

Host stage preference, juvenile mortality and functional response of *Trioxys pallidus* (Hymenoptera: Braconidae, Aphidiinae)

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Host stage preference, juvenile mortality and functional response of the walnut aphid parasitoid wasp, *Trioxys pallidus* were studied in laboratory constant conditions ($26 \pm 2^\circ\text{C}$, $60 \pm 5\%$ relative humidity, 16 L:8 D photoperiod). Populations of the walnut aphid, *Chromaphis juglandicola* and its parasitoid were collected from the field and reared on walnut seedlings in a growth chamber. Juvenile mortality of the parasitoid was 53.46, 8.01, 2.27 and 6.72% for the 1st to 4th instar nymphs of host aphid, respectively. *Trioxys pallidus* had a greater preference for the 3rd and 4th instar nymphs than the others. The functional response of the parasitoid was type III.

Key words: *Trioxys pallidus*, host stage preference, juvenile mortality, functional response.

Introduction

Trioxys pallidus (Haliday, 1833) (Hymenoptera: Aphidiinae) is a parasitoid of the Drepanosiphinae aphids attacking the walnut aphid, *Chromaphis juglandicola* (Kaltenbach, 1843). It was introduced to California from France in 1959 in order to control the walnut aphid (VAN DEN BOSCH et al., 1962). Its establishment was successful with high effectiveness in some areas (VAN DEN BOSCH et al., 1962). Another population of *T. pallidus* was introduced from Iran to California in 1960 for the same purpose (VAN DEN BOSCH et al., 1962). Adaptation of the Iranian strain of *T. pallidus* brought *C. juglandicola* under control in California

walnut orchards (VAN DEN BOSCH et al., 1970).

Although there are well established data concerning the relationship between *T. pallidus* and its aphid hosts very little information is available on the host stage preference, juvenile mortality and the functional response of this parasitoid. The present work is an attempt in this direction. Host stage preference can have considerable consequences for the population growth of both host and parasitoid if the development and reproduction of the parasitoid are affected by the host nymph instar at the time of parasitisation (PANDEY & SINGH, 1999). It may also be important with respect to the rearing techniques used in the mass production of the parasitoid and of the

experimental design in parasitoid studies (HAGVAR & HOFVANG, 1991). Functional response is the number of hosts attacked per parasitoid as a function of host density (SOLOMON, 1949). Handling time is defined as the time required for killing, eating or parasitizing and resting.

Material and methods

The populations of walnut aphid and parasitoid wasp were cultured on seedlings of *Juglans regia* L. grown in large plastic pots, kept in cylindrical net cages (100 × 20 cm). The studies were conducted at a constant temperature of approximately 26 ± 2 °C, relative humidity 60 ± 5% and a 16 L : 8 D photoperiod. In most experiments the testing areas were surrounded by a plastic clip cage 10 cm in diameter and 2 cm in height. Parasitoid wasps were exposed to their hosts in the clip cages attached to walnut leaves. Two sides of the clip cages were covered with a cloth mesh for ventilation in order to maintain conditions inside the cages similar to those existing in the growth cabinet (KAVALLIERATOS et al., 2002; RAKHSHANI et al., 2000).

Some parts of the experiments were directed at oviposition behaviour of the female parasitoid wasp. The behaviour of female parasitoids was observed under a stereomicroscope with a soft light for at least 30 min. The experiment was performed for 6 parasitoid wasps (replicates).

Juvenile mortality of T. pallidus per each aphid nymph instars

Nine to ten adult, allata (parthenogenic viviparous) aphids were introduced into each clip cage attached to the walnut leaves. One day later, when approximately 50–60 1st instar nymphs had been produced in each cage, the adult aphids were removed. The testing unit for the 1st instar nymphs was ready, but four additional experimental series from the 2nd instar nymph to adult needed to be prepared. Thus, cultures of the 1st instar nymphs were set up to produce 2nd, 3rd, 4th nymphs and adults. The aphid nymphal instars were identified by the number of ecdysis. When the testing area was ready, one young (2–3 days old) newly mated female wasp was introduced into each clip cage. The parasitoids were left for a period of 24 h for oviposition in the aphids, and then removed using an aspirator. The procedures were repeated 5 times for each aphid instar.

