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Case-Building Behavior, Persistence, and Emergence Success of *Pycnopsyche guttifer* (Walker) (Trichoptera: Limnephilidae) in Laboratory and *in situ* Environments: Potential Trade-offs of Material Preference

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Abstract

When removed from their cases in a non-flow laboratory environment, 5th instar *Pycnopsyche guttifer* (Walker) larvae were always successful in constructing a new case within 24 h when woody debris was present as a material choice. Most were successful within 1 h. Larvae were never successful at case building in the absence of wood in a non-flow environment. These laboratory-constructed 'emergency cases' were flimsy, lacking in shape, and larger than field cases. Laboratory case size, shape, and material preference remained constant after repeated daily evacuations over a series of 10 days. Larvae could be induced to construct a case composed of mineral particles only in the absence of wood and when placed in a laboratory stream with simulated flow conditions, or *in situ* in a natural stream. The emergence success of *P. guttifer* specimens induced to build these mineral cases, however, was significantly higher than that of larvae remaining in their field cases or of larvae that built wood cases. This result is likely due to a fungal infection that affected only larvae in wood cases. Our results demonstrate a scenario where a clearly non-preferred case construction material appears to increase survival.

Caddisflies constitute a taxonomically rich and ecologically diverse order of aquatic insects, abundant in nearly all types of freshwater ecosystems (e.g., Wiggins 1996). Caddisflies exhibit little morphological differentiation relative to their ecological diversity, however. Instead, the ability of the order to exploit different habitats and food resources is related to the production of silk from glands in their labium, with subsequent construction of portable cases and fixed retreats (Mackay and Wiggins 1979). Two monophyletic caddisfly lineages are currently recognized: the net spinning Annulipalpia and the tube-case making Integripalpia (Holzenthal et al. 2007a, b). The members of a third—questionably monophyletic—group, the Spicipalpia, construct a variety of case types; a few of these 'spicipalpians' do not construct cases until pupation. Our study focused on a species of tube-case maker. Tube cases have been variously proposed as respiratory devices, camouflage, and as physical protection against desiccation, predation, and cannibalism (Williams et al. 1987, Johansson 1991, Otto and Johansson 1995, Zamora-Muñoz and Svensson 1996, Wissinger et al. 2004, Boyero at al. 2006, Nislow and Molles 2006).

While cases are necessary for the survival of caddisfly larvae, they are also a liability. Silk production is energetically expensive, as is transportation of heavy cases (Stevens et al. 1999, Otto 2000). Case construction can lead to difficult trade-offs when larvae do not have easy access to preferred building material (Eggert and Wallace 2003, Statzner et al. 2005). In natural streams,

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larvae will sometimes have to travel up to 4 m to find construction particles, even venturing into oxygen-poor habitats that contain the appropriate materials (Elliot 1971, Jackson et al. 1999, Statzner et al. 2005). In laboratory experiments, most larvae will use larger or smaller particles than usual if their preferred sizes are not available (Hanna 1961, Tolkamp 1980). Some can be forced to switch to a different type of mineral (Gaino et al. 2002), and a few will switch from minerals to pieces of vegetation (Hanna 1961, Tolkamp 1980). Some will even construct laboratory cases composed of gold or other precious metals in the absence of other materials (Duprat and Besson 1998). It is not clear how these changes in case particle composition might affect the survival of a larva in nature.

Despite the liabilities of repeated building, many caddisflies construct a new case at each instar. Many will also abandon their cases when stressed by low flow or high temperature, and will readily build another case (Waters 1962, Anderson and Bourne 1974). When forcibly evacuated from their cases in a laboratory environment, many species will immediately construct an 'emergency case' (Houghton and Stewart 1998), a structure that tends to be flimsy, lacking in interstitial silk, and giving a mosaic view of the larva. Emergency cases are temporary shelters, and are often improved upon in subsequent hours or days, or else abandoned entirely for a newly-constructed case. Emergency case-building has been documented in both the Spicipalpia and the Integripalpia, suggesting a widespread behavior within Trichoptera (Houghton and Stewart 1998, Gupta and Stewart 2000, Stuart and Currie 2001, Norwood and Stewart 2002).

