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# Natural prey of the crab spider *Thomisus onustus* (Araneae: Thomisidae), an extremely powerful predator of insects

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## Abstract

The natural prey of the crab spider *Thomisus onustus* inhabiting *Eryngium* plants was studied in the Absheron Peninsula, Azerbaijan. The total percentage of specimens of *T. onustus* found while feeding was low (9.1%). However, solitary late instar and adult females exhibited a very high feeding percentage (29.9%). Other sex–age groups of *T. onustus*, including small juveniles, adult males, and females guarding egg sacs, were found feeding significantly less frequently. Investigation has shown that *T. onustus* is a polyphagous predator, with representatives of four arthropod orders found in its diet. The primary food of *T. onustus* was Diptera and Hymenoptera, which collectively accounted for 94.2% of total prey. Worker ants constituted about one-fifth of the prey, suggesting that *T. onustus* is a myrmecophagic spider. The length of prey killed by *T. onustus* ranged between 1.25 and 16.00 mm (mean 6.21 mm) and constituted from 34.4 to 587.9% (mean 194.9%) of length of their captors. The most frequently captured were large arthropods, exceeding the size of the spiders (83.1%). Small and medium-sized juveniles captured considerably larger prey (in terms of prey–predator length ratio) than late instar and adult females. Over half of their prey constituted arthropods more than two-fold larger than the spiders.

**Keywords:** *Araneae, crab spiders, diet, myrmecophagy, prey length*

## Introduction

Crab spiders (Thomisidae) belong to the group of so-called cursorial spiders, which do not use silk for prey capture. Instead, they lie in ambush and wait until prey comes within reach of their long raptorial forelegs (Foelix 1996). With over 2000 described species, the Thomisidae is among the largest families of spiders (Platnick 2006). However, despite their great diversity and potential predatory significance, few studies have addressed the natural prey of thomisids. A survey of arachnological literature revealed that quantitative data on natural diets are available for only 14 species of crab spiders (Broekhuysen 1948; Nyffeler and Benz 1979; Tarabaev 1979; Morse 1981, 1983; Ricek 1982; Lubin 1983; Dean et al. 1987; Agnew and Smith 1989; Castanho and Oliveira 1997; Schmalhofer 2001; Romero and Vasconcellos-Neto 2003; Guseinov 2006; Huseynov 2007).

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In the present paper I report on the prey of *Thomisus onustus* Walckenaer, 1805 which has not so far been studied in this respect. It is a common flower-dwelling crab spider, widely distributed throughout the Palaearctic (Marusik and Logunov 1994). *Thomisus onustus* is a medium-sized spider with adult female body length reaching up to 11 mm. The females are well known for the ability to change their colour (white, pink, yellow) to match the colour of flowers on which they take up residence (Thiery and Casas 2002). Males are much smaller than females (2–4 mm) and have constant brown coloration. In Israel, *Thomisus onustus* is characterized by an unusual and complicated life cycle (Levy 1970). There are two generations per year in this species. The first, spring, generation is much more numerous than the second, summer one. Females of both generations complete their development through the whole year and attain maturity at the respective seasons of the next year. In contrast, the lengths of developmental periods of males from different generations differ strikingly. Spring generation males grow quickly and become adult in the summer along with the second-generation females of the previous year. The developmental period of summer-generation males is extended. They pass through a larger number of moults, overwinter and reach maturity in the spring of the following year together with the first-generation females. Moreover, the developmental rates of both males and females even of the same generation are highly variable, so that individuals of various ages can be found at any time throughout the year, especially in the summer. Such a situation provides an excellent opportunity to compare the diets of different age–size classes of this species. The life cycle of the *T. onustus* population reported upon here was similar, on the whole, to that described by Levy (1970) for Israeli conspecifics, with the only difference being that summer adult spiders appeared in June at the study site, while in Israel they were found only in the second half of the summer.