The aphid-infested leaves in the clip cages were left in the growth chamber until mummification. Then leaves with mummies were clipped from the plant and placed in petri dishes for adult wasp eclosion. In all treatments, the number of developed and healthy adult aphids was assessed. The surviving aphids produced several offspring. The gross rate of juvenile mortality was calculated by subtracting the number of emerged wasps plus surviving aphids from the number of tentative nymphs. These procedures were carried out using of 90, 130, 90 and 90 1st, 2nd, 3rd and 4th instar nymphs, respectively. For the determination of the net

juvenile mortality of the parasitoid, the juvenile mortality of host aphids in each nymphal instar needed to be evaluated. Following the same procedures described, the colonies of 1st to 4th instar nymphs were prepared and allowed to develop to adults. Aphid juvenile mortality (%) was determined by subtracting the number of adult aphids from the number of initial nymphs. These procedures were carried out on 117 first, 100 second, 100 third and 95 fourth instar nymphs. The allata aphids that developed from the parasitized nymphs, produced no progenies. They accounted for the number of aphid natural mortalities. The net juvenile mortality of the parasitoid was estimated using Abbott's formula (ABBOTT, 1925):

1) Abbott's formula

$$100 \times \frac{(P_M - A_C)}{(P_M)}$$

where: P_M – gross juvenile mortality of parasitoid; A_C – aphid juvenile mortality

Host stage preference

To determine host aphid nymphal instars accepted for oviposition by *T. pallidus*, 50 aphids, 10 of each instar were placed randomly on leaves inside the clip cages. A newly mated female wasp was introduced into the test area for 24 hours, and then removed. After one day the 2nd to 4th instar nymphs and adult aphids were moved using a needle to other leaves, surrounded by a clip cage, and allowed to develop. The number of mummified aphids was recorded. The procedure was repeated 12 times.

Functional response

In order to determine the functional response of *T. pallidus*, different host densities were exposed to the parasitoid for constant periods and areas. Because the age and experience of the female wasps had important effects on the rates of parasitism, all female wasps had an equal 24 hours experience on aphid-infested leaves, 12 h after eclosion. The experiments were carried out with densities of 2, 4, 6, 8, 10, 12, 14, 18, 20, 30 and 40 3rd instar nymphs on leaves with five leaflets and a total area of 230 cm². A 36 h old female wasp was placed on each leaf, caged in a net bag for 24 h and then removed. Each density had five replications. The number of parasitized aphids was estimated from mummification. The results were analyzed using JULIANO's (1993) equations, with the use of a non-linear regression in SAS.

2) Holling Model

$$N_a = aTN_0/1 + aT_h N_0$$

3) Rogers Model

$$N_a = N_0[1 - \exp(a(T_h N_a - T))]$$

4) Full model

$$a = (d + bN_0)/(1 + cN_0)$$

5) Reduced model I

$$a = d + bN_0 \quad c = 0$$

6) Reduced Model II

$$a = bN_0 \quad c = 0, d = 0$$

Table 1. Percentages of juvenile mortality of walnut aphid and the parasitoid wasp, *T. pallidus* in different aphid nymph instars.

	Aphid nymph instars			
	Instar 1	Instar 2	Instar 3	Instar 4
Mortality to adult (mean \pm SD)	22.09 \pm 6.00	14.71 \pm 4.55	7.91 \pm 1.25	2.33 \pm 1.45
Mortality per each instar	7.38	6.8	5.58	2.33
Gross juvenile mortality of <i>T. pallidus</i>	64.44	21.58	10.00	8.88
Juvenile mortality of <i>T. pallidus</i> in mummies	20.00	5.82	6.65	5.84
Total net juvenile mortality of <i>T. pallidus</i>	54.36	8.01	2.27	6.72

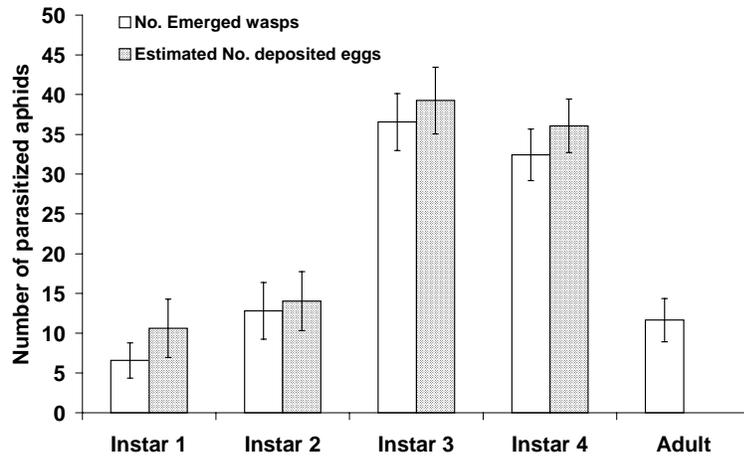


Fig. 1. Host stage preference of *C. juglandicola* by female *T. pallidus*, according to the deposited eggs and emerged wasp from each nymph instar. Data represent mean \pm SD.

