Density-distribution patterns of egg parasitoids in freshwater habitats

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Abstract: Similar in effect to predators, egg parasitoids could have a significant effect on the distribution of host and its' population dynamics. However, knowledge about the biology and ecology of aquatic parasitoids and their effects on the host are very limited. The aim of this study was to determine whether the density of parasitoids is affected by several environmental determinants and if there is a temporal change of density during the season, particularly in relation to the host population dynamics (from order Odonata in this study). In total, 266 individuals of parasitoid wasps (from four families utilizing damselflies as hosts) were identified. The density of parasitoids did not change significantly during the season regardless of the population dynamics of model host *L. sponsa* and other odonates, while there was a significant effect of habitat type on the density of parasitoids. This indicates that eggs of Odonata represent only one of several host taxa. This indicates that egg parasitoids of aquatic invertebrates are host generalists preferring open over afforested habitats.

Key words: habitat quality, egg parasitism, parasitoids, host–parasitoid dynamics

Introduction

Although parasitoids are among the largest groups of organisms on Earth, knowledge of their biology, taxonomy and ecology is very limited, especially of the species that are not widely used for purposes of biological pest control. While there are several parasitoid taxa in another six orders (mainly Diptera), most of the parasitoids belong to the order Hymenoptera (Godfray 1994; Footit & Adler 2009). Whereas almost all hymenopterans are terrestrial, development in aquatic environments has evolved independently in at least 11 families (Bennett 2008). All known species ($n \sim 150$) of aquatic Hymenoptera are parasitoids in which the female enters the water to search for hosts (Bennett 2008). A wide range of aquatic insects and other invertebrates (spiders) are known as hosts of parasitoids (Roble 1985; Fursov 1995). The majority of aquatic parasitoids are host generalists, attacking plenty of hosts from different taxa (Fursov 1995).

Aquatic Hymenoptera are mainly solitary endoparasitoids, preferring the egg life stage and with only one egg developing inside each host (Askew & Shaw 1986, Bennet 2008). They are classified as idiobionts that attack a host life stage that is immobile (e.g. an egg or pupa) and then consume the host tissues immediately after the parasitization (Askew & Shaw 1986; Hassell 2000). Developing the abilities to stay underwater, find a host, and undergo further development has required several adaptations (Thorpe 1950; Bennett 2008).

Significant adaptation may be also related to behaviour enabling location of a specific host. Little is known about the foraging behaviour of aquatic egg parasitoids, but several authors have assumed an active search for eggs similar to that seen in terrestrial species (e.g. LaPlante 1975; Corbet 1999). Higher density of hosts can be associated with higher rates of parasitism. Henriquez and Spence (1993) assume that parasitoids may use both visual and chemical cues to locate their hosts. Some observations of foraging behaviour among small scelionid wasp species indicate that these parasitoids use phoresis on female Odonates as a means to reduce costs of movement and especially facilitate the detection of eggs (Clausen 1976; Corbet 1999).

Moreover, the hosts are able to detect parasitoids. Females are able to memorize the risk associated with high density of parasitoids before oviposition (Hirayama & Kasuya 2009). Hosts are in several ways enabled significantly to reduce the risks of egg mortality due to

parasitoids, including by physiological defence and, in particular, site selection for oviposition (e.g. Amano et al. 2008; Harabiš et al. unpubl.). Distribution of parasitoids is related to habitat features. The distribution of parasitoids within habitats is non-random and is closely related to the structure and quality of habitat patches (Roland & Taylor 1997; James et al. 2009; Mlynarek et al. 2011). One of the most frequently mentioned aspects of patch quality is vegetation structure (Roland & Taylor 1997; Fraser et al. 2007). Significantly lower rates of parasitism occur in low-quality habitats (fragmented patches) than in complex habitat patches (Roland & Taylor 1997; Holtzschuh et al. 2010). This does not apply to all species, however (Roth et al. 2006).

As parasitoid has an intimate relationship with its host, it also has similarities with classical parasitism (Godfray & Shimana 1999). Numerous case studies provide evidence of the close relationship between parasites and their hosts (see Møller 2005; Kohler 2008). For example, water mites (Forbes et al. 2008) and gregarines (Forbes et al. 2011) occur mainly during the period when the population densities of hosts are at their highest levels. Yet, the effect of seasonality in host-parasitoid interaction has not been well documented for egg parasitoids. The main aim of the study is to analyse the effect of key factors on overall distribution of aquatic parasitoids and in particular to evaluate temporal changes in predation pressure caused by egg parasitoids.

