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Mineral grain availability and pupal-case building by lotic caddisflies: Effects on case architecture, stability and building expenses

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ABSTRACT

The retreat-making larvae of many lotic caddisflies build entirely new pupal cases with fine gravel and sand that they collect in the neighbourhood of the building place to fix it with silk to cobbles in swift flow (where finer sediments are generally rare). Previous field observations on *Hydropsyche siltalai* pupal cases illustrate that natural local resource limitations of the preferred grain fraction (2.5–3.15 mm) produced chained effects across other grain fractions, as the alternative use of more grains in the 1.6–2 mm fraction (an unlimited resource) induced an increased use of more grains in the 0.315–0.5 mm fraction (another unlimited resource). To examine the implications of these observations for *H. siltalai*, we used (1) mesocosms to created minor deviations in the availability of the natural grain size composition of the building material of pupal cases at otherwise carefully replicated natural stream habitat conditions and (2) recently developed technologies to assess many case characteristics so far ignored in studies of caddisfly cases. When the preferred coarser grains (2.5–3.15 mm) were unavailable, more grains with intermediate size (1.25–2.0 mm) were used (and not other, still available coarse grains) and fewer larvae built cases in groups, thereby not only loosing the benefits (lower costs for grain transport and silk) but also avoiding potential disadvantages associated with grouped cases (more aggressive encounters with conspecifics for rare building material, less flow exposure and thus reduced water renewal in the pupal chamber). Unavailability of 2.5–3.15-mm and 0.315–0.5-mm grains caused a reduction of larvae building in groups, more use of grains with intermediate size, changes of several other grain characteristics (e.g. number, circularity) and considerable investment into silk to maintain the case resistance. Finally, grain availability deviating most from that observed in nature (no grains of 2.5–3.15 mm and 1.6–2.0 mm) caused dramatic responses, as mortality increased so that fewer pupal cases were built, using typically more coarse grains so that many cases had an elevated resistance against crushing forces; in addition, many males had a retarded development, whereas female development was unaffected. Thus, the response of *H. siltalai* to any of the three types of grain limitations differed, illustrating an immense diversity to respond to grain-size shortage.

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1. Introduction

Building cases or tubes from or among particles is a widely used technique within many groups of aquatic (e.g. Brennan and McLachlan 1979; Dudgeon 1990; Statzner et al. 2005; Koller et al. 2006) and terrestrial (e.g. Bucheli et al. 2002; Farji-Brener 2003; Chaboo et al. 2008) animals. Among aquatic organisms, such structures are build by many species of protozoans, rotifers, molluscs, annelids (particularly polychaetes) and arthropods (crustaceans and insects), and the ways of particle selection for these buildings and related functional implications for the builder (or its surrounding environment) have been a major thread in studies of the biology and ecology of these animals (Dudgeon 1990). For example, architecture of such animal buildings and/or building behaviour served in cladistic analyses (e.g. Stuart and Currie 2001), assessments of habitat requirements of the builder (e.g. Tolkamp 1980; De Moor 2005) and the description of refugia for other organisms (e.g. Bergey 1999).

Among the building insects, caddisfly larvae construct cases from mineral and/or organic particles that are cemented with silk threads, an ability that has been viewed as a key for the evolutionary success of this order (Mackay and Wiggins 1979). The diversity and beauty of the cases built by these “underwater architects” fascinated biologists for more than a century (e.g. Lampert 1899; Wiggins 2004). When the preferred case material is available, the natural case architecture is often so typical that it can serve for the identifications of species, genera or families (e.g. Waringer and Graf 1997; Higler 2005). When experimentally limiting the availability

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of the naturally preferred material, however, larvae typically construct with material being as close as possible to the preferred one (Gorter 1931). Species building with mineral grains, for example, would use grain sizes near the size range of the usually preferred but unavailable grain size (Hanna 1961; Tolkamp 1980). If available mineral grain sizes are too different from the preferred ones or no mineral grains are available, larvae construct irregular silk cases or may use organic material instead (e.g. Haller 1948; Hanna 1961; Tolkamp 1980).

For lotic caddisflies building cases with a typical architecture in a given development stage, unavailability of the preferred mineral material has been considered as limiting factor at the scale of stream or habitat types (e.g. Hanna 1961; Tolkamp 1980; Nijboer 2004). This should be less relevant for larvae carrying their cases with them, as they can migrate over distances of meters (Elliott 1971; Jackson et al. 1999) to find places with the preferred building material (Mackay 1977; Podgornyi and Nepomnyashchikh 1999). Correspondingly, solid evidence that these case-carriers are limited by the unavailability of suitable case-building material is lacking (Dudgeon 1990). In contrast to these mobile species acquiring case-building material where it can be found, other caddisflies (larval retreat-makers; Wiggins 2004) depend entirely on local grain availability when building a pupal case. For example, hydropsychid and rhyacophilid larvae build entirely new pupal cases, using fine gravel and sand, which they fix to the surface of coarser particles (Haller 1948; Waringer and Graf 1997), i.e. they have to transport the grains to their building site. Typically, these taxa build their pupal cases in fast-flowing riffles (Sattler 1958; Lepneva 1970; Waringer and Graf 1997), where cobble substrates provide solid surfaces for case attachment and the fast flow facilitates oxygen uptake, whereas the amount of sand and fine gravel is reduced by the prevailing erosive forces of the flow (Hynes 1970; Newbury and Gaboury 1993). Thus, these taxa have conflicting resource requirements. As a result, the seemingly overabundant finer streambed sediments can be a locally limited resource for them. Therefore, the overall mass use in pupal cases build by larvae of *Rhyacophila* and particularly *Hydropsyche* significantly increased with local mass availability of their building material in the French Furan River (Statzner et al. 2005). In addition, the species *Hydropsyche siltalai* Döhler significantly changed the case architecture if the preferred case material was a locally limited resource in the Furan, which should have implications for functional case properties and building expenses for the builder (Statzner et al. 2005). Our aim in the present study was to assess these potential implications in a flume experiment that we designed addressing the previous field observations on *H. siltalai* in the Furan.

