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Hiding among traps? Mortality of early instar odonate larvae in the presence of bladderwort plants

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We investigated the effects of the presence of bladderwort plants on survival of early instar larvae of one coenagrionid and two libellulids in laboratory experiments. In all three species survival was reduced compared to treatments with a non-carnivorous submerged plant, with effective mortality that could be related to bladderwort being 19–45% dependent on the prey species. Individuals of all species were found in capture bladders. We also recorded the microhabitat use of the early instar larvae and found that the species with highest use of vegetation had highest mortality due to bladderwort. We conclude that bladderwort may have effects on odonate larvae that translate into natural conditions and we discuss factors that may affect predation by bladderwort on odonates in the field.

Introduction

Odonate larvae possess many natural enemies, such as fish, water birds, amphibia and various invertebrate predators including other odonate larvae (Corbet, 1999). The presence or absence of fish in particular often shapes odonate communities, as confirmed for *Enallagma* and *Lestes* communities in North America (McPeek, 1990; Stoks & McPeek, 2003). Dragonfly larvae have developed diverse behavioural and morphological features serving to reduce predation pressure, which involve traits for defence, escape, and crypsis (Suhling et al., 2015, table 35.2). The latter comprises behavioural traits such as reduced locomotory activity, which may be fixed as well as flexible, and depending on the type or species of predator (Johnson, 1991; Wohlfahrt, Mikolajewski, Joop, & Suhling, 2006). Particularly in species that have larvae belonging to the sprawler type, such as most Coenagrionidae and many Aeshnidae and Libellulidae (Corbet, 1962; Suhling et al., 2015), hiding among aquatic vegetation serves to reduce predation against fish as well as against invertebrates (Elkin & Baker, 2000; Henrikson, 1993; Thompson, 1987; Wellborn & Robinson, 1987). Predation pressure decreases with increasing weed density (Thompson, 1987) and is also influenced by the plant growth forms (Dionne, Butler, & Folt, 1990; Dionne & Folt, 1991). However, if it is generally assumed that aquatic plants may reduce the predation risk of

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odonate larvae (Corbet, 1999, p. 164), there may be exceptions if the plant itself is the predator (Martens & Grabow, 2011).

Bladderworts (genus *Utricularia*, Lentibulariaceae) are globally distributed carnivorous plants in freshwater systems. The plants capture small invertebrates by means of bladder-like traps (Reifenrath, Theisen, Schnitzler, Porembski, & Barthlott, 2006; Sanabria-Aranda et al., 2006), which provide additional nutrients (Friday, 1989). Whereas the relevance of the carnivory for the plant is debated (Kibriya & Iwan Jones, 2007; Knight, 1992; Richards, 2001), there is no doubt that many different organisms get trapped in the bladders. Enclosure experiments revealed that predation by bladderwort caused a decrease in prey density over time (Baumgartner, 1987; Harms, 2002). The known prey includes various microalgae, Protozoa, Oligochaeta, Rotifera, Crustacea (Cladocera, Copepoda, Ostracoda), and insect larvae, including Diptera (Chironomidae, Culicidae), Heteroptera (Corixidae), and Ephemeroptera (Caenidae) (Alkhalaf, Hübener, & Porembski, 2009; Baumgartner, 1987; Harms, 1999; Sanabria-Aranda et al., 2006; Walker, 2004). The prey organisms all have a size comparable to early instar odonate larvae. But, only recently, early instar larvae of Coenagrionidae and Aeshnidae have been discovered in capture bladders of *Utricularia australis* R. Brown in a garden pond (Herzog & Martens, 2013; Martens & Grabow, 2011).

We became interested in these observations because bladderwort can be a dominant aquatic vegetation at sites with huge dragonfly populations and one should expect clearly detectable interactions. On the other hand, even in studies where the prey captured by bladderwort was carefully compared against the assemblages of organisms, living in its plant stand, Odonata larvae remained undetected in traps of *Utricularia* (Baumgartner, 1987; Sanabria-Aranda et al., 2006). Thus, is predation by bladderwort on early instar larvae just a matter of random misfortune or could it have quantitative effects on the populations? Our aim was to quantify predation by bladderwort. We analysed mortality caused by the common bladderwort *Utricularia vulgaris* Linnaeus by comparing decreases in numbers of early instar larvae in containers with bladderwort and a non-carnivorous plant in the laboratory. We did that for three species of Odonata, one Coenagrionidae and two Libellulidae. Finally, we also recorded microhabitat use by the larvae of the three species in treatments with and without bladderwort.