Material and methods

Study area

Sampling took place in six freshwater habitats in the foothills of the Beskydy Mountains (within an area of about 80 km²) in the vicinity of the cities Valašské Meziříčí and Rožnov pod Radhoštěm in the north-eastern part of the Czech Republic. The individual sites were not significantly different in terms of their water conditions (pH, conductivity) or altitude (Table 1). Each habitat type was classified with regard to structure of vegetation cover and degree of shading as 1) open habitats (shading < 20%), 2) fragmented habitats (shading 20–50%), or 3) habitats with continuous vegetation cover (shading > 50%) (Table 1). All sites had been uninterruptedly freshwater habitats at least from 2006, were extensively formed by human activities, and contained well-developed emergent vegetation. Another criterion for selection of sites was initial occurrence of *L. sponsa* in previous years.

Sampling

Sampling was carried out during June to September 2011 between 10:00 and 16:00. Adult parasitoid wasps were sampled using Möricke 'pan' traps (Möricke 1951). Yellow and blue pans were installed at sites near the water surface at least 3 m apart. The installed pan traps were filled with water, with the addition of salt as a preserving agent. To increase the traps' efficiency, detergent was added to reduce surface tension of the water. Eight pan traps (4 yellow + 4 blue) were placed at each site. At localities where it was not possible to place the specified number of traps without violating the sampling design, lower numbers of traps were installed. This was taken into consideration in the subsequent statistical evaluation.

Colour of pan traps was included as a factor into the analysis mainly because we wanted to eliminate the variability of traps caused by their colour. Yellow pan traps are commonly used for trapping of micro-hymenoptera parasitoids, but there are several taxa of Hymenoptera (especially pollinators) that are better attracted by different colour plates (mainly blue). The efficiency of yellow pan traps was significantly higher than was that of blue traps. This effect was significant for all families except for Trichogrammatidae (Table 2). Given the low number of trapped individuals in the latter family, it was not possible objectively to evaluate the efficiency of pan traps for that family. Traps were placed at sites in 10-day intervals. After 3–4 days, the content of each trap was filtered and stored in 80% ethanol for subsequent determination in the laboratory. The parasitoids were identified according to Goulet & Hubert (1993) and Pitkin (2004).

Additionally we analysed seasonal phenology of damselfly *Lestes sponsa*, as a potentially important host species. *Lestes sponsa* is a widespread generalist whose distribution ranges from Western Europe to Japan. The biology of this species is well known, as it often is used as a model species. The period of oviposition occurs in late July and August, and eggs are laid into the stems of macrophyte vegetation. The generation cycle is univoltine. Endophytically laid eggs fall into diapause and the individuals overwinter in the egg life stage. Immediately after laying, the eggs become targets for egg parasitoids that undergo the life cycle before the start of the winter season.

Table 1: Details of sampling sites (Beskydy Mountains, Czech Republic), including habitat type and overall species richness of Odonata

Locality	GPS position		Elevation (m a.s.l.)	Number species	Habitat
Loc_01	49°25'18.69"N	18°13'18.42"E	450	6	fragmented
Loc_02	49°27'47.40"N	18°04'42.53"E	340	7	open
Loc_03	49°27'20.28"N	18°04'02.67"E	335	6	continuous
Loc_04	49°28'57.64"N,	18°02'58.12"E	390	2	continuous
Loc_05	49°28'05.41"N	17°59'59.69"E	305	12	open
Loc_06	49°31'08.12"N	17°54'18.95"E	275	13	fragmented

Table 2: Effect of variables on density of parasitoids. Number of *Lestes* refers to abundance of *Lestes sponsa*. Habitat refers to vegetation structure. Species richness refers to the number of Odonata species. Seasonality refers to date of sampling. Trap colour refers to yellow or blue pan traps.