Our study explored the liabilities of emergency case construction in *Pycnopsyche guttifer* (Walker), a tube-case making integripalpian widespread throughout Michigan and abundant in woodland streams (Houghton et al. 2011a). *Pycnopsyche* cases tend to be constructed of woody debris, although some species will occasionally utilize some small mineral fragments (Wiggins 1996). The specific objectives of our study were to: determine particle preference in *P. guttifer* emergency case construction; assess changes in the size and weight of these emergency cases over repeated forced evacuations; and test if forcible emergency case construction, materials provided for case reconstruction, or environment affected emergence success of adults.

Materials and Methods

Collecting and laboratory design. Several hundred fifth instar *P. guttifer* larvae were collected from the Saint Joseph (N 41.92°, W 84.82°) and the Little Manistee (N44.03°, W85.73°) Rivers in the lower peninsula of MI. The former population was tested in 2008 and the latter in 2010. The Saint Joseph River is surrounded by a primarily agricultural watershed, although the specific collection site was within the Lost Nations game preserve and had >75% intact riparian habitat (Houghton et al. 2011b). The Little Manistee River features naturally-reproducing populations of native brook trout, *Salvelinus fontinalis* (Mitchill); our specific collecting site was within the Manistee National Forest and, likewise, had intact riparian habitat. Thus, *P. guttifer* specimens were abundant at both sites. The populations were separated by nearly 300km and were assumed to be allopatric. In between experiments, larvae were housed in a Living Stream™ system (Frigid Units, Toledo, OH) with simulated river temperature, photoperiod, and flow regime. All larval field cases appeared to be composed predominately or exclusively of woody material (Fig. 1a).

Three different environments were used during case-building trials. 1) Non-flow: containers of 16×16×6 cm dimension kept at simulated river temperature and with continual water changes, without simulated flow regime. 2) Living Stream: flow-through containers of 32×10×16 cm dimension with simulated river temperature, photoperiod, and flow regime. 3) *In situ*: flow-through containers of the same size placed into a natural stream environment.

