askari & Stern (1972) found that survival of *O. insidiosus* nymphs decreased when the number of accompanying adults increased. Thus, for mass-rearing purposes it seems worth to avoid accidental transfer of adults, when bean pods with *Orius* eggs are collected. Cannibalism on eggs was not investigated, but does occur in anthocorids. *N. marginata* and *X. flavipes* seem to be unable to pierce their own eggs (Peet, 1973; Arbogast, 1979), but *A. nemorum*, *S. mississippiensis*, and *L. elongatus* were observed feeding on their own eggs (Hill, 1957; Schmitt & Goyer, 1983). In a mass-rearing system, egg cannibalism would be difficult to cope with, but in the stock colony *Orius* predatory bugs were never observed preying on conspecific eggs.

Cannibalism may also occur among adult anthocorids, e.g. *A. nemorum* (Hill, 1957). Barber (1936) reported female *O. insidiosus* frequently feeding upon males. In the present study, survival of adult *O. insidiosus* was relatively low in groups, but the difference with single pairs was not significant, when food supply was adequate. In the laboratory colony survival was also relatively low in the oldest jar, especially in males. *Orius* density during nymphal development may also influence adult survival, since mortality of females was negligible for more than a month after adult eclosion, when they were kept singly from hatching (Chapter 1). The relatively high mortality in the culture does not necessarily result from cannibalism. Lower food intake or increased frequency of escape reactions may also play a role.

Mortality of adults, before pigmentation was complete, appeared to be considerable in the laboratory colony, and was higher in females than in males. This difference may be explained by cannibalism when the developmental time of males is shorter than that of females. Females that are in the vulnerable period just after adult eclosion, may be cannibalized by males that have already passed this period. Originally there was no difference in developmental time between sexes in this laboratory colony. However, during a 3-year rearing period developmental times of *O. insidiosus* decreased (Van den Meiracker, 1994). This decrease was greater in males than in females, which caused a difference between sexes. As a result, predation by males on newly-eclosed females may increase. This is a potential risk for a mass rearing. Therefore it is worth checking regularly if the proportion of dead unpigmented females does not become too high.

Fecundity of insects often decreases with increasing population density (Watt, 1960; Peters & Barbosa, 1977). The ovipositional rate of *O. insidiosus* was 12% lower in groups than in single pairs. In the laboratory colony of *O. insidiosus* the ovipositional rate even more than 50% lower than in single pairs. Alauzet et al. (1992) kept 40-50 *Orius majusculus* (Reuter) pairs per 0.6 l jar (one third of the
density in the present study), which resulted in ovipositional rates of 4-5 eggs per female per day. This is also approximately 50% of the daily egg production they found in individual females at 25°C (temperature in the culture was not mentioned). In the laboratory colony of *O. insidiosus* food supply may be insufficient. Males do not eat more than approximately 3 eggs per day, whereas for females a daily supply of 8 eggs is needed for normal oviposition (Chapter 2). With approximately 200 females and 200 males in each jar, the weekly requirement would be 15,400 moth eggs, which approximates weekly supply. However, consumption may also be reduced when the accessibility of the *E. kuehniella* eggs in the culture is lower than in single female experiments. In the culture eggs are strewn into the jars, and this often results in aggregations of prey eggs on the bottom of the jar. These aggregations are not simultaneously accessible for all predatory bugs. Providing prey eggs regularly glued on paper sheets will increase accessibility, and enables removal of empty eggs.

The ovipositional rate may also be reduced by mutual interference, and that in four ways. First, although the amount of food may be adequate, interference may lead to reduced food intake through disturbance at feeding sites. This may in turn affect the number of eggs produced. Due to the adverse effect of the density of the predatory mite *Phytoseiulus persimilis* Athias-Henriot on the number of prey killed per individual, its fecundity also decreased with increasing predator density (Eveleigh & Chant, 1982a,b). In the experiment with 16 individuals of *O. insidiosus*, interference did not apparently not reduce food intake, since consumption rates equalled those of single pairs. However, interference may have reduced consumption in the laboratory colony. Second, interference may increase mobility. As a result of continuous disturbance a smaller part of the ingested food intake can be allocated to oviposition. This type of interference could be reduced by increasing the number of hiding places in a rearing container. Third, although enough mature eggs are present in the ovary, interference may directly reduce oviposition through disturbance on oviposition sites. In an *Orius* mass culture the remedy would be to supply more beans. Fourth, reduction of oviposition activity may occur merely as a response to the detection of conspecifics (to prevent offspring from starvation as a result of too much competition). This detection may have a chemical basis (Evans, 1976), and in that case it will be difficult to enhance oviposition in a mass culture.

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