## Material and methods

The investigation was carried out on Absheron Peninsula, Azerbaijan. The three primary study sites were located near Shagan, Gres, and Bina villages (40°27–30'N, 50°04–08'E), where over 95% of total observation time was spent. Additionally, there were two secondary study sites located near Gala village and Ganly-Gyol Lake. The study sites were areas of ephemeral semi-desert covered with dwarf shrubs, *Eryngium biebersteinianum* Nevski, *Alhagi pseudoalhagi* (MB), *Noaea mucronata* (Forsk.), and herbs and grasses, predominantly *Calendula persica* C.A.M., *Senecio vernalis* Willd. & Kar., *Medicago denticulata* Willd., *Carduus arabis* Jaqu., *Hirschfeldia incana* (L.), *Erodium cicutarium* (L.), *Hedypnois cretica* W., *Pterotheca marschalliana* (Rchb.), *Anagalis coerulea* Schreb., *Poa bulbosa* L., *Aegilops biuncialis* Vis., *Avena ventricosa* Bal., *Hordeum leporinum* Link., *Koeleria phleoides* (Vill.). The habitats near Shagan, Bina, and Ganly-Gyol were additionally characterized by artificially planted pines, *Pinus eldaricus* Medw., while others were treeless.

During the study period *Thomisus onustus* was abundant only on *Eryngium biebersteinianum*, therefore observations were concentrated exclusively on this plant. The prey of spiders was sampled during three successive years: 1997 (2 July to 9 August), 1998 (14 June to 25 July), and 1999 (14 June to 31 July). A total of 50 surveys were conducted during these periods which took a total of about 113 h. All surveys were done in daylight hours between 11:00 and 21:00 h. During the surveys, *E. biebersteinianum* plants were thoroughly searched for *T. onustus*, and the mouthparts of each individual found were inspected with a hand-lense of  $\times 4$  magnification to avoid overlooking small prey. Spiders with prey in their chelicerae were captured with a transparent cup, placed in separate vials

containing 75% ethyl alcohol, and brought back to the laboratory for measurement and prey identification. Spiders without prey were left in the field. At the same time, all spiders observed were classified into the following groups: (1) adult males, which could be easily distinguished by their coloration; (2) small juveniles, including all spiders less than 5 mm in length, except for adult males; (3) solitary late instar and adult females, comprising all spiders exceeding 5 mm in length and without egg sacs; (4) females guarding their egg sacs. During every survey the numbers of spiders with and without prey were counted separately within each of these groups.

## Results

In total, 1329 specimens of *Thomisus onustus* were observed, 120 of which (9.0%) had prey in their chelicerae. One juvenile was consuming two prey items simultaneously. Thus the actual percentage of feeding events was slightly higher (9.1%). Among spiders observed, 117 males (five prey records, ~4.3%), 1091 small juveniles (90 prey records, ~8.2%), 77 solitary late instar and adult females (23 prey records, ~29.9%), and 44 females with egg sacs (three prey records, ~6.8%) were recorded. The percentage of feeding specimens among solitary late instar and adult females was significantly higher than those among other sex-age groups ( $\chi^2=44.663$ ;  $df=3$ ;  $P<0.001$ ). In contrast, there was no statistically significant difference between small juveniles, males and egg-guarding females in this respect ( $\chi^2=2.379$ ;  $df=2$ ;  $P>0.1$ ).

The prey of *T. onustus* were distributed among four orders of arthropods (Table I), including three from the class Insecta (Diptera, Hymenoptera, Heteroptera), and one from the class Arachnida (Araneae). The dominant prey orders were Diptera and Hymenoptera, which collectively made up 94.2% of total prey. The majority of dipterans (93.8%) constituted flies (Brachycera and Cyclorhapha). The most frequently captured flies were *Cytherea dispar* Loew, 1873 (Bombyliidae) and *Phthiria* sp. (Phthiriidae), which accounted for over half of the dipteran prey and were, respectively, the first (24.8%) and the third (11.6%) most abundant prey species of *T. onustus*. Other brachycerans included various representatives of Syrphidae, Scenopinidae, Milichiidae, Calliphoridae, Tachinidae, Stratiomyidae, Mythicomyiidae, and Chloropidae. Nematocerans were represented by two species of Lestremiidae and two of Ceratopogonidae. Among hymenopteran prey the most abundant were Formicidae (42.8%). The bulk of ants (16 individuals) consisted of *Cataglyphis aenescens* Nylander, 1849, which was the second abundant prey species in the total diet (13.2%). Additionally, three *Cataglyphis setipes* (Forel, 1894) and two *Plagiolepis* sp. were caught by *T. onustus*. All captured ants were workers. Bees of the family Halictidae were also a considerable prey component. Most of these were represented by *Nomioides* sp. (13 individuals), followed by three *Halictus* spp. Other hymenopterans included venomous wasps, Sphecidae (four *Tachisphex* spp. and one *Cercerys* sp.), and parasitic wasps (two Bethyloidea and five Chalcidoidea). The rest of the insect prey was a heteropteran bug (Anthocoridae). Spiders constituted only 5.0% of the total prey. They were represented by five juvenile conspecifics and one juvenile *Kochiura aulica* (C. L. Koch, 1838) (Theridiidae). In the cases of cannibalism, the predators were an adult male, a pre-adult female, and three juveniles.