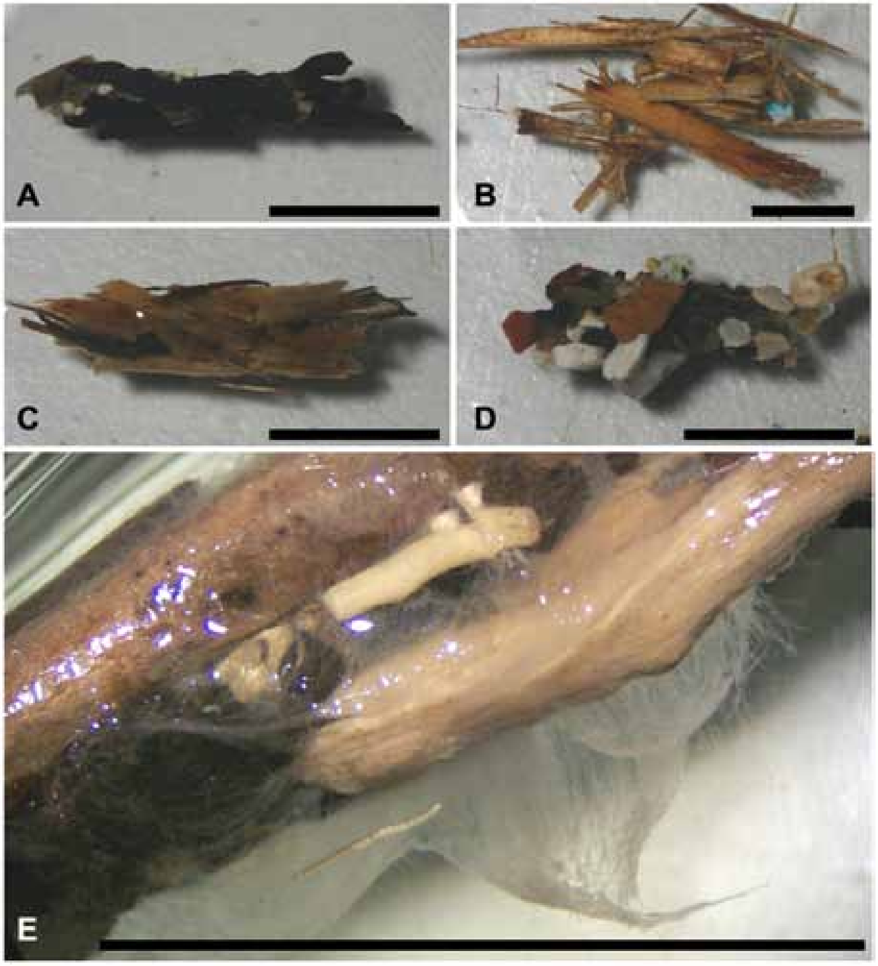

Figure 1. *Pycnopsyche guttifer* cases. A: typical field case. B: typical emergency case constructed within 1 h in the non-flow environment. C: typical case constructed over 24 h from woody debris *in situ*. D: typical case constructed over 24 h from mineral particles *in situ*. E: Close-up of *Mucor* (brown) and *Epicoccum* (white) infections on a woody case. Scale bars = 1 cm.

The bottoms of these environments were covered with three different types of case building materials depending on the treatment group. Some were covered with woody garden mulch broken into pieces approximating the size range (1–20 mm) of woody material found in *Pycnopsyche* field cases. Others were covered with non-colored aquarium gravel, likewise broken into a variety of particles sizes (0.5–5 mm). Other groups were given a mixture of both wood and mineral particles in approximately equal volumes and placed randomly within the environment so a larva would have the same access to either material type. The bottoms of all environments included large-diameter (5–10 mm) mineral particles to serve as a natural substrate. None of these larger particles were incorporated into constructed cases.

In all trials, larvae were gently prodded with soft touch forceps through the posterior opening of their case until they evacuated. All statistical tests were conducted using JMP for Windows™ software (JMP 2002). Voucher specimens and cases are deposited in the Hillsdale College insect collection.

Emergency case-building behavior. To test how the available case-building materials affected success at building emergency cases over a short period of time, larvae were given either mineral particles only, or a mixture of minerals and woody debris, and their behavior was closely observed for 1 h. Behaviors were placed in three categories: 'wandering' throughout the environment without any attempt to manipulate the materials, 'hiding' by burying into the substrate, and 'building' an emergency case. If a larva was successful in building a case, its behavioral sequence was noted. 'Case-building success' was defined as a larva using silk to attach enough particles together to cover itself, regardless of case integrity. While building was considered the most adaptive behavior, hiding was considered more adaptive than wandering since erratic wandering is one of the best predictors of predation risk in nature (Johansson 1991). Furthermore, a caseless larva buried in the substrate was engaging in a behavior in which it also engages with a case (e.g., Wiggins 1996). If a larva exhibited more than one behavior, the more adaptive behavior was recorded. The Saint Joseph River population was tested in the non-flow environment. The Little Manistee River population was tested in both the non-flow and the *in situ* stream environment.

Particle preference. To test how the available case-building materials affected case construction over a longer (24 h) period, larvae were given either mineral particles only, woody debris only, or equal volumes of both materials. After 24 h, larvae were removed from the environment and larval success in building an emergency case was noted. The Saint Joseph River population was tested in the non-flow environment. The Little Manistee River population was tested in both the non-flow and the *in situ* stream environment.

Changes to subsequent emergency cases. To determine changes in emergency case construction over time, larvae from the Saint Joseph River population were given both woody debris and mineral particles in the non-flow environment. After 24 h the larvae were re-evacuated from their cases and placed back into the non-flow environment. This process was repeated for a total of 10 days and the successive cases compared. Each successive emergency case was air-dried for 12 h, after which they were weighed, and their volumes measured by water displacement. A sample of cases was re-measured 2 months later to assess any changes over time that may have resulted from continued drying. No changes were found; thus, the 12 h drying period likely was sufficient.

