BioOne COMPLETE

Host Specificity and Temporal and Seasonal Shifts in Host Preference of a Web-Spider Parasitoid Zatypota percontatoria

Authors: Korenko, Stanislav, Michalková, Veronika, Zwakhals, Kees, and Pekár, Stano

Source: Journal of Insect Science, 11(101) : 1-12

Published By: Entomological Society of America

URL: https://doi.org/10.1673/031.011.10101

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Journal of Insect Science
www.insectscience.org

Host specificity and temporal and seasonal shifts in host preference of a web-spider parasitoid *Zatypota percontatoria*

Stanislav Korenko[1,2,a*], Veronika Michalková[3,b], Kees Zwakhals[4,c], Stano Pekár[2,d]

[1]Department of Agroecology and Biometeorology, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague 6, Suchdol, Czech Republic
[2]Department of Botany and Zoology, Masaryk University, Faculty of Science, Kotlářská 2, 611 37 Brno, Czech Republic
[3]Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, 845 06 Bratislava, Slovakia
[4]Dr. Dreeslaan 204, NL-4241 CM Arkel, Netherlands

Abstract

Current knowledge about polysphinctine parasite wasps' interactions with their spider hosts is very fragmented and incomplete. This study presents the host specificity of *Zatypota percontatoria* (Müller) (Hymenoptera: Ichneumonidae) and its adaptation to varying host availability. Two years of field observations show that *Z. percontatoria* is a stenophagous parasitoid that parasitizes only five closely related web-building spiders of the family Theridiidae (Araneae). Within the Theridiidae it attacks only species belonging to a small group of species, here called the "*Theridion*" group. These hosts have a similar biology, but are available at different levels of abundance and at different sizes over the season. Laboratory experiments showed that this wasp species ignores linyphiid, araneid or dictynid spiders and accepts only theridiid spiders of the "*Theridion*" group. In the field study, wasp females preferred older juvenile and sub-adult female spider instars with intermediate body size. Only 5% of the parasitized spiders were males. Parasitism in the natural population of theridiid spiders was on average 1.3%. Parasitism was most frequent on two species, *Theridion varians* Hahn in 2007 and *Neottiura bimaculata* Linnaeus in 2008. The parasitization rate was positively correlated with spider abundance. The wasp responded adaptively to seasonal changes in host abundance and host body size and shifted host preference according to the availability of suitable hosts during, as well as between, seasons. In spring and summer the highest percentage of parasitism was on *T. varians* and in autumn it was on *N. bimaculata*.

Keywords: foraging strategy, host-parasitoid interaction, *Neottiura bimaculata*, *Theridion varians*
Correspondence: [a*] korenko.stanislav@yahoo.com, [b] vmichalkova@yahoo.com, [c] keeszwakhals@yahoo.com, [d] pekar@sci.muni.cz, *Corresponding author
Editor: Jay Rosenheim was Editor of this paper.
Received: 17 December 2010, **Accepted:** 31 December 2010
Copyright : This is an open access paper. We use the Creative Commons Attribution 3.0 license that permits unrestricted use, provided that the paper is properly attributed.
ISSN: 1536-2442 | Vol. 11, Number 101

Cite this paper as:
Korenko S, Michalková V, Zwakhals K, Pekár S. 2011. Host specificity and temporal and seasonal shifts in host preference of a web-spider parasitoid *Zatypota percontatoria*. *Journal of Insect Science* 11:101 available online: insectscience.org/11.101

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Introduction

Foraging is one of the central issues in ecology as it shapes the interactions between predators and their prey. Foraging of a parasitoid includes attack on a single free-living host and oviposition of an egg that develops only on the host tissue leading to complete host consumption. Due to this restriction, parasitoids have evolved adaptive foraging and host-selection strategies that enable them to survive in situations when host sources are restricted (Godfray and Shimada 1999).

Two different parasitoid developmental strategies exist: idiobiosis and koinobiosis. Idiobiont species develop on a paralyzed and non-growing host (Askew and Shaw 1986), hence their host resource is static in terms of size during their development. Parasitoid size is thus a function of host species size at the time of attack. By contrast, koinobiont species attack hosts that continue to feed and grow (Askew and Shaw 1986). The amount of resources exploited by such parasitoid larvae for growth and development is not fixed; their development depends upon host feeding rate and growth (Godfray 1994).

Hymenopteran parasitoids show a great variety of host specializations. The host range of specialist parasitoids, assessed at the taxonomic level, is often very narrow, whereas generalists exploit a broad range of hosts (e.g., Shaw 1994; Shaw and Aeschlimann 1994). They tend to attack a group of host species that share a similar set of characteristics, either ecological or phylogenetic. When encounters with one host species become infrequent, generalist parasitoids expand their host selection criterion to include other (even less profitable) host species (Henry et al. 2009). As a result, generalist parasitoids can have multiple generations per season (Pyke et al. 1977).

Koinobionts are generally more host-specific than idiobionts (Althoff 2003). In strictly specialized parasitoids, their life history is tightly coupled with that of their host species. Such parasitoids occur only in the habitat of their host and synchronize their development with them (Barrantes et al. 2008). Examples of rather specialized parasitoids include polysphinctine ichneumonids that attack spiders (e.g. Fitton et al. 1987).

