Trophic behaviour of the dragonfly Cordulegaster boltoni (Insecta: Odonata) in small creeks in NW Italy

This is the author's manuscript

Original Citation:

Availability:
This version is available http://hdl.handle.net/2318/1727846 since 2020-02-16T18:52:10Z

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Research Paper

Living Apart Together: On the Biology of two Sympatric Leuctra Species (Plecoptera, Leuctridae) in an Apenninic Stream, Italy

key words: Stoneflies, Leuctra fusca, Leuctra hippopus, life cycle, feeding habits

Abstract

Leuctridae is the richest stonefly family on the European continent, with many species of Leuctra often coexisting in sympathy in the same lotic environment. In this work we studied the life cycle and feeding habits of two species, Leuctra fusca and L. hippopus, coexisting in a small Italian Apennine stream. The life cycles of the two species are non-overlapping, i.e., periods of faster nymphal growth and adult emergence separate them. Nymphs of both species feed mainly on detritus, but quantities of coarse particulate organic matter (CPOM) and diatoms are also ingested. Larger nymphs of both species ingest more CPOM and fewer diatoms. This suggests a similar trophic behaviour through their development. For example, they act as collector-gatherers in their earlier instars and as collector-gatherers or as shredders in their later instars.

1. Introduction

Aquatic insects represent the most diversified and abundant group of invertebrates in freshwaters, and in particular Plecoptera is one of the most important and often dominant orders in stream ecosystems (FOCHETTI and TIERNÓ DE FIGUEROA, 2008a).

Leuctridae Klapálek represents the most species-rich family of the European stonefly fauna with the genus Leuctra, including fifty-nine species, currently described for Italy (FOCHETTI and TIERNÓ DE FIGUEROA, 2008a, VINÇON and GRAF, 2011). Leuctra are small-sized stoneflies. The nymphs are long, slender and light coloured, and the adults are brown to blackish and are characterized by wings wrapped around the abdomen. Leuctra nymphs are generally detritivores, feeding mainly on coarse particulate organic matter, although their diet may also include algae, fungi and bacteria (FEMINELLA and STEWART, 1986). Adult emergence usually occurs at night. The duration of adult activity is variable, but is generally long and adults can feed on pollen, cyanolichens, cyanoprocariota and fungal hyphae (TIERNÓ DE FIGUEROA and SÁNCHEZ-ORTEGA, 2000).

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Many studies have indicated that different species of *Leuctra* can coexist in the same stream reach. For example, Ravizza and Ravizza Dematteis (1976) reported that four *Leuctra* species can live in sympatry in an Alpine creek while, more recently, Bo et al., (2009) reported that six species cohabit in the Curone creek, an Apenninic lotic system. Because several species of this genus may coexist in the same environment, this genus represents an excellent subject for ecological-evolutionary studies. The aim of this research was to study the biology of two populations of *Leuctra*, one of *L. fusca* (Linnaeus) and one of *L. hippopus* (Kempny) that inhabit a small creek. We tried to analyze their occurrence, diet, life-cycle, adult phenology, and discuss the results within the framework of an ecological approach.

2. Methods

The study was conducted in the Albedosa Creek (4°41’14” N, 8°43’19” E; 190 m a.s.l.), an Apenninic small tributary of the Orba River, north-western Italy. The climate is temperate-Mediterranean, with high autumnal rainfalls. The stream flows through a small valley in a secondary deciduous forest. The riparian vegetation is dominated by *Robinia pseudoacacia* (Linnaeus), *Alnus glutinosa* (Gaertn), *Corylus avellana* (Linnaeus) and scattered *Castanea sativa* (Miller) and *Quercus* spp. In the sampling station, the channel width was about 2.5–3.5 m, with a mean depth of 25–30 cm. The stream substrate consisted mainly of sands (40%), gravels (30%), cobbles (20%), and other masses (10%). Samples were collected randomly in the stream bed, in order to represent every possible microhabitat. We used a Surber sampler (area: 0.0625 m²; mesh size: 250 μm). All macroinvertebrates were collected and preserved in 85% ethanol. In the laboratory, *L. fusca* and *L. hippopus* nymphs were separated, counted and measured. Nymphs identification was done following Hynes (1977) and Consiglio (1980).

We measured total body length and pronotum width of each nymph with the micrometer of a binocular microscope. A high correlation existed between both measures in both species (Gamma correlation = 0.85, \( P < 0.05 \) for *L. fusca* and Gamma correlation = 0.71, \( P < 0.05 \) for *L. hippopus*). Therefore, only total length was used for all analyses. Nymphs were classified in 1 mm length size intervals. The life cycle was represented by means of size-frequency graphs obtained with FiSAT II software (Gayani et al., 2002).