Variable	df	Chi	P
Eulophidae			
Number of <i>Lestes</i>	1	0.83	0.362
Habitat	2	8.65	0.013
Species richness	1	19.08	0.141
Seasonality	6	2.16	0.004
Trap colour	1	19.08	< 0.001
Mymaridae			
Number of <i>Lestes</i>	1	0.00	0.977
Habitat	2	10.05	0.007
Species richness	1	2.95	0.086
Seasonality	6	23.07	0.001
Trap colour	1	4.96	0.026
Scelionidae			
Number of <i>Lestes</i>	1	3.61	0.057
Habitat	2	8.36	0.015
Species richness	1	7.08	0.008
Seasonality	6	25.60	< 0.001
Trap colour	1	10.47	0.001
Sum of parasitoids			
Number of <i>Lestes</i>	1	2.36	0.125
Habitat	2	17.63	< 0.001
Species richness	1	10.00	0.002
Seasonality	6	50.71	< 0.001
Trap colour	1	25.85	< 0.001

Adult individuals of *L. sponsa* were sampled according to timed survey method (Kadlec et al. 2012). For this purpose were searched specific habitats, especially macrophyte vegetation in order to catch as many individuals over time. To avoid duplicate counting, the specimens were collected and later released. All localities were sampled at equal intervals (0.5 h for each locality) to obtain precise comparable estimates. During the sampling we have also recorded the occurrence of other species of Odonata as model organisms (presence/absence only) that were identified according to Dijkstra & Lewington (2006).

Statistical analysis

Non-linear mixed-effects models (NLME) with Poisson error distribution (link = log) were used to analyse the effects of vegetation structure, density of *L. sponsa* and the overall species richness of Odonata on the abundance of parasitoids (by individual families). The effect of sampling period (seasonality) was also included in the model. Given the small number of individuals found within it, the family Trichogrammatidae was not analysed separately. In order to reflect the site differences and different number of traps at each site, a split-plot design was selected (Bates et al. 2011). In the model, *L. sponsa* density, overall species richness, and vegetation structure were treated as fixed effects and locality as the random effect. Individual traps as sub-units were nested in locality. To analyse differences in the efficiency of pan traps, colour was used as a fixed effect. Within NLME, we used the glmer function, which is a part of the lme4 package (Bates et al. 2011).

To find the minimum adequate model, all non-significant variables ($P > 0.05$) were excluded step-by-step, using the backward selection procedure (Crawley 2007). The model selection was based on AIC criterion (Crawley 2007). Each minimal adequate model was verified using standard statistical diagnostics in the end, i.e. by residuals and standardized residuals versus fitted and predicted values and by Cook's distances (Crawley 2007). Post hoc comparisons of pairwise differences between the number of parasitoids for each habitat type were made using the multiple comparisons of means: Tukey contrasts; Multcomp package in R (Bretz et al. 2010). All analyses were performed using the statistical program R 2.15.0 (R Development Core Team 2011).

Results

In total, 266 egg parasitoid individuals were found during the study. The most abundant parasitoid family comprised the Scelionidae (119 individuals), followed by Mymaridae (71) and Eulophidae (65). The least abundant family was Trichogrammatidae, in which only 11 individuals were found (Fig. 1).

Fig 1: Total number of parasitoid wasps found in pan traps. White columns denote yellow pan traps, while black column denotes blue pan traps.

There was no significant relationship was found between the number of parasitoids (all families) and the recorded abundance of *L. sponsa* (Table 2). Possible linkage (but one not determined to be statistically significant) to the abundance of *L. sponsa* was found in the family Scelionidae (Table 2). High numbers of parasitoids were found even at sites where there was no documented occurrence of *L. sponsa* in the year of the survey (but had been

documented in previous years). Effect of seasonality on the abundance of parasitoids was significant for all families (Table 2). A similar trend was observed in the recorded occurrence of Odonata and was probably caused by significant changes in temperature during the season. Except for the families Mymaridae and Eulophidae, there was significant correlation between the number of parasitoid wasps and the species richness of Odonata (Table 2). However, the sampling design did not allow for differentiating whether this was a coincidence of parasitoids and Odonata or it was caused by interaction between hosts (Odonata) and their parasitoids.