Emergence success. To determine emergence success after emergency case construction, larvae were removed from their cases and given either mineral particles only, or else mineral particles and woody debris. Larvae from the Saint Joseph River population were tested in the Living Stream environment. A control group composed of individuals remaining in their original field cases was also placed in the Living Stream and given mineral particles to act as a natural substrate. It was assumed that larvae of the control group would not construct new cases. Treatments were divided into 5 groups of 8 individuals within a flow-through container, for a total sample size of 40 for each treatment. Containers were randomly distributed throughout the Living Stream. Living Stream temperature and photoperiod were adjusted throughout the summer and fall to match the conditions of the Saint Joseph River. Larvae were checked after 3 d to confirm that they had constructed cases and then were not disturbed until adult emergence in September. After emergence, pupal cases were examined for any obvious abnormalities. Any fungi present were identified by preparing specimens with a lacto-fuchsin stain (Dhingra and Sinclair 1995) and mounting them on glass slides.

This experiment was repeated using the Little Manistee River population in 2010. The experimental design was the same as with the Saint Joseph population except that larvae were also tested in the *in situ* environment simultaneously with those in the Living Stream environment. Also, due to a limited number of larvae, and based on the results of the Saint Joseph experiment and of previous studies showing no difference in the emergence success of control groups (Houghton and Stewart 1998, Stuart and Currie 2001), no control group was used in the Little Manistee River experiment.

Results

Fifty percent of the larvae in the Saint Joseph population given woody debris in the non-flow environment built emergency cases within 1 h, a significantly higher number than those who engaged only in wandering or hiding behaviors (Fig. 2a). Larvae provided with only mineral particles wandered more than they hid and none built a case. For the Little Manistee population, there was no significant difference in the mean number of larvae that engaged in wandering, hiding, or case-building behaviors in the non-flow environment when provided with woody debris (Fig. 2b). Nearly all were able to construct cases within 1 h in the *in situ* environment using woody debris. As with the Saint Joseph population, all larvae provided mineral particles wandered more than they hid and none were able to construct a case in the non-flow environment. In the *in situ* environment, however, over 50% of larvae were successful at building mineral cases within 1 h, a significantly higher number than the number of larvae that engaged in wandering or hiding (Fig. 2c).

All larvae of both populations followed a similar emergency case-building sequence: collect pieces of debris, align them parallel to each other, attach them together to form a rudimentary shelter, and hide underneath the shelter with their dorsal side facing downward. Larval emergency cases bore little resemblance to field cases in this or other experiments. Instead they were loosely-constructed piles of debris (Fig. 1b). Larvae left in non-flow environments for several days after emergency case construction remained in these cases until they died without any noticeable changes to case composition.

When given minerals and woody debris, all larvae built emergency cases almost exclusively out of wood at least twice in succession within the 24 h periods; 85% rebuilt at least 5 times, and almost 60% built for all 10 days of the experiment (Fig. 3). Mean weights (0.30 g) and volumes (0.42 mL) of emergency cases were significantly larger than those of field cases (0.20 g and 0.28 mL) (Independent T-test, $P < 0.02$ for both). Subsequent emergency cases, however, did not change in either weight or volume over time ($R^2 < 0.5$, $P > 0.05$ for all 12 specimens).

In the Saint Joseph population, 100% of larvae were successful at case construction within 24 h when provided with woody debris in the non-flow environment and 0% successful when provided with only mineral particles in the same environment (Table 1). In the Little Manistee population, larvae