Methods

Study species and study area

Our study organisms included early instar larvae of three odonate species and two water plants. The odonates were *Ischnura elegans* (Vander Linden, 1820), *Crocothemis erythraea* (Brullé, 1832), and *Libellula quadrimaculata* Linnaeus, 1758. First experiments were done with *L. quadrimaculata* larvae in 2018 for reason of availability of egg clutches. But, since in nature the larvae of *L. quadrimaculata* mainly dwell on bottom substrates and less so in vegetation (Wildermuth & Martens, 2019), we aimed to compare with species that use submerged vegetation as main microhabitat in 2019. Both *I. elegans* and *C. erythraea* are such species, although larvae can be found on bottom substrates of ponds, *C. erythraea* more commonly so than *I. elegans* (Wildermuth & Martens, 2019).

For obtaining young instar larvae, we caught females in the field. In *I. elegans* the female was kept for 12 hours over night in a small closed container with air contact, water, small sticks and a filter paper as a macrophyte replacement, which was accepted for oviposition. The eggs of the two libellulids were collected by dipping the abdomen into a jar with water, which was followed by immediate egg laying (cf. Schenk, Suhling, & Martens, 2004). We used one egg clutch of *I. elegans*, one of *C. erythraea* and two of *L. quadrimaculata*. The eggs were kept in the laboratory at 20°C until hatching of the larvae. For all experiments second instar larvae were used.

The water plants used in our experiments were *U. vulgaris* and *Myriophyllum spicatum* L. Both plants were collected from an aggregation of several ponds situated in the northeastern suburban area of the city district of Braunschweig (52.33032°N, 10.58186°E), which are rich in aquatic vegetation and odonate species (Suhling, Martens, Leipelt, Schütte, & Hoppe-Dominik, 2009). In the case of *U. vulgaris* these ponds are the major habitat in the area and *U. vulgaris* is among the dominant plants there. *Myriophyllum spicatum* occurs in many ponds in the area. Stems of both plants were taken from the ponds and transferred to the laboratory where they were kept at ambient temperature of 20°C and a day/night rhythm of 14/10 hours. The light intensity was 1600 lux.

The bladderwort *U. vulgaris* is free-floating and does not put down roots. The stems can attain lengths of > 1 m in a single growing season. From the main axis branch off smaller stems with photosynthetic leaves with about 20 traps or bladders (Friday, 1992). The bladders are 0.3–5.0 mm in diameter and closed with a trap door. Antennae trigger the trap mechanism after being touched (Friday, 1989; Meyers & Strickler, 1979). Within 10–15 ms, the trap door opens and the prey are drawn in by a negative pressure of –15 to –17 kPa. That mechanism resets within 30 minutes (Adamec, 2011). The main stem grows at one end while it slowly dies at the other but 1200–2700 bladders are functional simultaneously (Friday, 1989). *Myriophyllum spicatum* is a submerged, aquatic perennial that can have stems 1.8–6 m in length with soft and feather-like leaves, and each mature submerged leaf has a central midrib with 12–20 filiform segments on each side. Although the two plants are not fully similar in appearance we assumed that they may be similar enough that both may serve as shelter for odonate larvae.

Experimental design and analyses

We compared survival of young instar larvae in the presence of stalks of *U. vulgari*s with treatments where stalks of *M. spicatum* were provided as perches. The experiments were conducted in containers 6 cm wide, 7.5 cm long, and 2.5 cm high, which were half filled with dechlorinated tap water. The temperature and light conditions were as above. The vegetation density was kept equal in the experimental containers: the water volume was about 80% filled with plant material. For convenience, the treatments will be termed *Utricularia-* and *Myriophyllum*-treatment in the following. In each replicate 20 larvae were introduced immediately after hatching from the egg (Figure 1). The replicates were started successively when enough larvae (i.e. 40) had hatched to prepare at least one replicate for each treatment. Each run of the experiment was stopped after 10 days. *Artemia salina* naupliae were added to the containers once per day serving as prey for the odonate larvae. For each replicate we used new odonate larvae as well as new plant material.