Host size or developmental stage vary during the season. Therefore, choosing suitable hosts is fundamental to the parasitoid–host relationship. Some parasitoids, for example, attack hosts only at a certain developmental stage or size (Henry et al. 2006). Henry et al. (2009) demonstrated that smaller parasitoids receive the greatest benefits from selecting small, but less defended and abundant hosts. Hosts, such as web spiders, are habile hunters that can easily overcome the handling capabilities of smaller parasitoids (Gentry and Dyer 2002; Henry et al. 2006). The host's ability to physically defend itself typically increases with host age and size. Female parasitoids must make a choice between increased handling time and risking injury in attempting to oviposit on larger dangerous hosts (Gerling et al. 1990).

The koinobiont ectoparasitoid wasp, *Zatypota percontatoria* (Müller) (Hymenoptera: Ichneumonidae), belongs to polysphinctine pimplines, which exhibit a unique trait within the Ichneumonidae in terms of development (Fitton et al. 1987). A wasp larva develops externally on an active spider and the spider host is killed and consumed shortly before the

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

ichneumonid's pupation. Biologically and morphologically, polysphinctines belong to the most specialized Pimplinae (Fitton et al. 1987). Overall, the trophic relationship between polysphinctines and spiders is clearly highly specialized, and *a priori* it is expected that the host ranges of these species are narrow (Shaw 1994). Our knowledge about this host – parasitoid system still remains very fragmented and incomplete.

The few available records about the *Zatypota* species show that it attacks spiders from several different families (Aubert 1969; Shaw 1994; Gauld and Dubois 2006). Shaw (1994) summarized host records of *Z. percontatoria* and concluded that this species attacks spiders from several web-building families, namely Araneidae, Dictynidae, Tetragnathidae and Theridiidae. However, Gauld and Dubois (2006) presumed a misidentification of the reared wasp in several cases and questioned all hosts other than theridiid spiders. Thus, verified records of hosts of *Z. percontatoria* include only a few spider species from the family Theridiidae: *Phylloneta impressa* (L. Koch), *Platnickina tincta* (Walckenaer), *Theridion varians* Hahn, *T. simile* Koch and *T. melanurum* Hahn (Aubert 1969; Fitton et al. 1987; Gauld and Dubois 2006).

The aim of this study was to investigate the foraging strategy of *Z. percontatoria* in terms of host specificity at a taxonomic, developmental and sexual level.

Materials and Methods

Field study

A population of *Z. percontatoria* was investigated in an apple orchard situated in Brno, Czech Republic (49° 09′ 37″ N, 16° 33′ 35″ E). The orchard consists of two tree varieties, Golden Delicious and Champion, both between 27 and 30 years old. The orchard was under an integrated pest management regime during our study.

The percentage of parasitism (defined as the total number of cases of parasitized spiders in the population at a given time, divided by the number of individuals in the population) was investigated during 2007 and 2008, by collecting potential and parasitized hosts. The hosts, arboreal spiders, were collected by beating apple tree branches. This was done from spring (April) to late autumn (October) each year. Spiders were collected in a square shaped beating net (1 m^2 area) placed beneath the tree crown. A single sampling consisted of beating the branches of 25 trees. The sampling was performed on 12 days in April, May, August, September, and October in 2007 and on 10 days in April, May, June, July, August, and September in 2008. On each investigated day three samples were taken. All spiders were fixed in 70% alcohol and identified to species/genus level using Heimer and Nentwig (1991), Roberts (1995) and Pekár (1999). The spider nomenclature is according to Platnick (2009).

During both years, 11 theridiid spider species were identified to species level based upon adult specimens. The majority of these belonged to the "*Theridion*" group. In the terms of this study the "*Theridion*" group includes the following closely related species with a similar biology and web architecture (see, e.g. Heimer and Nentwig 1991): *Theridion varians* Hahn, *T. pinastri* L. Koch, *Phylloneta impressa* Linnaeus, *Neottiura bimaculata* (Linnaeus), *Platnickina tincta* (Walckenaer), *Heterotheridion nigrovariegatum* (Simon) and *Paidiscura pallens* (Blackwall). The remaining species are *Dipoena melanogaster* C. L. Koch, *Enoplognatha latimana* Hippa and Oksala, *E.*

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

ovata (Clerck) and *Parasteatoda lunata* (Clerck). The body size (prosoma length), developmental stage (juvenile or adult), and sex of each parasitized spider were determined with an Olympus stereomicroscope SZ 40.

The sex ratio of both unparasitized (N = 204) and parasitized (N = 75) "*Theridion*" spiders was estimated from individuals of sub-adult and adult growth stage. The sex of spiders could be recognized only at later juvenile and sub-adult stages, i.e. when their prosoma was larger than 0.7 mm. At these stages, males were recognized by swollen pedipalps and females by a swollen and dark area of the epigyne. The length of the prosoma is a commonly used parameter for body size because unlike the length of the abdomen it changes only during molting (Schaefer 1987).