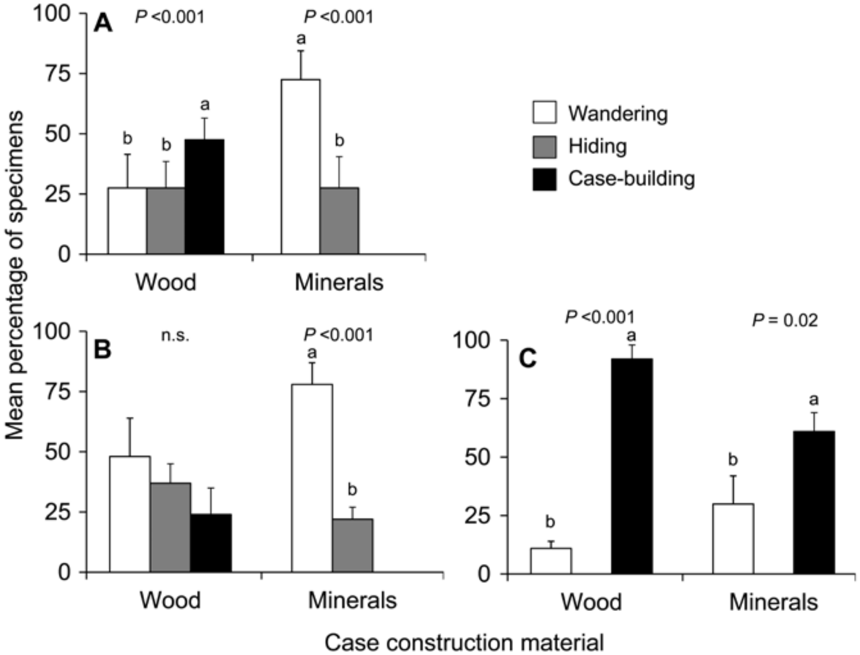

Figure 2. Mean (+1 SE) percentage of *Pycnopsyche guttifer* larvae ($n = 20$ for all treatments) that engaged in each of three types of behaviors during 1 h emergency case construction experiments, based on case material provided within different years and habitats. A: Saint Joseph non-flow laboratory environment. B: Little Manistee non-flow environment. C: Little Manistee *in situ* environment. Letters denote statistically distinct groups (1-way Analysis of Variance with *post-hoc* Tukey test). n.s. = not significant.

provided with woody debris in the non-flow environment were as successful as those provided exclusively with mineral particles in the *in situ* environment. Larvae provided with both woody debris and mineral particles were able to construct cases 100% of the time in the *in situ* environment. As with the Saint Joseph population, larvae provided exclusively with mineral particles in the non-flow environment were unable to construct a case within 24 h. All cases constructed during the 24-h periods were similar in appearance to field cases, and constructed more solidly than were emergency cases (Fig. 1c–d).

Nearly 100% of larvae constructed a case suitable for pupation within 3 d in both the Living Stream and *in situ* environments regardless of material provided. In the Saint Joseph population, emergence success in the Living Stream environment was highest in the mineral case treatment group and lowest in the control and woody debris treatment groups (Fig. 4a). There was no difference in the length of time spent in pupation between the three groups (1-way Analysis of Variance, $P = 0.37$). In the Little Manistee population, larvae in the Living Stream environment given access exclusively to minerals, as well as larvae given access to both minerals and woody debris, had higher adult emergence success than those given access exclusively to woody debris; the woody debris treatment group had 0% emergence (Fig. 4b). In the *in situ* environment, however, there was no significant difference in emergence success between the treatment groups (Fig. 4c).

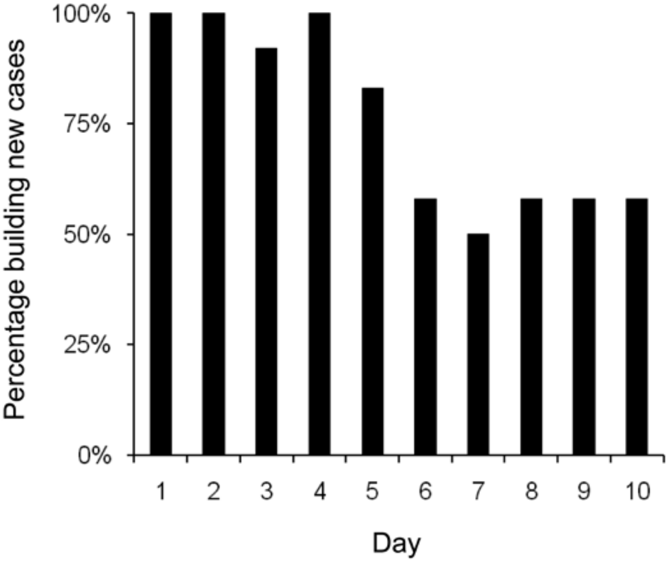

Figure 3. The percentage of *Pycnopsyche guttifer* larvae ($n = 12$) from the Saint Joseph population in a non-flow environment that constructed a succession of emergency cases throughout the 10 days of our experiment.

Table 1. Results of 24 h case construction experiments from the Saint Joseph and Little Manistee River populations. Each population constituted a distinct experiment. Groups determined by a *Chi*-square Goodness of Fit test ($P < 0.001$ for both) followed by Pairwise *Chi*-square Goodness of Fit tests (with Yates Correction if df < 2), $P < 0.01$ for all significant pairwise comparisons.