7) Integrated model for type III response

$N_a = N_0 \{1 - \exp[(d + bN_0)(T_h N_e - T)/(1 + cN_0)]\}$ where N_a – the number of parasitized hosts, N_0 – host densities, P – number of parasitoid wasps, T – duration of experiment, b , c and d – constant values, a – searching efficiency and T_h – handling time.

For type II and III functional response, the precise form of the model arises when the full model (eq. 4) integrates with Holling (eq. 2) or Rogers (eq. 3) models, respectively. If the confidence intervals of the parameters (b , c and d) include the zero, meaning those parameter(s) has no significant difference with 0, and must be eliminated from the model. Finally we used the reduced model II, in which the parameters c and d were eliminated and only two parameters b and T_h were assessed. b value is the searching efficiency of parasitoid in each host densities ($a = bN_0$).

Results

Juvenile mortality

In all experiments, the initial number of nymphs differs from the subsequent adult number of aphids, indicating juvenile mortality. The majority of the perished nymphs were 1st and 2nd instar.

The juvenile mortalities of aphids from each instar nymph to adult and per each nymphal instar is shown in Table 1. The percentage of mortality in pre-adult stages of the parasitoid wasp, *T. pallidus* during development time and the pupal stage was assessed (Tab. 1). Net juvenile mortality was measured using Abbott's formula (ABBOTT, 1925) and aphid juvenile mortality per nymphal instar. Although the parasitoid mortality was higher in the 1st and 2nd instar nymphs, the parasitized nymphs were dead before reaching the adult stage and became smaller mummies.

Host stage preference

The female parasitoid oviposited in all 4 nymph instars and newly moulted adults of the host. From 103 emerged wasps, 6.58% \pm 2.21 (mean \pm SD) emerged from the 1st instar nymphs, 12.81% \pm 3.56 from the 2nd instar nymphs, 36.55% \pm 3.57 from the 3rd instar nymphs, 32.41% \pm 3.24 from the 4th instar nymphs and 11.65% \pm 2.71 emerged from adult aphids. There was a significant difference between the numbers of emerged wasps from the different aphid instar nymphs (ANOVA, $F =$

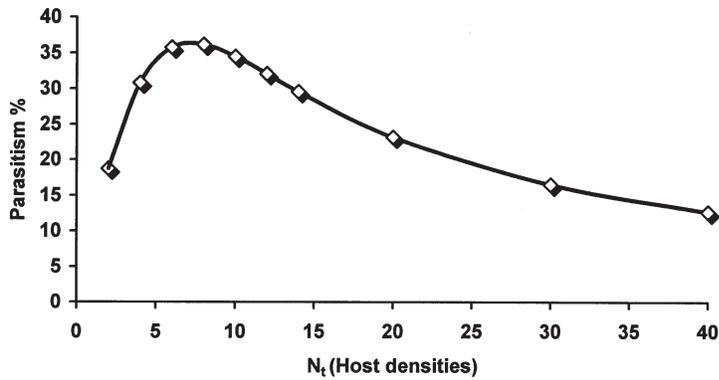


Fig. 2. The rate of parasitism by *T. pallidus* in different densities of 3rd instar nymphs of *C. juglandicola*.

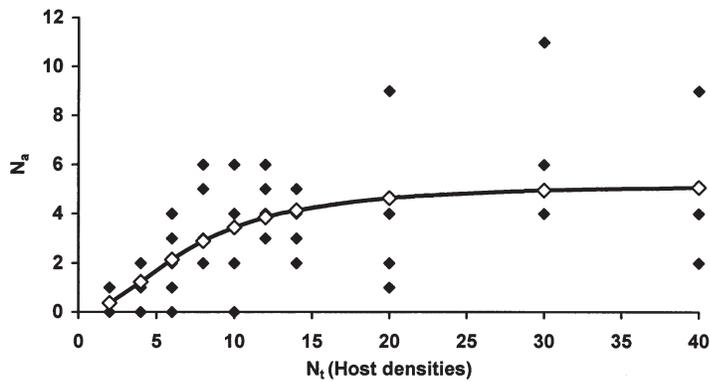


Fig. 3. Functional response of *T. pallidus* to different densities of *C. juglandicola*. N_a – number of attack.