Wasp rearing

Living parasitized spiders were collected in the same periods but in a different part of the orchard. Parasitized spiders (N = 138) were collected by means of branch beating. Hosts with parasitoids were placed singly in cylindrical containers (diameter 35 mm, height 40 mm) with a layer of plaster of Paris at the bottom. The plaster was moistened at three-day intervals. Spiders were kept at room temperature 22 ± 3.5° C under a natural L:D regime and fed with a surplus of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). The spiders were reared until the wasps' emergence. Spider hosts were identified and the results were included into host-specificity frequencies. Hatched wasps were identified using Fitton et al. (1988) and Zwakhals (2006). The nomenclature of the polysphinctines follows Fitton et al. (1988) and Yu and Horstmann (1997). Some of these wasps were used in the experiments described below.

Laboratory experiments

The host preference of *Z. percontatoria* was investigated under laboratory conditions in two experiments. In the first one, the preference for hosts of four spider genera belonging to four families was tested; in the second one, the preference for spider species of one family was tested. A similar experimental set-up was used in both experiments. After hatching, the virgin female wasps were placed singly in glass vials (height 85 mm, diameter 55 mm), with a cotton ball soaked in 20% aqueous honey solution at the bottom. Three days later three spiders (potential hosts) were released into each vial simultaneously and acceptance of a particular spider host was recorded within 48 hours. Arrhenotokous parthenogenesis of virgin females seems to be common in *Z. percontatoria* (Korenko, unpublished).

In the first experiment with 18 wasp females, web-building spiders, specifically *Araniella* sp. (Araneidae, N = 12), *Meioneta* sp. (Linyphiidae, N = 11), *Dictyna* sp. (Dictynidae, N = 13), and *Theridion* spp. (Theridiidae, N = 18) collected in the orchard, were offered as potential hosts. The prosoma length of these spiders was between 0.6 and 1 mm. All spiders were juvenile and did not build a complete web in such a short time. If the spider built a dense web, it was destroyed with a stick in order to prevent the female wasp from becoming caught in the web.

In the second experiment with 30 wasp females, six species of the family Theridiidae were offered. The following species were used: *N. bimaculata* (N = 17), *P. impressa* (N = 11), *T. varians* (N = 30), "*Theridion*" (N = 15), *Dipoena melanogaster* (N = 9) and *Enoplogntha* sp. (N = 8). All spiders were

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

juvenile with a prosoma length between 0.6 and 1 mm.

Data analysis of the laboratory experiments

Data were analyzed using various methods within the R environment (R Development Core Team 2009). The Chi-square "goodness of fit" test was used to compare frequencies of abundance of potential hosts with the rate of parasitized hosts. The Proportion test was used to compare proportions of each sex among available and parasitized hosts. ANOVA was used to compare host sizes during each season, as the response variable was continuous and residuals were homoscedastic. The results of laboratory experiments were analyzed using two different methods. As in both experiments, observations of the frequency of parasitization were not independent due to blocked design, therefore methods that can handle correlated data were used. The first experiment included only 18 vials (blocks); thus, the Generalized Linear Model with a quasibinomial setting (GLM) was used to correct for over-dispersion due to the correlated response within vials (Pekár and Brabec 2009). The second experiment included 30 vials (blocks); therefore, Generalized Estimating Equations with binomial error structure (GEE) were used (Hardin and Hilbe 2003). Within this model an exchangeable association structure was used.

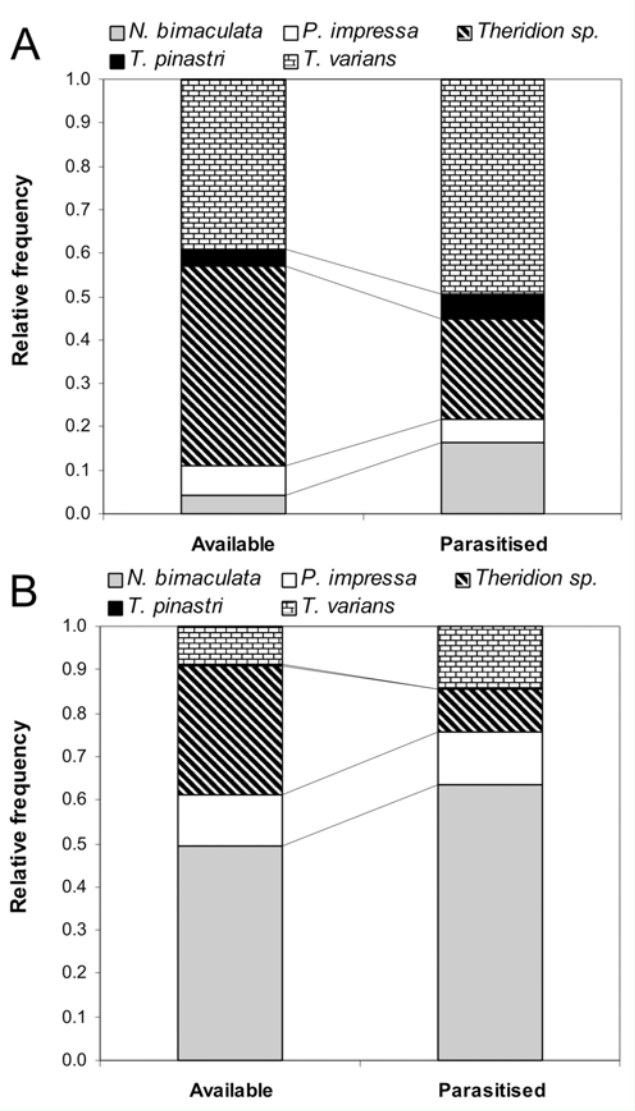


Figure 1. Comparison of relative frequency of available and parasitized "*Theridion*" spider hosts in the field in 2007 (A) and 2008 (B). High quality figures are available online.