In total 118 prey items were measured. Their length varied from 1.25 to 16.00 mm (mean  $\pm$  SD,  $6.21 \pm 3.31$  mm) and constituted from 34.4 to 587.9% ( $194.9 \pm 97.1$ %) of the length of their captors, which ranged from 1.37 to 10.50 mm ( $3.61 \pm 2.38$  mm). The size distribution of the prey in relation to the sizes of their captors, which are divided into four

Table I. Prey of *Thomisus onustus* classified by order and family.

Prey	N	%
Insecta		
Diptera	[65]	[53.7]
Bombyliidae	30	24.8
Phthiriidae	14	11.6
Syrphidae	4	3.3
Scenopinidae	4	3.3
Milichiidae	4	3.3
Stratiomyidae	1	0.8
Calliphoridae	1	0.8
Tachinidae	1	0.8
Mythicomyiidae	1	0.8
Chloropidae	1	0.8
Lestremiidae	2	1.6
Ceratopogonidae	2	1.6
Hymenoptera	[49]	[40.5]
Formicidae	21	17.4
Halictidae	16	13.2
Sphecidae	5	4.1
Bethylidae	2	1.6
Chalcididae	2	1.6
Pteromalidae	1	0.8
Eurytomidae	1	0.8
Eulophidae	1	0.8
Heteroptera	[1]	[0.8]
Anthocoridae	1	0.8
Arachnida		
Araneae	[6]	[5.0]
Thomisidae	5	4.1
Theridiidae	1	0.8
Total	121	100.0

groups including adult males and three size classes of juveniles and females (see Table II), is shown in Figure 1. The prey not exceeding the length of spiders constituted only 16.9% of total prey measured, while the rest of the prey items were larger than their captors. Over half (52.6%) of the large prey exceeded the length of their captors more than twice. These very large prey were captured almost exclusively by small and medium-sized *T. onustus*, whereas only one prey of late instar and adult females exceeded 200% of spider body length (Figure 1). Even prey more than three times greater than the lengths of the spiders constituted a considerable fraction (>20%) in the diet of small juveniles (Figure 1).

Table II. Length of prey of different sex-age groups of *Thomisus onustus*.

Sex-age group	n	Length of spiders (mm)		Length of prey (mm)		Length of prey (%)	
		Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
Males	4	2.30–3.30	2.73 $\pm$ 0.42	2.35–8.00	4.59 $\pm$ 2.41	87.0–242.4	164.3 $\pm$ 65.7
Small juveniles	69	1.37–3.00	2.08 $\pm$ 0.43	1.25–9.70	4.57 $\pm$ 2.54	55.0–587.9	217.2 $\pm$ 107.9
Medium-sized juveniles	22	3.05–5.75	4.03 $\pm$ 0.85	1.25–12.50	7.86 $\pm$ 2.46	36.5–310.4	201.6 $\pm$ 74.5
Late instar and adult females	23	6.15–10.50	7.93 $\pm$ 1.29	2.15–16.00	9.82 $\pm$ 2.52	34.4–228.6	126.8 $\pm$ 40.6