The density of parasitoids (from all families) was significantly affected by habitat type (Table 2). The gradual gradient of parasitoid density in the direction: open > fragmented >> continuous tree cover indicates that parasitoids had a considerable preference for open habitats over continuously afforested habitats. For the sum of parasitoids, this trend was significant between continuous : open ($t = -3.63$, $P < 0.001$) and continuous : fragmented ($t = -4.57$, $P < 0.001$) habitats, while there was no difference in the case of open : fragmented habitats ($t = 0.78$, $P = 0.695$). The strength of this relationship was significantly different between families. In the family Mymaridae, there was a similar trend for the sum of parasitoids in the cases of continuous : open ($t = -2.57$, $P = 0.025$) and continuous : fragmented ($t = -3.64$, $P < 0.001$) habitats, but there was no significant relationship for open : fragmented ($t = 0.315$, $P = 0.940$). There was a significant gradient in the family Scelionidae. The highest density of these wasps was in open habitats [open : continuous ($t = 3.11$, $P = 0.004$); open : fragmented ($t = 2.40$, $P = 0.037$)], while the lowest density was in continuously afforested habitats [continuous : fragmented ($t = -2.55$, $P = 0.024$)]. Post hoc tests did not show significant differences between habitat types in the family Eulophidae.

Discussion

This study demonstrates that the density of egg parasitoids is affected mainly by habitat type (in particular vegetation cover) but not by the abundance and seasonal dynamics of their host (e.g. Odonata). The initial assumption that the oviposition strategy of individual host taxa leads to a very close linkage in host–parasitoid population dynamics and therefore that the density of parasitoids should correlate with the occurrence of their hosts and the period of hosts' oviposition probably does not apply for egg parasitoids of Odonata.

Except for a period of unsuitable weather conditions (mainly characterized by a significant decrease in temperature), the density of parasitoid wasps (all monitored families) did not change significantly throughout the season. This suggests that egg parasitoids are able to use a wide range of hosts for their development. This finding has appeared across multiple studies concerned with parasitoids of aquatic invertebrates (see Fursov 1995; Corbet 1999; Bennett 2008). They are idiobionts, that attack their hosts always at the time of oviposition and usually parasitize yet undifferentiated tissues and do not need adaptations enabling them to overcome the mechanical and physiological defence of their hosts (Askew & Shaw 1986). There is no pressure, therefore, for egg parasitoids to specialize on single host taxa, and idiobionts are able to attack a wider range of hosts than are koinobionts (Althoff 2003). Thus, we assume that *L. sponsa* (endophytically laid eggs) and other odonates are not the main hosts, but rather constitute just one of many host taxa.

The question remains how wasps detect endophytically laid eggs, and especially those laid underwater. LaPlante (1975) describes foraging behaviour of parasitoid wasps as a random process in which a female seeks for eggs laid on vegetation. It can be assumed that the parasitoids are better able to detect eggs enclosed within vegetation. This does not require specialization upon single taxa, however, since most aquatic invertebrates prefer aquatic plants for oviposition (Footit & Adler 2009).

This study shows that there is a strong linkage of parasitoids on vegetation and habitat type. These aspects are most often cited as factors affecting the distribution of parasitoids (e.g.

Roland & Taylor 1997; Fraser et al. 2007). Similar to the situations for other invertebrates, while rich vegetation cover may be important for several species of parasitoids it may represent a barrier to other species (Roth et al. 2006). Based on the results of our study, it can be assumed that aquatic parasitoids fall into the second category, namely that they prefer more open habitats. In order to work through the potentially general applicability of this trend, it is necessary to extend the research to a larger number of sites.

The results of this study suggest that the density of parasitoids was positively correlated with the species richness of Odonata, but the cause of this correlation is unresolved. As mentioned earlier, the distribution of parasitoids is closely related to vegetation structure (Roland & Taylor 1997). But this applies also to the order Odonata (e.g. Corbet 1999; Sahlén & Ekestubbe 2001). Although it can be assumed that the densities of Odonata and aquatic egg parasitoids are closely associated with habitat quality (mainly vegetation structure), the methodology of this study did not allow us to distinguish whether this was only coincidental for the two ecological groups or if this was due to the host–parasitoid relationship.

With the possible exceptions of several groups of parasitoids attacking pests of economically important crops, there is but very limited information about the behaviour and ecology of parasitoids. This scarcity ensues from the low level of knowledge about the taxonomy of micro-hymenoptera. Moreover, there is still little known about the significance of key environmental factors on the distribution of aquatic parasitoids. Future research should examine also the adaptation of other hosts as well as additional attributes of the host–parasitoid relationship.

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Appendix 1: Ten most abundant families of Hymenoptera trapped in pan traps. White columns denote yellow pan traps, black columns denote blue pan traps, and hatched columns denote sum of individuals.

Appendix 2: Ten most abundant parasitoid families of Hymenoptera trapped in pan traps. White columns denote yellow pan traps, black columns denote blue pan traps, and hatched columns denote sum of individuals.

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