19.29; $df = 4.55$; $P < 0.01$), but the difference between the numbers of emerged wasps from the 3rd and 4th instar was not significant ($T = 0.17$; $df = 21$; $P > 0.05$). Using the percentage of juvenile mortalities of the parasitoid wasp the number of deposited eggs per each aphid instar nymph was estimated. According to this, using the total number of eggs, $10.62\% \pm 3.66$ were laid in the 1st instar, $14.04\% \pm 3.70$ in the 2nd instar, $39.25\% \pm 4.19$ in the 3rd instar and $36.08\% \pm 3.37$ in the 4th instar (Fig. 1).

The higher percentage of eggs laid in 3rd and 4th aphid instar nymphs showed the preference of the female parasitoid to oviposit in older nymphs. There was no significant difference between eggs laid in the 1st and the 2nd instar nymphs ($T = 0.45$; $df = 21$; $P > 0.05$).

Oviposition behaviour

Female parasitoids walked around continually searching the leaf surface with their antennae pointing forwards. The duration of oviposition was usually less than 4 s. Female parasitoid

had problems with oviposition on the 1st instar nymphs. Sometimes, female wasps inserted their ovipositor in the exuvia or in a dead aphid.

The 3rd and 4th instar nymphs showed defensive behaviour with their hind legs, when encountering a female parasitoid. Sometimes the female parasitoid exhibited unusual behaviour when encountering 3rd or 4th instar nymphs. It flapped its wings and moved around the nymphs. The adult aphid often escaped from parasitoid attack, and the female parasitoid was not able to oviposit in adults. Insertion of the ovipositor in the hind portion is impossible, because of the large wings of the adult aphid.

Functional response

The results of parasitism on the 3rd instar nymphs are shown in Fig. 2. Increase in aphid density from 2 to 4, had a great effect on parasitism rate. There was a sharp increase with densities from 4 to 8, which however, was followed by a slight decline. The rate of parasitism, gradually decreased

when more than 30 aphids were offered. *T. pallidus* displayed a type III functional response to different densities of 3rd instar nymphs of *C. juglandicola*. The sigmoid functional response is shown in Fig. 3. Searching efficiency (b coefficient) or a' was 0.0042 ± 0.0016 arena/h. In the type III functional response, searching efficiency is dependent on host density. The handling time (T_h) of the parasitoid was 4.5823 ± 0.5418 h. Maximum attack rate ($1/T_h$) was 2.451 mummies/h.

Discussion

Juvenile mortality

Mortality rate in aphids decreased with an increase in age of the nymphs. The greatest mortality was observed between the 1st and the 2nd nymph instar, whereas the lowest mortality was observed between the 4th nymphal instar and the adult. Similar observations concerning higher mortality in the lower instars have been made by VALDIVIA & VILLATA (1986) who showed that the mortality rate in *Acyrtosiphon kondoi* (Shinji, 1938) is greater in the 1st instar and decreases with age. Aphids parasitized in the 1st instar did not reach the adult stage and failed to reproduce, as reported by HAGVAR & HOFVANG (1986) parasitoid eggs as well as the larvae have a juvenilizing effect on the parasitized aphid (SINGH & SINHA, 1982).

The percentage of net juvenile mortality of the parasitoid, *T. pallidus* decreased with the age of parasitized nymphs. This is in accordance with PANDEY & SINGH (1999) who showed that 1st and 2nd instar nymphs are unsuitable hosts for *Lysiphlebia mirzai* Suja-uddin, 1975. However, mortality in the 4th instar nymphs was higher than in the 3rd instar nymphs. The greatest juvenile mortality was in the 1st instar nymphs (54.36%), so that the female parasitoid had low preference on 1st instar nymphs. The development rate of the parasitoid is slower in earlier aphid instars than later ones (TALEBI et al., 2002). This preference for particular instars is often considered to be optimal for the parasitoid in term of offspring survival (HAGVAR & HOFVANG, 1991).