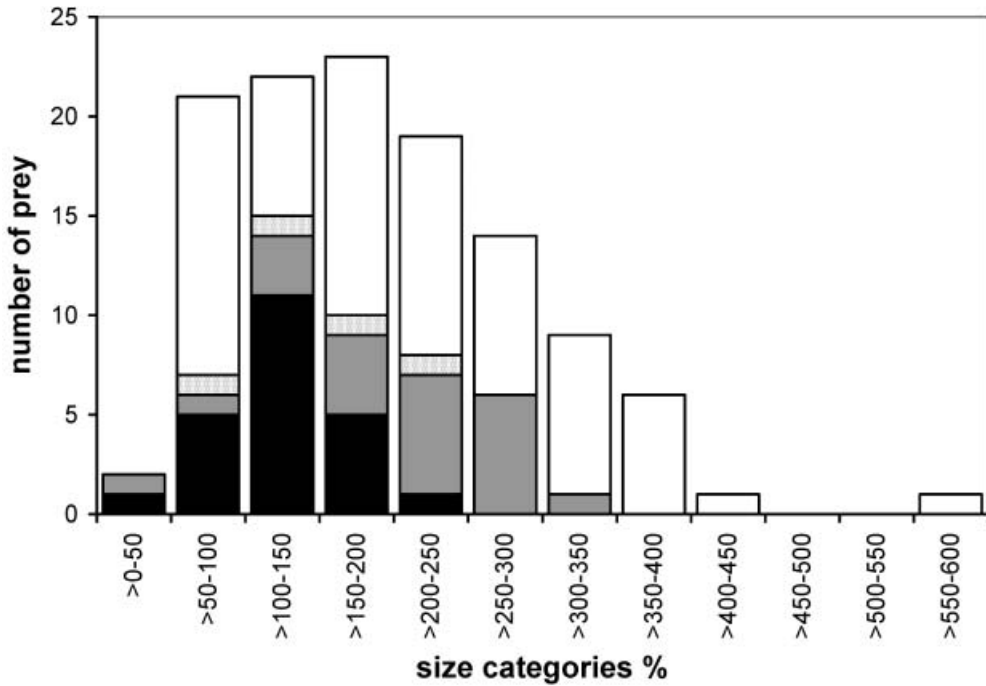


Figure 1. Distribution of prey of different sex-age groups of *Thomisus onustus* (black, late instar and adult females; grey, medium-sized juveniles; dotted, adult males; white, small juveniles) in different size categories (body lengths of prey expressed as percentages of the body lengths of their captors).

Because of this fact the mean relative lengths of prey of small and medium-sized juveniles were considerably greater than that of late instar and adult females (Table II). This difference in relative length of prey captured between various age-size groups of *T. onustus* is due to the ability of small- and medium-sized juveniles to catch prey as large as that caught by late instar and adult females. All groups of large Diptera (Bombyliidae, Phthiridae, Syrphidae) captured by females were also taken in numbers by small and medium-sized juveniles (Table III). While these flies on average only slightly exceeded the length of large *T. onustus*, their mean length was more than twice larger than that of medium-sized juveniles and more than three times larger than that of small juveniles. Moreover, small juveniles captured large ants, *Cataglyphis setipes*, which exceeded their length by more than three times. The only other group which fed on this ant was males with size comparable to that of small juveniles (Table III).

## Discussion

The total percentage of specimens of *Thomisus onustus* found while feeding is comparable to those recorded in other crab spiders (Nyffeler and Benz 1979; Dean et al. 1987; Romero and Vasconcellos-Neto 2003). However, the percentage of feeding specimens among solitary late instar and adult females is unusually high (29.9%), i.e. nearly every third observed spider was in possession of prey. I am unaware of such a high feeding percentage reported for any other cursorial spider. It might be suggested that this fact is due to the exceptionally large numbers of insect visitors to *Eryngium*, but solitary late instar and adult

Table III. Prey of different sex-age groups of *Thomisus onustus* classified by body length and ecological categories.