Population	Material	Environment	*n*	% successful	Group
Saint Joseph	Wood	Non-flow	6	100%	a
Saint Joseph	Mixed	Non-flow	5	100%	a
Saint Joseph	Mineral	Non-flow	8	0%	b
Little Manistee	Mixed	*In situ*	15	100%	a
Little Manistee	Mixed	Non-flow	15	60%	b
Little Manistee	Mineral	*In situ*	15	53%	b
Little Manistee	Mineral	Non-flow	15	0%	c

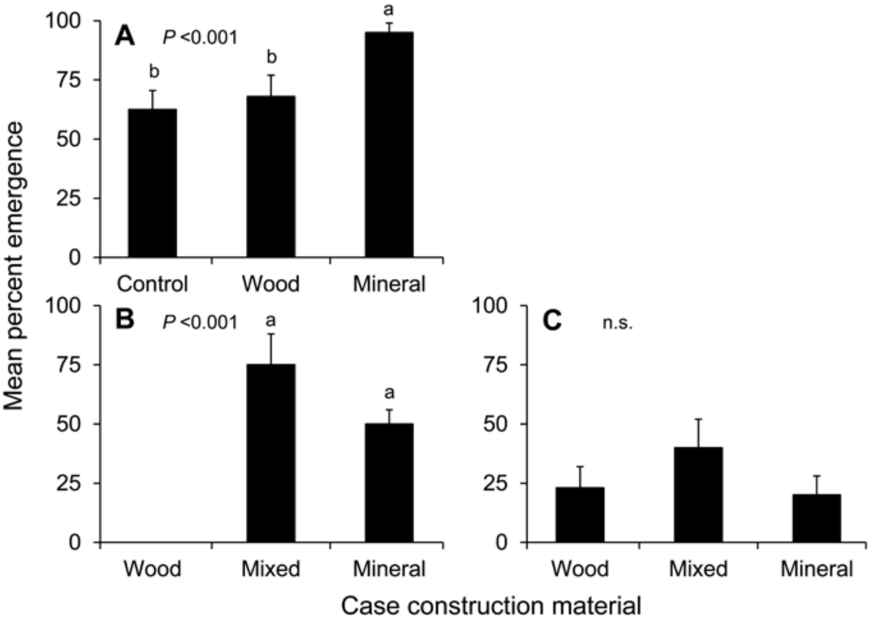

Figure 4. Mean (+1 SE) emergence success of *Pycnopsyche guttifer* adults based on the material of their emergency cases (*n* = 40 for all treatments) constructed by each population and under various conditions. A: Saint Joseph Living Stream environment. B: Little Manistee Living Stream environment. C: Little Manistee *in situ* environment. The control group was not forced to construct a laboratory case. Letters denote statistically distinct groups (1-way Analysis of Variance with *post-hoc* Tukey test). n.s. = not significant.

In both populations, both the control cases and those constructed from woody debris became infected while in the Living Stream environment during the summer by two fungal species: the dematiaceous mold *Epicoccum purpascens* (Ehrenb.) (Ascomycota: Dothideomycetes), and the zygomycete *Mucor* sp. (*incertae sedis* in the Zygomycota) (Fig. 1e). No individuals or cases within mineral case treatment groups appeared to be infected despite the random arrangement. Based on subjective observation, cases constructed from a mixture of woody debris and mineral particles appeared to have an intermediate level of fungal infection. No cases in the *in situ* environment appeared to be infected, regardless of case construction material.

Discussion

Emergency case construction within the Trichoptera. Emergency case construction appears to be a common and possibly homoplastic behavior in the Trichoptera. Within the Integripalpia, for example, Stuart and Currie (2001) found only three families: Brachycentridae, Helicopsychidae, and Odontoceridae, as well as the genus *Ceraclea* (Leptoceridae), that did not construct emergency cases. Taxa that build emergency cases represent both of the major monophyletic divisions of the Integripalpia: Brenventoria and Plenitentoria (Holzenthal et al. 2007a, b). Furthermore, the behavior has been found in the 'Spicipalpia' (Houghton and Stewart 1998), which is considered sister to the Integripalpia.