Results

Host specificity from the collected spiders

Of 9,314 spider specimens collected in the field, the potential spider hosts, i.e. the web-building spiders, were represented by five families amounting to 85.7% of all collected spiders. These were Theridiidae (92%, N = 7,353), Araneidae (6.2%), Dictynidae (0.5%), Tetragnathidae (0.6%) and Linyphiidae (0.6%). The parasitoid, however, attacked only Theridiidae (100%, N = 105).

Using all data from both the samples from the parasitism rate study (N = 105) and the rearing of wasps (N = 138), it was shown that parasitized theridiid spiders belonged mainly to *Theridion varians* (43%, N = 104), *Neottiura bimaculata* (24.4%), *Phylloneta impressa* (6.6%), *T. pinastri* (4.5%) and unidentified juveniles of the "*Theridion*" group (21.5%). The frequency of attacked theridiid hosts did not correspond to their

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

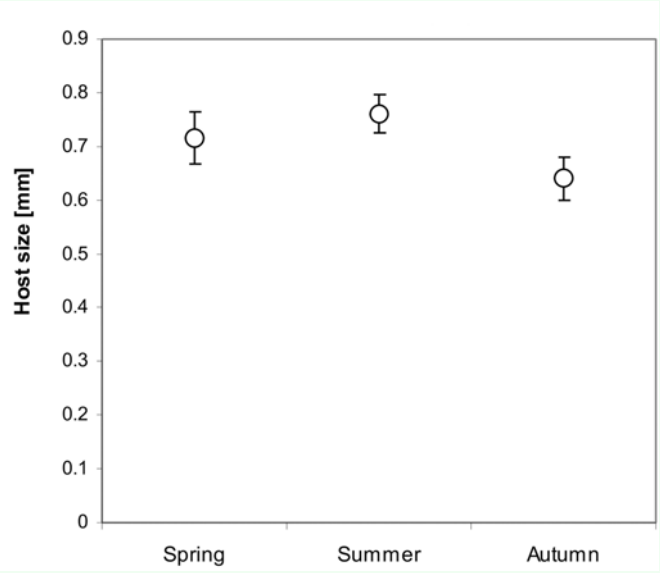


Figure 2. Comparison of the size (prosoma length) of available juvenile "*Theridion*" hosts during season. Points are means; uncertainty bars represent 95% confidence intervals. High quality figures are available online.

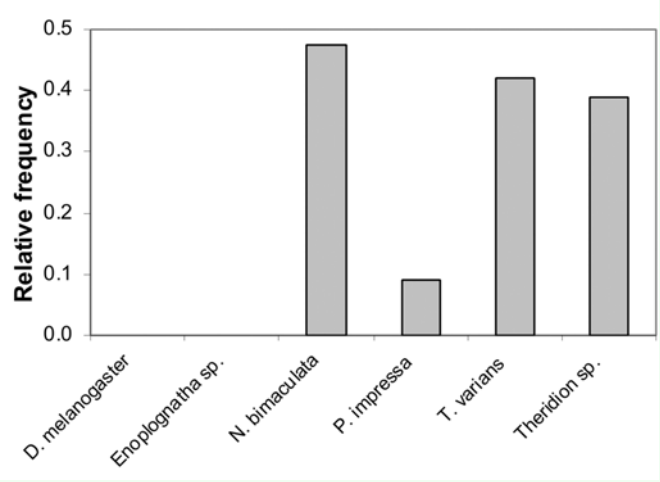


Figure 3. Relative frequencies of six taxa parasitized by wasps in laboratory experiments. High quality figures are available online.

availability both in 2007 (Goodness of fit, $\chi^2_4 = 1674$, $p < 0.0001$) and in 2008 (Goodness of fit, $\chi^2_4 = 1137$, $p < 0.0001$), (Figure 1).

The vast majority of the parasitized spiders (89.5%) were at the juvenile stage (from N = 105). Adults, which comprised 10.5% of all parasitized hosts, were parasitized merely in August 2007, and these were exclusively females of *T. varians*. The mean size of the prosoma of the parasitized host was 0.71 mm (N = 105, SE = 0.013) and changed somewhat during the season (Figure 2).

The natural sex ratio of subadult and adult "*Theridion*" spiders was biased in favor of females, as only 25% (from N = 204) of spiders were males. The sex ratio of parasitized "*Theridion*" spiders was significantly skewed in favor of females, as only 5% (from N = 75) of spiders were males (Proportion test, $\chi^2_1 = 12.2$, $p = 0.0005$).