To study the diet of the nymphs, we used the method proposed by Bello and Carrera (1999), as done in other papers on Plecoptera nymphal feeding (e.g., López-Rodríguez and Tierno de Figueroa, 2006; Fenoglio et al., 2009; Kozáčeková et al., 2009). Once each nymph was measured (to the nearest 0.01 mm), each individual was placed in a vial completely cover with Hertwigs’ liquid and heated in an oven at 65 °C for approximately 24 hours. Afterwards individuals were mounted on slides to study their gut content under the microscope. We use a microscope equipped with an ocular micrometer to estimate the percentage absolute gut content at 40 × (as percentage of total area occupied by the contents in the whole digestive tract) and the relative abundances of food items in the gut content at 400 × (as percentage area occupied by each component of the total gut contents). We calculated the mean, standard deviation, minimum and maximum of each component. We also studied the correlation between nymphal size and gut contents using a Gamma correlation.

All the statistical analyses were performed under STATISTICA v.7.1 software (StatSoft, 2005). As the analysed variables had a non-normal distribution, nonparametric statistics were used.

3. Results and Discussion

Both species have a univoltine life cycle in the studied site, but nymphal development was not synchronized (Fig. 1). The average nymphal development period of *L. fusca* is usually 3 months, from July to September, although some medium-size nymphs may be found in October. The latter nymphs, despite being smaller, were mature. The flight period of this species begins in September and ends in November.
In contrast, *L. hippopus* has a longer nymphal development period, ranging from September to February–March though, even in February, some small nymphs are collected. The flight period of *L. hippopus* is shorter than *L. fusca*, and adults were only captured in March. Quantitatively, more nymphs of *L. fusca* were captured than of *L. hippopus* (*N* = 345 and *N* = 41, respectively; Fig. 1). The nymphal feeding study shows that both species feed mainly on detritus, but both also ingest quantities of coarse particulate organic matter (CPOM) and diatoms (Table 1). In the gut of some nymphs of both species, mineral particles were present. Positive significant correlations between size and percentage of occurrence in the gut are found for fungi hyphae and spores, and CPOM in *L. fusca*, and for fungi hyphae, CPOM, and mineral matter in *L. hippopus* (Table 2). Negative significant correlations were found for diatoms and mineral matter in *L. fusca*, and for diatoms in *L. hippopus*.

The univoltine life cycle of the Albedosa population of *L. fusca* is similar to the one found in other parts of Europe, such as Great Britain, Sweden, France and Norway (Hynes, 1941; Brinck, 1949; Lavandier and Dumas, 1971; Lillehammer, 1988). Nymphal growth is also fast in this species. The first nymphs reach maturity in just the three months of summer. A

Table 1. Nymphal gut contents of the studied species in the Albedosa Creek.

<table>
<thead>
<tr>
<th></th>
<th>Leuctra fusca</th>
<th>Leuctra hippopus</th>
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<tbody>
<tr>
<td></td>
<td>N  Mean SD</td>
<td>Min Max</td>
</tr>
<tr>
<td>% detritus</td>
<td>61  57.61 24.44</td>
<td>0.00 95.00</td>
</tr>
<tr>
<td>% hyphae</td>
<td>61  2.34 3.39</td>
<td>0.00 15.00</td>
</tr>
<tr>
<td>% spores</td>
<td>61  0.85 1.80</td>
<td>0.00 10.00</td>
</tr>
<tr>
<td>% CPOM</td>
<td>61 16.46 22.35</td>
<td>0.00 100.00</td>
</tr>
<tr>
<td>% pollen</td>
<td>61  0.61 1.45</td>
<td>0.00 8.00</td>
</tr>
<tr>
<td>% diatoms</td>
<td>61 15.82 17.79</td>
<td>0.00 65.00</td>
</tr>
<tr>
<td>% mineral matter</td>
<td>61  6.64 4.36</td>
<td>0.00 15.00</td>
</tr>
</tbody>
</table>
maximum nymphal growth in summer was recorded by several authors (e.g., Brinck, 1949; Lillehammer, 1988) in different populations, but not as rapid as we observed. For instance, Lavandier and Dumas (1971) pointed out that nymphs of _L. fusca_ are more abundant in spring and summer, and that they require eight to nine months for nymphal development. These authors collected nymphs from January to November (a longer period than occurring in our study in Albedosa Creek). In our study, several mature nymphs were also collected in October, but with a relatively smaller size than those of the September collections. They would be either males (generally of smaller size) or some nymphs that did not achieve a higher size before the arrival of the emergence period. The flight period in the Albedosa creek is mainly autumnal (as recorded in several studies, Tierno De Figueroa et al., 2003; Fochetti and Tierno De Figueroa, 2008b), though in some parts of Europe, the period may extent into winter (e.g., Luzón-Ortega et al., 1998). Adults may also be present after one month of the capture of the last nymph. This probably indicates that they can survive several weeks in this stage.