For detecting larvae, the plant stalks were transferred carefully to a Petri dish filled with water and searched for larvae. The numbers of larvae found by this method were considered as survivors. To avoid disturbance, we did not check bladders of *U. vulgaris* for larvae during the experiment. However, we examined samples of bladders after the experiment using a dissecting microscope. Because of these limitations, we cannot provide absolute numbers of larvae captured in bladders. A somewhat makeshift method was used for identifying microhabitat use by the larvae. For this it was noted how many larvae were climbing to the plants and how many were found on the bottoms of the containers when checking for larvae. Since the numbers of survivors usually did not resemble the initial numbers of larvae in the container we used the proportions of larvae on plants in relation to the surviving larvae per container for later analysis.

For statistical analyses, we ran two-way ANOVAs with species and treatment as independent factors. Numbers of survivors per container and proportions of larvae on plants served as response variables in two separate analyses. The data were log $(x + 1)$ transformed for the purpose of the tests. In figures the original data are shown. We used Tukey's posthoc tests for
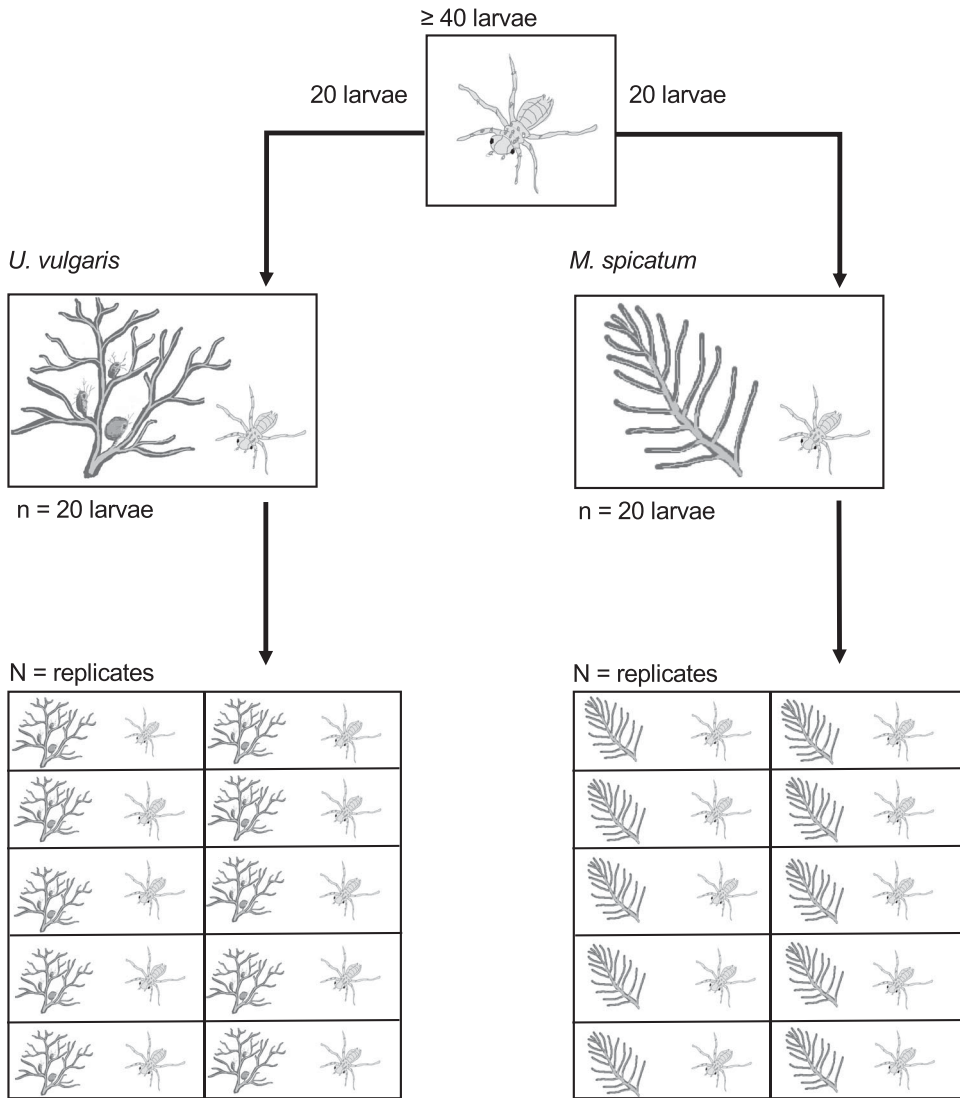
Figure 1.   Flow chart depicting the methods. Odonate larva and plant are not to scale; compare to photos in Figure 3.

pairwise comparisons between the treatments in each odonate species. The analyses were run in the software Past 3.24 (Hammer, Harper, & Ryan, 2001). The numbers of replicates are presented in Table 1.