Ovopositioning results in the laboratory

Under laboratory conditions, *Z. percontatoria* attacked exclusively spiders of the family Theridiidae and ignored linyphiid, araneid or dictynid spiders (GLM, $F_{3,32} = 19.1$, $p = 0.004$). When six taxa of the family Theridiidae (N = 30) were offered, parasitism differed significantly among them (GEE, $\chi^2_5 = 87.2$, $p < 0.0001$). *N. bimaculata*, *T. varians* and "*Theridion*" were parasitized with similarly high frequency, *P. impressa* was parasitized with a low frequency, and *D. melanogaster* and *Enoplognatha* sp. were not parasitized at all (Figure 3).

Host shifts

In 2007 the rate of parasitism by *Z. percontatoria* wasps on theridiid spiders was 1.74% (from N = 4,814). In 2008 the rate halved to 0.83% (from N = 2,539). Comparison of the host spectrum between the two seasons, 2007 and 2008, revealed a shift in host preference. While in 2007 the highest portion of parasitized hosts was represented by *T. varians*, in 2008 it was represented by *N. bimaculata* (Figures 1A, B). In 2007 (April – August) *T. varians* was the most abundant species with a mean abundance of 40.1 specimens (N = 7, SD = 23.5). This species was also the most parasitized (49.5%) spider host (Figure 1A). In 2008, the abundance of *T. varians* decreased to 12.9 (N = 8, SD = 13.8),

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

and its parasitized portion decreased to 14.6%. *Neottiura bimaculata* had a lower abundance in 2007, specifically 4.3 (N = 7, SD = 4.4) spiders and a parasitized portion 16.3%. In 2008, it was the most abundant species with 20.9 specimens (N = 8, SD = 6.5) and a higher portion of parasitism (63.4%) (Figure 1B). The abundance of *P. impressa* was similar in both years, i.e. 7 specimens per day (N = 7, SD = 9.8) in 2007 and 5.4 specimens (N = 8, SD = 4.84) in 2008. Its portion of parasitism increased from 5.4 to 12.2% between years.

The body size of parasitized hosts changed significantly according to the seasons (ANOVA, $F_{2,102} = 10.4$, $P < 0.0001$): it was smallest in autumn and largest in summer (Figure 2). The frequency of occurrence of the three main hosts, *T. varians*, *N. bimaculata* and *P. impressa*, at a size preferred by the parasitoid, also changed with the seasons. In spring, all three host species were juvenile and thus occurred at high frequencies at the preferred body size (Figure 4A). In spring (of both years) the highest parasitized portion was in *T. varians* (43.5%, N = 10), followed by *N. bimaculata* (26%), the "*Theridion*" group (15.5%), *P. impressa* (13%) and *T. pinastri* (2%). In summer, spiders with a suitable body size were rare, as the majority of them had reached adulthood. The prosoma size of adult *T. varians*, however, falls within the preferred host range and adult females were thus accepted as host (Figure 4B). This was not the case in *P. impressa*, whose adult prosoma length was far larger than 1.1 mm. Neither the first instar spiderlings (prosoma size < 0.5 mm) of *T. varians* or *N. bimaculata* that hatched from egg sacs were accepted as hosts (field data). In summer, the highest parasitized portion was observed on *T. varians* (57%, N = 26), followed by indeterminable spiders at early instars (prosoma > 0.6 mm) of the "*Theridion*" group (26%), *N. bimaculata* (8.7%), and *P. impressa* (6%) and *T. pinastri* (2.3%). In autumn, spiderlings (prosoma size > 0.6 mm) of all three species were accepted by the wasp (Figure 4C). The parasitized

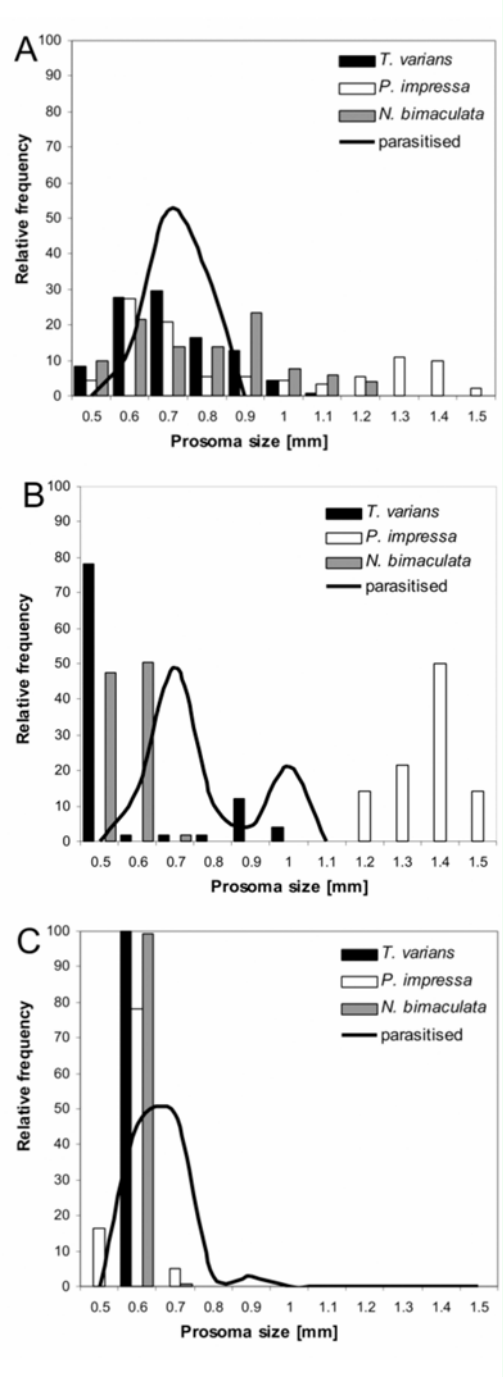


Figure 4. Relative frequencies of prosoma sizes of three major available host species (bars) and parasitized individuals (line) in spring (A), in summer (B) and in autumn (C). Bars were generated from spider relative abundance in the particular prosoma size (for each species separately). Lines were generated from all parasitized spiders in the particular prosoma size collected in the field in the particular season. High quality figures are available online.