Host stage preference

Female wasps laid their eggs in all 4 aphid instars and adults. The total number of eggs laid and the total number of parasitized aphids varied among instars when parasitoids were given a choice between equal numbers of each instar. *T. pallidus* had a higher preference on the 3rd and 4th instar nymphs than on others. It also suggested that de-

fensive behaviour in these instars had no significant effect on parasitism. Similarly, the parasitoid wasps, *Trioxys indicus* Subba Rao et Sharma, 1959 (SINGH & SINHA, 1982) and *Lysiphlebia mirzai* (Pandey & Singh, 1999) preferred the 3rd instar nymphs of its host aphids for oviposition. In contrast *Binodoxys angelicae* (Haliday, 1833) had a preference on the 1st instar nymphs of *Aphis pomi* de Geer, 1733 (CIERNIEWSKA, 1976). *Trioxys cirsii* (Curtis, 1831) and *Monoctonus pseudoplatani* (Marshall, 1896) parasitoids of platanus aphid, *Drepanosiphum platanoides* (Shrank, 1801) oviposit in younger nymphs and rarely parasitize the older nymphs (HAMILTON, 1974). HOFVANG & HAGVAR (1986) studied the oviposition behaviour of the parasitoid wasp, *Ephedrus cerasicola* Stary, 1962, in addition to the handling time and aphid defensive behaviour and concluded that the 1st instar nymphs of *Myzus persicae* (Sulzer, 1776) were most easily parasitized, but *T. pallidus* had some problems in parasitising the 1st instar nymphs of *C. juglandicola*. The high juvenile mortality of the parasitoid in the 1st instar nymphs suggested that 1st instar nymphs are not a suitable stage for parasitisation.

Difference in the host stage preference by a parasitoid depends on several factors. MACKAUER (1983) indicates that host stage preference is not constant, but influenced by test duration and by the parasitoid functional responses to densities. The parasitism of an aphid nymphal instar, influenced the development and fecundity of the aphid as well as their parasitoid (HAGVAR & HOFVANG, 1991). Although the older nymphs are most hazardous, aphids parasitized in 3rd and 4th instar nymphs can emerge as adults and reproduce before being killed. Thus parasitism of the aphid instar plays an important role in this respect (STARÝ, 1988).

Oviposition behaviour

The time spent by *T. pallidus* for parasitisation of the 1st instar nymphs was much longer than for the other instars of *C. juglandicola*. Host size does not only influence oviposition preference of the parasitoids, but also the duration of oviposition (HOLLING, 1959). The duration of oviposition of *T. pallidus* in the 2nd, 3rd and 4th instar nymphs was very short (less than 4 seconds). This time differs among Aphidiinae. The shortest time is about 1-2 seconds in *Aphidius* spp. (MACKAUER, 1983). The species of *Ephedrus* have a long oviposition time. *Ephedrus californicus* Baker, 1909 spends 6 or more seconds for oviposition (CHOW & MACKAUER, 1986). The time in *Ephedrus cerasicola* is at

least 9 seconds and depends on the aphid nymphal instar (HOFSVANG & HAGVAR, 1986).

When the parasitoid wasp, *T. pallidus* encounters different nymphs of *C. juglandicola*, the probability of parasitism partly depends on nymph behaviour. The 3rd and 4th instar nymphs showed defensive behaviour, but the higher percentage of eggs laid in these instars suggest the low value of this defensive behaviour.

Functional response

A sigmoid functional response type III was observed in *T. pallidus* to its host *C. juglandicola*. Among all natural enemies, only species with a type III functional response are able to regulate their host populations (HASSELL, 1978). A parasitoid with functional response type III is density dependent and increases its searching efficiency on higher densities of the host. The functional response of Aphidiinae is often type II (HAGVAR & HOFSVANG, 1991), but type III is also reported for *Trioxys indicus* (SINGH & SINHA, 1983). The essential premise of the type III response is that the parasitoid is able to discern host density and adjust its searching efficiency (O'NEIL, 1990). The handling time (T_h) in parasitoid insects is defined as the time interval between ovipositions (ROGERS, 1972). This time defines the suitability of biological agents for distributing their time for attacking the host.