Results

Mortality

The numbers of surviving larvae varied significantly with the treatment (ANOVA, $F_{1,86} = 70.46$, $p < 0.001$) and between the odonate species ($F_{2,86} = 19.90$, $p < 0.001$) (Figure 2). Pairwise posthoc tests revealed that the numbers of surviving larvae differed between the treatments in all three odonate species, with survival always lowest in presence of *Utricularia*. There was

Table 1. Numbers of replicates in the different treatments and analyses. In each replicate 20 larvae were exposed to the plants. Note that the replicates for the microhabitat analysis is lower because in the first runs with *L. quadrimaculata* the larval position was not noted.

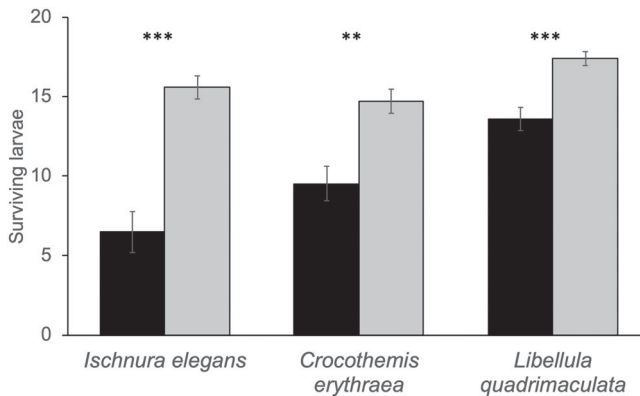| | Replicates per treatment | | | |
| | *Utricularia*-treatment | | *Myriophyllum*-treatment | |
Odonate species	Survival	Microhabitat	Survival	Microhabitat
Ischnura elegans	10	10	10	10
Crocothemis erythraea	13	13	11	11
Libellula quadrimaculata	23	17	25	15

Figure 2. Mean numbers of surviving larvae ($\pm$ SE) in treatments with *Utricularia vulgaris* (black bars) and *Myriophyllum spicatum* (shaded bars). Pairwise posthoc tests: **$p < 0.01$, ***$p < 0.001$.

also a significant interaction between treatment and species ($F_{2,86} = 5.24$, $p = 0.007$), i.e. the effect of treatment differed in strength between species. The decline of survival in the *Utricularia* treatment was much more severe in the case of *I. elegans* compared to the two other species. The proportions of mortality in the *Utricularia*-treatments relative to the *Myriophyllum*-treatments, where mortality was quite similar in all species, were 45.5% for *I. elegans*, 25.9% for *C. erythraea*, and 18.9% for *L. quadrimaculata*.

On closer examination, we found small larvae of all three odonate species in the bladders of *U. vulgaris*, one of *I. elegans*, two of *C. erythraea* and 11 of *L. quadrimaculata* (cf. Figure 3a). This did not comprise all larvae missing from the replicates, which was not surprising due to the 10-day running time of the experiment and the fact that we did not check for larvae in all the bladders.