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

portion was highest on *N. bimaculata* (37%, N = 13), followed by *T. varians* (28.6%), indeterminable spiders at early instars of "*Theridion*" group (25.7%), *P. impressa* (5.7%) and *T. pinastri* (3%).

Discussion

Both field and laboratory data show a strong preference of *Z. percontatoria* for web-building spiders of the family Theridiidae. It is known that host identification may be based on visual and chemical cues and the attacking behavior may be dependent on the invasion of the host web (Fellowes et al. 2005). The limitations of the performed laboratory experiments (i.e. with only virgin females enclosed in a small container and spiders deprived of their webs) could have influenced the searching and attacking behavior of the wasp. We assume that wasp females, which naturally mate in the field, may express different host acceptance behaviors. If female wasps allocate male offspring to smaller hosts and female offspring to larger hosts (e.g. Takasuka et al. 2009), then patterns of host preference for virgin females might differ from those of mated females.

Although laboratory experiments have limitations, they clearly support field data. The same spider species were accepted by wasps in the laboratory as in the field. Thus, as predicted by Gauld and Dubois (2006), previous records of hosts from other families, namely Agelenidae, Araneidae, Dictynidae and Tetragnathidae, cannot be supported. *Zatypota percontatoria* clearly attacks spiders building 3-dimensional webs with similar biology and web architecture. This study confirmed three hosts published previously (Aubert 1969; Fitton et al. 1987; Gauld and Dubois 2006) and revealed two new hosts: *N. bimaculata* and *T. pinastri*.

The results of this study provide data only for a single population. To identify the entire host spectrum of *Z. percontatoria*, studies in other places of its distribution area should be undertaken. This species has a Holartic distribution, but most of the records come from Europe, where about 30 spider species of the family Theridiidae belong to the potential pool of hosts.

Host size/stage preference

Within the "*Theridion*" group we found *Z. percontatoria* to select only hosts of a certain size range. Populations of spider hosts are generally characterized by a high degree of body size variation (Henry et al. 2009). Large hosts provide more resources and, therefore, produce larger parasitoids, which is a proxy mechanism positively correlated with parasitoid fitness (Sequeira and Mackauer 1994; Takasuka et al. 2009). Parasitoids can distinguish between high- and low-quality hosts and preferentially oviposit on higher quality ones (Godfray 1994). Fincke et al. (1990) observed an intermediate-size preference for juvenile female spiders by *Hymenoepimecis* sp. in Panama. This is because the developmental stage of a host becomes far more important for larva survival than the actual size of the host at the moment of parasitization (Henry et al. 2006).

Zatypota percontatoria is a medium-sized parasitoid and it attacks medium-sized spiders corresponding to older juvenile and sub-adult spider instars. It does not accept hosts that are either too small (early instars) or too large (adult specimens). Tiny spiders are probably not accepted because the larva would be too great a burden for the spider, likely decreasing its foraging efficiency, which would negatively affect the fitness of the parasitoid. *Zatypota percontatoria* females significantly

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

preferred female juvenile spiders as host. Generally, female spiders are larger, can be more abundant and have higher longevity (e.g. Schaefer 1987); therefore, they are a more profitable source of food for larvae than males. The selection of female sex in spider hosts is profitable due to divergent ontogenetic developmental trajectories. As females are larger than males at the adult stage, they have a higher foraging rate (Givens 1978), pass through more instars and attain a larger body size (Vollrath 1987). We can assume that adult males are avoided due to their short life expectancy, while large adult females are presumably avoided because of their stronger defenses against an ovipositing female wasp. It is, however, not known how wasps recognize the sex of immature spiders.

Host shifts

Zatypota percontatoria adaptively changed hosts according to their size, which was changing during the season. The two most preferred hosts, *T. varians* and *N. bimaculata*, attain an acceptable body size even at maturity, but the latter species was not parasitized at the adult stage. This is probably because adult female specimens of *N. bimaculata* are hidden while guarding their eggsac underneath the leaves of an herb layer (Korenko, unpublished). Thus adult females of *T. varians* were the only acceptable hosts of the preferred size in the middle of a season, presumably because they build webs at a higher vegetation stratum.

Species of the "*Theridion*" group are among the most abundant spiders in crowns of fruit trees (Pekár and Kocourek 2004). In central Europe, three species, *T. varians*, *N. bimaculata* and *P. impressa* are the most abundant 3-D web weavers, but they differ in phenology and body size during the season. *Zatypota percontatoria* responds adaptively to changes in abundance, body size and age of the three hosts. Spider hosts may become unavailable, for example due to reproduction when males die soon after mating, or due to large body size, which is not accepted by the wasp. This adaptive behavior is an effective means of maintaining a stable population dynamic throughout the season.