Our results indicate that, when developing biological control strategies for pest management in walnut, factors such as host stage preference and functional response must be taken into account. According to WAAGE & GREATHEAD (1988) the natural enemy functional response offers a good conceptual framework for understanding the action of agents in inundative releases. Further experimentation is required in order to investigate those factors between *T. pallidus* and other aphid hosts of economic importance.

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First records of braconids (Hymenoptera, Braconidae) from Slovakia

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In spite of relatively good knowledge of the braconid fauna on the territory of Slovakia (ČAPEK & LUKÁŠ, 1989) the finding of new species to this country is still possible. The investigation of little explored regions can also discover braconid species new to the fauna of Slovakia. During the last three years we recorded six braconid species which represent first records for Slovakia.

Doryctinae

Spathius polonicus Niezabitowski, 1910

Material examined: SW Slovakia, Malé Karpaty Mts, Devín env., Devínska Kobyla NNR (National Nature

Reserve) (7867 – grid reference number of the Database of the fauna of Slovakia), 10.II.2002, 2 ♂♂, 2 ♀♀, leg. J. Schlarmannová, det. J. Lukáš. Distribution: a rare species known from Poland, Armenia, Tadzhikistan, Uzbekistan (TOBIAS, 1986).

Hosts: *Lampra mirifica* Mulsant, 1855, *Melanophila decastigma* (F., 1787) (TOBIAS, 1986). In Slovakia it was bred from *Agrilus viridis* L., 1758.

Histeromerinae

Histeromerus mystacinus Wesmael, 1838

Material examined: SW Slovakia, Malé Karpaty Mts, Devín env., Devínska Kobyla NNR (7867), 10.V.2002,

3 ♀♀, leg. J. Schlarmanová, det. J. Lukáš. It belongs to category of vulnerable species in Slovakia (LUKÁŠ, 2001).

Distribution: W Europe, Crimea, Georgia (TOBIAS, 1986).

Hosts: *Leptura scutellata* F., 1781, *Strangalia aurulenta* (F., 1792), *Sinodendron cylindricum* (L., 1758), *Dicercia alni* (Fischer, 1824) (TOBIAS, 1986). In Slovakia was bred from Anobiidae.

Opiinae

Pokomandya curticornis Fischer, 1959

Material examined: SW Slovakia, Malé Karpaty Mts., Devín env., Devínska Kobyla NNR – Sandberg (7877), 9.VII.2001, 1 ♀, leg. et det. J. Schlarmanová. It belongs to category of vulnerable species in Slovakia (LUKÁŠ, 2001).

Distribution: Hungary, Turkey, Greece, Kazakhstan (TOBIAS & JAKIMOVICHUS, 1986) and Austria (FISCHER, 1972).

Hosts: unknown.

Orgilinae

Orgilus hungaricus Szépligeti, 1896

Material examined: E Slovakia, Východoslovenská rovina plain, Somotor (7596), 21.VII.2002, 1 ♀, leg. et det. J. Lukáš.

Distribution: Hungary, former Yugoslavia, Kazakhstan (TAEGER, 1989).

Hosts: unknown.

Cheloninae

Sigalphus irrorator (Fabricius, 1775)

Material examined: S Slovakia, Podunajská rovina plain, Čenkovská lesostep woodsteppe (8277), 22.VII.2001, 1 ♀, leg. et det. J. Lukáš. It belongs to category critically endangered species in Slovakia (LUKÁŠ, 2001).

Distribution: W Europe, Urals, Siberia, Far East, Japan (TOBIAS, 1986).

Hosts: *Acronicta psi* (L., 1758), *Acronicta tridens* (Denis et Schiffermüller, 1775), *Acronicta aceris* (L., 1758) *Mamestra pisi* L., 1758, *Calophasia lunula* (Hufnagel, 1766) (TOBIAS, 1986).

Euphorinae

Chrysopophthorus hungaricus (Zilahi – Kiss, 1927)

Material examined: SW Slovakia, Malé Karpaty Mts., Devín env., Devínska Kobyla NNR (7867), 22.VI.2003, 1 ♀, leg. et det. J. Lukáš. It belongs to category of vulnerable species in Slovakia (LUKÁŠ, 2001).

Distribution: C and S Europe, Azerbaidzhan (TOBIAS, 1986)

Hosts: *Chrysopa flavifrons* Brauer, 1851, *Chrysopa ventralis* Curtis, 1834, *Chrysopa carnea* Stephens, 1836 (TOBIAS, 1986).

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