Larval microhabitat use

Larvae were in most cases found more commonly on the bottom of the containers than on the plants, which may be to some extent an artefact of handling. However, even after handling many larvae were crawling on the plant stems, often in close vicinity of the bladders of *U. vulgaris* (Figure 3b, c). The mean proportion of larvae of *I. elegans* and *C. erythraea* found on the plants was higher than 0.5 in the *Utricularia*-treatments. In the *Myriophyllum*-treatments larvae were proportionally underrepresented on the plants in all cases (Figure 4). Two-way ANOVA revealed significant differences between the treatments ($F_{1,76} = 29.76$, $p < 0.001$) and also between the odonate species ($F_{2,76} = 6.41$, $p = 0.003$), while the interaction was not significant
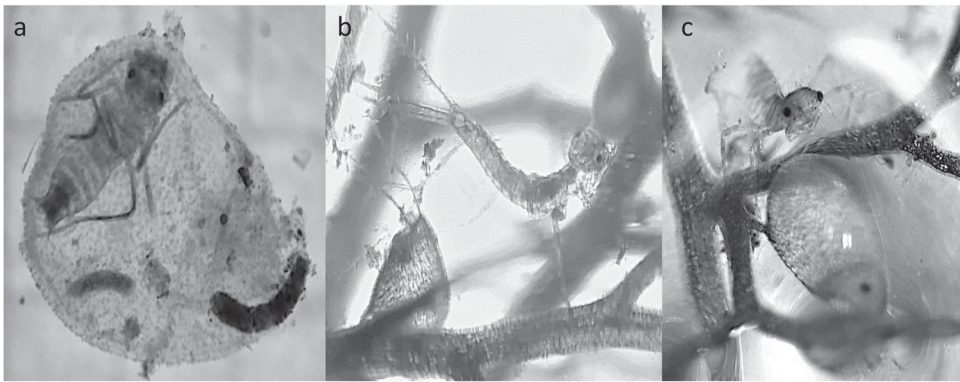
Figure 3.   (a) Second instar larva of *Libellula quadrimaculata* found dead in a bladder of *Utricularia vulgaris*. (b) Living second instar larva of *Ischnura elegans* next to a bladder of *U. vulgaris*. (c). Living second instar larva of *Crocothemis erythraea* next to a bladder of *U. vulgaris*.
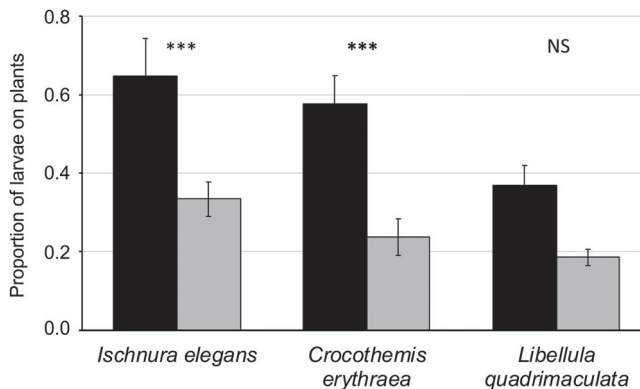

Figure 4.   Mean proportions ($\pm$ SE) of larvae perching on plants in treatments with *Utricularia vulgaris* (black bars) and *Myriophyllum spicatum* (shaded bars). Pairwise posthoc tests: ***$p < 0.001$, NS not significant.

($F_{2,76} = 1.61$, $p = 0.207$). Pairwise comparisons showed that significant differences between treatments occurred in *I. elegans* and *C. erythraea* but not in *L. quadrimaculata* (Figure 4).

Discussion

Early instar larvae of both Coenagrionidae and Aeshnidae have been recorded in bladders of *U. australis* (Herzog & Martens, 2013; Martens & Grabow, 2011). In our study, we add *U. vulgaris* to the (short) list of plants preying on early instar odonate larvae. We suppose that other bladderwort species are also capable of preying on early instar Odonata. We also confirm that larvae of Coenagrionidae can be victims of bladderwort and add two species of Libellulidae to the list of prey. We suppose that early instars of most odonate species may be affected – as long as they come somehow in contact with aquatic bladderwort plants.

So far, there was no quantification of the mortality risk for early instar odonate larvae due to bladderwort predation. We found that, at least under the experimental conditions, the number of larvae killed by *U. vulgaris* may be severe. This is under the assumption that the differences in survival between the *Utricularia*- and the *Myriophyllum*-treatments were caused by bladderwort. This is supported by the fact that we found larvae in the bladders at the end of the experiments and by the record of larvae in bladders in the field (Martens & Grabow, 2011).

There were significant differences in mortality between the three odonate species tested. Yet, the predatory effect by bladderwort is likely not species-specific. However, we suppose that the larval lifestyle and behaviour shapes the predation risk. In our experiments *I. elegans* was the species with the most distinct use of bladderwort versus the bottom, followed by *C. erythraea*, and *L. quadrimaculata*. This result fits relatively well expectations, considering the known pattern of habitat use of the three species, with *I. elegans* probably most clearly related to aquatic vegetation (cf. Study Species), whereas *L. quadrimaculata* larvae dwell in vegetation as well as in bottom substrates. It is likely that the more the larvae of a species sprawl in vegetation the higher their risk of becoming prey to bladderwort. However, prey behaviour may also play a role (Harms & Johansson, 2000). For instance, early instar larvae of *C. erythraea* are active, visual hunters; they move towards sensed prey when foraging (Suhling, Sahlén, Kasperski, & Gaedecke, 2005). During such actions they probably more regularly touch the antennae of *Utricularia* and, consequently, have higher risk of being captured than less active hunters. The same may be true for *I. elegans* (cf. Heads, 1985).