We also observed shifts in host preference between years. In the first year, 2007, *T. varians* was the dominant host, while in the second year, 2008, the parasitoid shifted to *N. bimaculata*. Parasitoids may influence parasitoid–host dynamics (Mangel and Roitberg 1992), which can further produce cascading effects on populations that shape the structure of the entire arthropod community (Petchey et al. 2008). Theridiid spiders are polyphagous predators, very abundant in agrobiocenoses and thus important for the natural control of pests (Bogya 1999). The rate of parasitism on theridiid hosts by *Z. percontatoria* was relatively low in both years. This complements observations on other related species: 1.4% in *Zatypota petronae* Gauld parasitized on *Theridion evexum* Keyserling (Barrantes et al. 2008) and 5% in *Zatypota albicoxa* (Walker) parasitized on *Parasteatoda tepidariorum* (C.L.Koch) (Tanaka 2007). In the study orchard, the frequency of parasitism did not exceed 6% throughout the season, except for the summer of 2007, when parasitism rate was 33% (sample in August). This high increase in parasitism rate was caused by a low abundance of acceptable theridiid hosts. Adult females of *T. varians* were frequently parasitized in the summer of the first year of the investigation (50% of all *T. varians* specimens). In general, such a situation could lead to a dramatic decline in the population of this species in the following year. The impact

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

of parasitism on the host population seems to be most disastrous when adult females are attacked. The high rate of parasitism on adult female hosts was observed by Eberhard (2000) and Gonzaga and Sobezak (2007), but they did not investigate how parasitism rate influences host population dynamics.

This study confirms that *Z. percontatoria* is a stenophagous parasitoid attacking a group of ecologically similar and taxonomically related spider hosts. Such narrow host specialization is advantageous because it requires similar attack and handling behavior. Not being strictly monophagous allows shifts between hosts when their availability changes during and between seasons.

Acknowledgements

We would like to thank J. Viktorín of Fruit-growing Company Brno – Starý Lískovec for permitting us to collect spiders at their commercial orchard. We also thank two anonymous referees for their constructive comments. Stanislav Korenko was supported by grant no. 526/09/H025 of the Czech Science Foundation and project MSM 6046070901 of the Ministry of Education, Youth and Sports of the Czech Republic. Stano Pekár was supported by project MSM 0021622416 of the Ministry of Education, Youth and Sports of the Czech Republic.

References

Althoff DM. 2003. Does parasitoid attack strategy influence host specificity? A test with New World braconids. *Ecological Entomology* l28: 500-502.

Askew RR, Shaw MR. 1986. Parasitoid communities: their size, structure and development. In: J Waage J, Greathead D, Editors. *Insect parasitoids*. pp. 22-234. Academic Press.

Aubert JF. 1969. Les Ichneumonides Ouest-Paléarctiques et leurs Hôtes. 1. Pimplinae, Xoridinae, Acaenitinae. *Laboratoire d'Evolution des Etres Organises,*, Paris.

Barrantes G, Eberhard WG, Weng JL. 2008. Seasonal patterns of parasitism of the tropical spiders *Theridion evexum* (Araneae, Theridiidae) and *Allocyclosa bifurca* (Araneae, Araneidae) by the wasps *Zatypota petronae* and *Polysphincta gutfreundi* (Hymenoptera, Ichneumonidae). *Revista de Biologia Tropical* 56: 749-754.

Bogya S. 1999. Spiders (Araneae) as polyphagous natural enemies in orchards. Ph.D. Thesis, Landbouwuniversiteit Wageningen.

Eberhard WG. 2000. The natural history and behaviour of *Hymenoepimecis argyraphaga* (Hymenoptera: Ichneumonidae) a parasitoid of *Plesiometa argyra* (Araneae: Tetraganthidae). *Journal of Hymenoptera Research* 9: 220-240.

Fellowes MDE, van Alphen JJM, Jervis MA. 2005. Foraging behaviour. In: Jervis MA, Editors. *Insects as natural enemies: a practical perspective.* pp. 1-71. Kluwer Academic Publishers.

Fincke O, Higgins L, Rojas E. 1990. Parasitism of *Nephila clavipes* (Araneae, Tetragnathidae) by an ichneumonid (Hymenoptera, Polysphinctini) in Panama. *Journal of Arachnology* 18: 321-329.

Fitton MG, Shaw MR, Austin AD. 1987. The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society* 90: 65-93.

Fitton MG, Shaw MR, Gauld ID. 1988. Pimpline ichneumon-flies. *Handbooks for the Identification of British Insects* 7: 1-110.

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Gauld ID, Dubois J. 2006. Phylogeny of the Polysphincta group of genera (Hymenoptera: Ichneumonidae; Pimplinae): a taxonomic revision of spider ectoparasitoids. *Systematic Entomology* 31: 529-564.

Gentry GL, Dyer LA. 2002. On the conditional nature of neotropical caterpillar defenses against their enemies. *Ecology* 83: 3108-3119.