Prey type	Late instar and adult females	Medium- sized juve- niles	Small juve- niles	Males
Large prey, >6 mm				
Flies (Bombyliidae, Phthiriidae, Syrphidae)	16	16	16	–
Wasps (Sphecidae)	4	1	–	–
Bees ( <i>Halictus</i> )	2	1	–	–
Ants ( <i>Cataglyphis setipes</i> )	–	–	1	1
Medium-sized prey, 3–6 mm				
Flies (Tachinidae, Stratiomyidae, Calliphoridae, Scenopinidae)	–	–	7	–
Wasps (Chalcididae)	–	–	1	–
Bees ( <i>Nomioides</i> )	–	3	9	1
Ants ( <i>C. aenescens</i> )	–	–	14	1
Small prey, <3 mm				
Flies (Milichiidae, Chloropidae, Mythicomyiidae, Lestremiidae, Ceratopogonidae)	–	–	9	–
Wasps (Bethyidae, Chalcididae, Pteromalidae, Eulophidae, Eurytomidae)	–	–	6	–
Ants ( <i>Plagiolepis</i> )	–	–	2	–
Spiders (Thomisidae, Theridiidae)	1	–	4	1
Bugs (Anthocoridae)	–	1	–	–

females of another crab spider inhabiting *Eryngium*, *Runcinia grammica* (C. L. Koch, 1837) fed ca 2.5 times less frequently (Huseynov 2007). So, the extremely high feeding frequency of solitary late instar and adult females of *T. onustus* remains to be explained.

After oviposition crab spiders attend their egg sacs. Unlike some other cursorial spiders (e.g. Salticidae, Clubionidae, Gnaphosidae), thomisid females do not construct a silken chamber enclosing the mother with her egg sac. Thus, they are able to catch prey during the egg-guarding period. The feeding rate of guarding females of flower-dwelling thomisid *Misumena vatia* (Clerck, 1757) was found to be rather low (Morse 1987). *Thomisus onustus* usually attach their egg sacs to *E. biebersteinianum* heads. This habit significantly increases the probability of prey capture by guarding females of this spider, in comparison to *M. vatia*, females of which deposit their sacs on leaves, far away from flowers (Morse 1985). Indeed, guarding females of *T. onustus* fed more frequently than those of *M. vatia* (6.8% versus 0.6%).

The investigation has shown that *T. onustus* is a polyphagic predator feeding primarily on insects. Among the dominant prey groups of *T. onustus*, Diptera and winged Hymenoptera are typical prey of flower-dwelling crab spiders, but ants are not (Broekhuysen 1948; Nyffeler and Benz 1979; Morse 1981, 1983; Ricek 1982; Schmalhofer 2001). Worker ants possessing effective defensive equipment (strong mandibles, formic acid, hard cuticle) are not palatable prey to most cursorial spiders and laboratory experiments have shown that *M. vatia* avoid attacking them (Nentwig 1986). The high proportion of worker ants in the diet of *T. onustus* found during the present study unambiguously indicates that it is a competent ant predator. The only other flower-dwelling thomisid found to feed frequently on ants is *Misumenops argenteus* (Mello-Leitao, 1929) from Brazil (Romero and Vasconcellos-Neto 2003).

Among non-web-building spiders thomisids are prominent for their ability to catch large prey, a fact that has been repeatedly emphasized by thomisid students (Lovell 1915; Hobby

1931, 1940; Bristowe 1941; Morse 1981; Ricek 1982). In feeding experiments, most cursorial spiders preferred prey not exceeding 100% of their size, whereas crab spiders, *Xysticus cristatus* (Clerck, 1757), readily accepted insects larger than themselves (Nentwig and Wissel 1986). It was not unexpected, therefore, to find that *T. onustus* fed mostly on large prey, exceeding its own size. However, small juveniles of this species frequently captured exceedingly large prey. It was surprising to find that most common prey of these spiders exceeded their length more than twofold (mean relative prey length 217.2%), and the greatest prey–predator length ratio was nearly 600%. Sometimes the prey (especially flies) were so large compared to the size of their captors that spiders were almost invisible near their victims' bodies (Figure 2A–C). In such cases attention was attracted only by the unnatural position of flies hanging from flowers without any visible support. After careful inspection a tiny spider consuming the fly and preventing it from falling was always found. It is difficult to understand how these minute spiders could hold their heavy victims and even more difficult to imagine how they could overcome the struggle of flies during the first seconds after capture. The task becomes even more difficult when the prey is a large ant with hard cuticle and strong mandibulae. However, juvenile *T. onustus* occasionally captured workers of *C. setipes*, which is the largest ant at the study area (Figure 2D). To my knowledge, none of the cursorial spiders studied so far is comparable to juvenile *T. onustus* in this respect. The question arises: why did not *T. onustus* females catch prey exceeding their size so much? Adult crab spiders have been reported to feed on very large prey such as