We found much less use of *M. spicatum* than of *U. vulgaris* by the odonate larvae. This has no relevant effect on the interpretation of the predatory effects of bladderwort, since the non-carnivorous plant was less used than the carnivorous one. Nevertheless, it demands some explanation. We only can imagine that the plant structure, which is a bit simpler in *M. spicatum*, may have caused larvae to slide off the leaves more often when being transferred to Petri jars for counting. We actually cannot exclude that that happened with both plants, but maybe less so with bladderwort. The consequence would be that the use of plants in both cases may be underestimated.

A mortality of 19% due to bladderwort was found in *L. quadrimaculata* and 45% in *I. elegans*; however, the most relevant question is whether mortality under experimental conditions somehow translates into natural conditions. Several factors may affect the predation by bladderwort on odonate larvae. The efficiency of bladderwort to catch prey depends on age, size and position of bladders (Friday, 1989) as well as on the condition of the plant. The optimal conditions for building traps are complex and not fully understood, particularly the influence of nutrient availability, which depends on the environment (Englund & Harms, 2003; Knight, 1992). Under bad conditions, such as low carbon dioxide concentrations in the water and low light intensity, the investment in trap building declined or stopped (Friday, 1989; Harms, 2002). Then, predation by bladderwort would be massively reduced. Also, phenology of plant and odonate larvae have to be synchronised. At least in our experimental system this seems to be the case. Usually, fully functional traps are built in the middle of April and trap building continues during summer (Friday, 1989). That resembles the reproductive season of Odonata in the region, so traps would be present at all times together with early instar larvae of at least some species.

In nature, high density of other prey such as microcrustaceans may prevent odonate larvae from being captured. In our experiments *Artemia* was present at least once per day. But, since the survival time of *Artemia* is not very long in fresh water there was probably not enough other prey for the bladderwort than the odonates. On the other hand, it seems that plankton prey is less common in bladders compared to organisms living among vegetation (Harms, 1999). Also, interactions between prey species may cause that certain prey species to be overrepresented as prey (Harms & Johansson, 2000).

Finally, the predatory effect of bladderwort versus its efficiency as shelter against other predators is relevant. A mesocosm experiment, although with a different study aim, provided interesting results (Knorp & Dorn, 2016). Interactions of mosquitofish (*Gambusia holbrooki* Girard, 1859) and presence of vegetation were investigated with bladderwort being used as submerged vegetation. Dragonflies were able to colonise the mesocosms via oviposition and dragonfly emergence from mesocosms was measured. In the presence of fish, emergence was higher when bladderwort plants were present (Knorp & Dorn, 2016). Thus, compared to

conditions without any submerged vegetation the bladderwort is surely still reducing preda-tion by fish. However, with other vegetation the anticipated antipredation effect may be higher. So far there is no study on predation by fish or invertebrates in treatments comparing between bladderwort and non-carnivorous plants.

In conclusion, it seems possible that bladderwort can be a notable predator for early instar larvae, which use submerged aquatic vegetation as microhabitat, even if they have not often been recorded yet as prey. The predatory effects may be particularly relevant in species that hide between plants as an antipredation behaviour. Most likely, there will be only predation on very small larvae that fit the size of the bladders. It still has to be investigated to which size larvae are caught. For small larvae the bladderwort plant may provide a shelter against other predators but as well a trap. One may expect a behavioural conflict, comparable to conflicts such as anti-predation versus anti-parasite behaviour or anti-predation versus avoiding aggressive encounters with conspecifics (Baker & Smith, 1997; Elkin & Baker, 2000). Interesting in this context is that the larvae were running along stems of bladderwort without avoiding the bladders. Maybe they do not recognise the bladders as a threat. For a better evaluation of the population effects more studies are necessary, e.g. considering the plant density, the time of the year, and the mortality due to bladderwort in relation to the protection the plant may provide against other predators.

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