Gerling D, Roitberg BD, Mackauer M. 1990. Intraspecific defense of the pea aphid, *Acyrthosiphon pisum* – influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera, Aphelinidae). *Journal of Insect Behavior* 3: 501-514.

Givens RP. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). *Ecology* 59**:** 309-321.

Godfray HCJ. 1994. *Parasitoids: Behavioral and evolutionary ecology*. Princeton University Press.

Godfray HCJ, Shimada M. 1999. Parasitoids as model organisms for ecologists. *Population Ecology* 41: 3-10.

Gonzaga MO, Sobezak JF. 2007. Parasitoid-induced mortality of *Araneaus omnicolor* (Araneae, Araneidae) by *Hymenoepimecis* sp. (Hymenoptera, Ichneumonidae) in southeastern Brazil. *Naturwissenschaften* 94: 223-227.

Hardin JW, Hilbe JM. 2003. *Generalized Estimating Equations*. Chapman and Hall/CRC.

Heimer S, Nentwig W. 1991. *Spinnen Mitteleuropas*. Paul Parey.

Henry LM, Ma BO, Roitberg BD. 2009. Size-mediated adaptive foraging: a host-selection strategy for insect parasitoids. *Oecologia* 161: 433-445.

Henry LM, Roitberg BD, Gillespie DR. 2006. Covariance of phenotypically plastic traits induces an adaptive shift in host selection behaviour. *Proceedings of the Royal Society B* 273: 2893-2899.

Mangel M, Roitberg B. 1992. Behavioral stabilization of parasite–host dynamics. *Theoretical Population Biology* 42: 308-320.

Nielsen E. 1923. Contributions to the life history of the pimpline spider parasites (*Polysphincta*, *Zaglyptus*, *Tromatobia*) (Hym. Ichneumon.). *Entomologiske Meddelelser* 14: 137-205.

Pekár S. 1999. Life-histories and the description of developmental stages of *Theridion bimaculatum*, *Theridion impressum* and *Theridion varians* (Araneae: Theridiidae*). Acta Societatis Zoologicae Bohemicae* 63: 301-309.

Pekár S, Brabec M. 2009. *Modern Analysis of Biological Data*. 1. Generalised Linear Models in R. Scientia [in Czech].

Pekár S, Kocourek F. 2004. Spiders (Araneae) in the biological and integrated pest management of apple in the Czech Republic. *Journal of Applied Entomology* 128: 561-566.

Petchey OL, Beckerman AP, Riede JO, Warren PH. 2008. Size, foraging, and food web structure. *Proceedings of the National Academy of Science of the United States of America* 105: 4191-4196.

Platnick NI. 2009. The world spider catalogue, version 10.0. American Museum of Natural History. Available online, http://research.amnh.org/entomology/spiders/catalog/index.html.

Pyke GH, Pulliam HR, Charnov EL. 1977. Optimal foraging: a selective review of theories and tests. *Quarterly Review of Biology* 52: 137-154.

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Roberts MJ. 1995. *Spiders of Britain and Northern Europe*. Harper Collins Publishers.

R Development Core Team 2009 R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Availble online, http://www.R-project.org.

Schaefer M. 1987. Life cycles and diapause. In: Nentwig W, Editor. *Ecophysiology of Spiders*. pp. 331-347. Springer.

Sequeira R, Mackauer M. 1994. Variation in selected life-history parameters of the parasitoid wasp, *Aphidius ervi* – influence of host developmental stage. *Entomologia Experimentalis et Applicata* 71: 15-22.

Shaw MR. 1994. Parasitoid host ranges. In: Hawkins BA, Sheehan W, Editors. *Parasitoid community ecology*. pp. 111-144. Oxford University Press.

Shaw MR, Aeschlimann JP. 1994. Host ranges of parasitoids (Hymenoptera: Braconidae and Ichneumonidae) reared from *Epermenia chaerophyllella* (Goeze) (Lepidoptera: Epermeniidae) in Britain, with description of a new species of *Triclistus* (Ichneumonidae). *Journal of Natural History* 28: 619–629.

Takasuka K, Matsumoto R, Ohbayashi N. 2009. Oviposition behavior of *Zatypota albicoxa* (Hymenoptera, Ichneumonidae), an ectoparasitoid of *Achaearanea tepidariorum* (Araneae, Theridiidae). *Entomological Science* 12: 232–237.

Tanaka K. 2007. Seasonal life cycle of *Zatypota albicoxa* (Hymenoptera: Ichneumonidae), an ectoparasitoid of *Achaearanea tepidariorum* (Araneae: Theridiidae), in north Japan. *Entomological Science* 10: 421–423.

Vollrath F. 1987. Growth, foraging and reproductive success. In: Nentwig W, Editor. *Ecophysiology of Spiders*. pp. 357-370. Springer-Verlag.

Yu D, Horstmann K. 1997. Catalogue of world Ichneumonidae (Hymenoptera). *Memoirs of the American Entomological Institute* 58: 1–1558.

Zwakhals K. 2006. The European species of the genera *Zatypota* and *Sinarachna* (Hymenoptera: Ichneumonidae, Pimplinae, Polysphinctini). *Entomologische Berichten* 66: 34–37.

Downloaded From: https://bioone.org/journals/Journal-of-Insect-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use