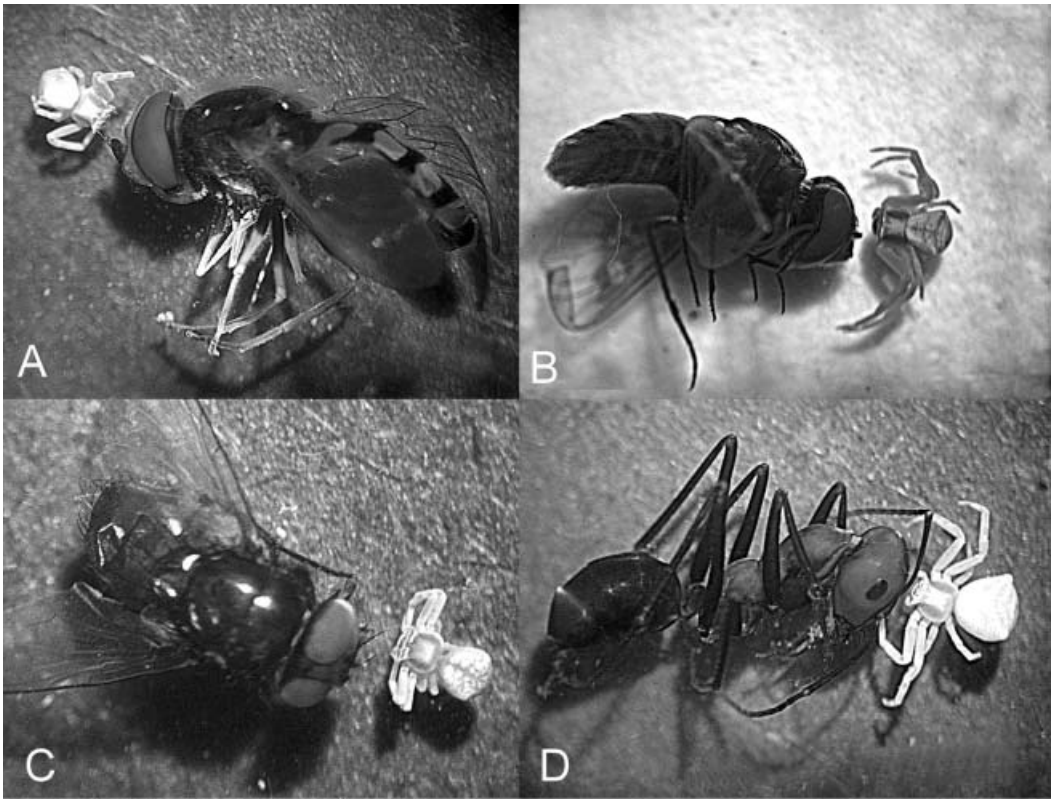


Figure 2. Some of the largest prey captured by *Thomisus onustus* juveniles together with their captors. (A) Syrphid fly; (B) bombyliid fly; (C) calliphorid fly; (D) *Cataglyphis setipes* ant.



bumblebees, dragonflies, large butterflies, and wasps (Lovel 1915; Hobby 1931; Bristowe 1941; Morse 1981). However, such large insects were not observed on *E. biebersteinianum*. The largest potential prey visiting this plant in more or less considerable numbers were sphecid wasps (*Tachisphe* spp.), with size comparable to that of honeybees. Thus, comparatively low mean relative length of prey of *T. onustus* females is probably due to the absence of very large insects in their habitat. This assumption is confirmed by the fact that medium-sized and large individuals of *T. onustus* had very similar diets. On another plant a *T. onustus* female was observed eating a praying mantid, *Empusa pennicornis* Pallas, 1773, which was approximately four times larger than the spider. This observation suggests that *T. onustus* females are capable of killing not only very large, but also very dangerous prey; mantids themselves are aggressive arthropod predators. Concerning *T. onustus* males, Levy (1970) wrote "...the adult males hardly feed at all, or at most, prey on fruit-flies or similar tiny insects". The present observations are in contrast to this assertion. Of four prey items taken from *T. onustus* males, three were considerably larger than their captors. Moreover, these were well-armed insects, such as worker ants and bees.

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