1.1. Pupal-case architecture of Hydropsyche: examining costs and benefits for the builder

Last (fifth) instar larvae of *H. siltalai* in the Furan used on average ∼300 grains weighting ∼0.5 g (dry-mass here and elsewhere) in the size range 0.125–5 mm to construct typically a domed case having its open silk window (lacking grains, see "domed" in Fig. 1) fixed to larger bedplates (Statzner et al. 2005). In addition to this typical case construct, other larvae built flat cases with two open silk windows between larger bed particles (being attached on both sides) or round cases without any silk window (being only secured by silk threads fixed to larger particles) (Fig. 1). These cases were typically detached from other pupal cases of the species, although relatively often cases were built in contact with other cases ("grouped" in Fig. 1). Across all these configurations, *H. siltalai* used the mass of coarser (2.5–5 mm) or intermediate (1.25–2 mm) grains as alternatives in the pupal cases, and each of these alternatives required the use of finer grains. Local resource limitations of the preferred grain fraction (2.5–3.15 mm) produced chained effects across other grain fractions, as the alternative use of more grains in the 1.6–2 mm fraction (an unlimited resource in the Furan) induced an increased use of more grains in the 0.315–0.5 mm fraction (another unlimited resource in the Furan) (Statzner et al. 2005).

Beginning with the three detached case types, the differences among them have obvious implications for case architecture and in turn for costs and benefits for the case builder. The three detached case types shown in Fig. 1 obviously require different numbers and sizes (and thus masses) of grains and different relative silk uses (fixing grains to each other, spinning silk windows). For example, laboratory observations suggested that *Hydropsyche* larvae never leave their building site and collect their building material for the entire pupal case from a surface of ∼15 cm^2 (Haller 1948; Sattler 1958), whereas field observations illustrated that larvae make shorter excursions into the neighbourhood of the building site to collect fine gravel and sand (Mogel et al. 1985). Thus, distances moved to collect the grains are related to grain number used in the cases and energy expended to transport them per unit distance is related to grain mass, i.e. grain number and mass are generating expenses for the building larvae. Consequently, building a flat case instead of a round one would reduce expenses for the transport of both number and mass of grains. In contrast, the potential implications of the chained effects across grain fractions at limited availability of the preferred grain size are more subtle: instead of a few coarse grains many finer grains were used (Statzner et al. 2005), i.e. costs for mass transport decreased whereas costs for collection trips increased.

Hydropsyche larvae are highly aggressive against other species of the genus and their conspecifics (Schuhmacher 1970; Jansson and Vuoristo 1979), kill and eat each other (Sattler 1958; Schuhmacher 1970) and fight for building material when building pupal cases close to each other (Mogel et al. 1985). Thus, shortage of preferred building material or thereby induced longer transport distances to bring it to the building site should increase the risk of aggressive encounters and thus of mortality. Another factor causing potential mortality or reduced development speed of the pupae relates to the decreased overall grain projection area when the preferred grain fraction was limited (Statzner et al. 2005), which should affect case and thus pupal-chamber size, and in turn the energy required for active ventilation (through abdominal undulations) to generate water renewal in the chamber (e.g. Sattler 1958). Concerning the grain properties of caddisfly cases, the amount of silk required to fix the grains of a case of a given size increases with decreasing grain size (Smart 1976; Becker 2001) and increasing grain surface roughness (Okano and Kikuchi 2009) (i.e. increasing grain perimeter; Statzner et al. 2005). Lighter thoraces and/or smaller wings of adults (reducing presumably their dispersal potential) compensate for such higher costs for silk use in pupal cases (Stevens et al. 1999, 2000). Furthermore, grain size (e.g. few big vs. many small grains) and grain shape (e.g. spheres vs. cubes) should affect the resistance of pupal cases against a crushing force generated by moving, unstable bottom substrates or the jaws of predators (Otto and Svensson 1980; Williams et al. 1983; Dudgeon 1990). Thus, for the three detached case types, there are already numerous potential implications of grain availability for case architecture and in turn costs and benefits for the builder.

Aggregation of pupal cases in groups increases the complications related to costs and benefits for the builders. We assume that such aggregates were not simultaneously built because of the aggressive behaviour among larvae from adjacent building sites (see above). Thus, the first builder in such an aggregate had to invest into an entire pupal case, whereas subsequent builders in it profited from the efforts of previous builders as they used parts of the neighbouring case walls for their own case. Furthermore, aggregation of pupal cases might reduce the predation risk (Otto and Svensson 1981; Wrona and Dixon 1991).

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