_Leuctra hippopus_ also has a univoltine pattern that coincides with the one pointed out in other European studies (e.g. Lavandier and Dumas, 1971; Lillehammer 1988). The growth of this species is slower than the growth of the previous one, lasting from seven to eight months, and is relatively constant. This period is similar to the one found in a population in the French Pyrenees, where first nymphs reach maturity in approximately eight months (Lavandier and Dumas, 1971). Nevertheless, in that study, the authors reported nymphs being present all 12 months of the year. In our study, nymphs were collected over eight months. As pointed out by Lillehammer (1988), local populations of _L. hippopus_ seem capable of giving rise to variable life histories. The egg hatching and nymphal development are dependent on temperature. Regarding this plasticity, some degree of asynchronous hatching was detected at our study site, because some small nymphs were collected in February. The latter nymphs probably represent individuals that hatched late and did not complete their nymphal development before the warmer spring period. In the Albedosa Creek, adults were captured only in March. In other parts of Europe, the flight period of _L. hippopus_ was also spring (Fochetti and Tierno De Figueroa, 2008b), spring-summer (Lillehammer, 1988) or even winter-spring, the latter in the French Pyrenees (in Tierno De Figueroa et al., 2003). However, marked differences were noted by Lavandier and Dumas (1971) who collected adults from February to June, a wider period than that of our population.

With regard to feeding habits, both species are mainly collector-gatherers. However, the relatively high content of CPOM and diatoms also suggests that nymphs of both species play an important role as shredders and scrapers too. The presence of mineral matter in the gut may indicate that nymphs swallowed these resources when collecting detritus. Nevertheless, their shredder role cannot be rejected, as CPOM is ingested in greater amount by

<table>
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<tr>
<th></th>
<th><em>L. fusca</em> total length (mm)</th>
<th><em>L. hippopus</em> total length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>% absolute</td>
<td>–0.05</td>
<td>0.11</td>
</tr>
<tr>
<td>% detritus</td>
<td>0.05</td>
<td>–0.20</td>
</tr>
<tr>
<td>% hyphae</td>
<td>0.36*</td>
<td>0.29*</td>
</tr>
<tr>
<td>% spores</td>
<td>0.35*</td>
<td>0.14</td>
</tr>
<tr>
<td>% CPOM</td>
<td>0.19*</td>
<td>0.53*</td>
</tr>
<tr>
<td>% pollen</td>
<td>0.05</td>
<td>0.00</td>
</tr>
<tr>
<td>% diatoms</td>
<td>–0.20*</td>
<td>–0.27*</td>
</tr>
<tr>
<td>% mineral matter</td>
<td>–0.26*</td>
<td>0.40*</td>
</tr>
</tbody>
</table>
larger nymphs, as well as hyphae (and spores in L. fusca). Larger nymphs, with more robust mouthparts, could break up and ingest CPOM and the fungi that colonize leaf surfaces. Feeding on detritus and CPOM by L. fusca and L. hippopus had been already reported by several authors (BRINCK, 1949; LILLEHAMMER, 1988), as well as ingestion of diatoms and mineral matter in L. fusca (BRINCK, 1949).

In this study the two Leuctra species seem to have different thermal requirements for nymphal development. It seems that nymphs of L. fusca as apparently need warmer temperatures for development than does L. hippopus. In fact, FOCCHETTI and TIERNO DE FIGUEROA (2008b) classified L. fusca as mesotherm reophil and L. hippopus as reophil and crenophil in Italy.

4. Conclusions

The fundamental question of how congeneric and similar species manage to coexist with one another in the same environment is an intriguing subject of study. The coexistence of two or more congeneric species in the same environment is possible because adaptive mechanisms have evolved. Indeed, related species are more likely to interact and/or compete because the great part of behavioural and ecological activities is linked with phylogenetic and morphological characters (e.g., GRANT and MACKAY, 1969).

The well-documented tendency of sympatry in Leuctra is a fascinating subject. Probably the most outstanding finding of our study is the complete absence of overlapping in the development of two congeneric and morphologically similar species: L. fusca and L. hippopus. We hypothesize that this offset in the life cycles could be due to: i) a strategy to minimize possible competition for trophic resources if they were limiting in the past. Because both species show detritivorous feeding habits, the temporal segregation of the period of rapid nymphal growth would be fundamental in minimizing trophic resource interaction, as pointed out in previous studies on other aquatic insects (BRITTAIN, 1982; LÓPEZ-RODRÍGUEZ et al., 2010). ii) The non-overlapping flight periods of both species results in segregation of the taxa.

Obviously, both hypotheses [decreasing the ecological competition in accordance with the principle of Gause (GAUSE, 1935) and strengthening reproductive isolation, according to the Wallace effect (SAWYER and HARTL, 1981)] may help to explain this asymmetry in the life cycles of these congeneric species. Nevertheless, according to KREBS (2009), Gause’s principle should not be used as a general ecological model for competition, since even the smallest differences can allow coexistence of closely related species. Moreover, in other parts of their distributional range, even when they do not coexist, they maintain these life history patterns (GRAF et al., 2009). Thus, this displacement in the life cycles of both species would be due to an evolutionary constraint of each species more than due to the “ghost of competition past” (CONNELL, 1980) in this stream.

5. Acknowledgements

Authors are actually grateful to two anonymous referees and to Professor KENTON M. STEWART, whose comments improved a previous version of the manuscript. This study was supported by Fondazione Cassa di Risparmio di Alessandria CRAL grants.
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Manuscript submitted June 29th, 2011; revised September 9th, 2011; accepted October 10th, 2011