The purpose of emergency cases appears to be immediate coverage of the larva while it is building its permanent case. Under the highly unnatural conditions of non-flow plastic containers with shallow water, *P. guttifer* larvae constructed such cases rapidly, often within 1 h. Likewise, most larvae were able to construct new emergency cases over consecutive days under these conditions, without notable changes in case size or material composition. Within the Trichoptera, emergency cases sometimes exhibit some superficial resemblance to permanent cases (Houghton and Stewart 1998) or may be barely recognizable as a caddisfly case. The latter was the situation with *P. guttifer*. Indeed, emergency cases were significantly larger than field cases, and were essentially piles of woody debris loosely attached with silk and covering the larva like a blanket.

Material preference and plasticity. It appears from our experiments that *P. guttifer* clearly prefers woody debris over mineral material to construct its cases. The presence of wood repeatedly induced the more adaptive behaviors. Larvae denied wood were unsuccessful in building any type of case in the non-flow environment. This preference for building with woody debris was seen over successive evacuations.

The preference of *P. guttifer* for woody debris in case construction is not surprising given that all field cases were also composed almost exclusively of wood. Other observations, however, raise some questions about this preference and its interaction with the case-building environment and length of time given for case building. For example, > 50% of larvae were able to construct cases exclusively out of minerals when placed *in situ* in a natural stream environment for 1 h. Within 24 h, larvae were as successful at constructing mineral cases *in situ* as were larvae in the non-flow containers using the preferred woody debris. Nearly 100% of larvae were able to construct a mineral case for pupation within 3 d in the Living Stream and *in situ* environments.

Perhaps the more natural flow, temperature, and photoperiod of the natural stream and the Living Stream were more conducive to larval adaptation to a non-preferred case-building material than was the non-flow environment. Stuart and Currie (2001) found that “certain species” (unspecified) would not construct cases of any type unless exposed to current flow, suggesting the importance of a more natural environment for adapting to non-programmed case-building activities. The length of time given to a larva for case reconstruction may have also been an important factor in adapting to non-preferred building materials. Stuart and Currie (2001) found that some species took up to 4 days to build a case. Thus, the 24 h that *P. guttifer* larvae were in the non-flow containers in our experiment may not have been sufficient to induce construction of a case with non-preferred materials, whereas 3 days in the Living Stream was sufficient. In the most natural environment of the *in situ* stream, however, 1 h was sufficient time for more than half of the larvae to build a case from non-preferred materials.

Likewise, the more natural conditions of the Living Stream may have been conducive to constructing cases similar to those found in the field instead of the loosely-constructed emergency cases produced in the non-flow environment. Houghton and Stewart (1998) found that *Culoptila cantha* (Ross) (Glossosomatidae) built exclusively emergency cases when placed in a non-flow environment, but built typical cases when placed in a Living Stream environment overnight. The length of time given to larvae may have also been an important factor in determining the type of case that it built. Larvae in our experiment built emergency cases within 1 h in the Living Stream and *in situ* environments, and built typical cases in these environments within 24 h. Time alone cannot explain this difference, however, since larvae in non-flow environments always built emergency cases regardless of the amount of time available. A larva in the unnatural environment of a non-flow container may simply respond by only building an emergency case.

Emergence success. It appears that forcing *P. guttifer* to build emergency cases does not lower its emergence success. In the Saint Joseph population, there was no significant difference between the mean emergence of the control and wood case treatment groups, and the mean of the mineral case treatment group was actually higher than that of the control. Houghton and Stewart (1998) found similar results for *C. cantha*: larvae forced to rebuild their cases in the Living Stream from preferred materials had the same emergence success as those not forced to rebuild. Although forced rebuilding in nature may lead to greater mortality due to predation or other factors, it appears that this activity is not inherently harmful to the larva. Our results corroborate many observations in the field of caddisflies abandoning their cases to drift, or when stressed by adverse environmental conditions.

We found, rather surprisingly, that *P. guttifer* larvae forced to build a case from minerals—a clearly non-preferred material—actually had higher emergence success than those not forced to rebuild their case. These confounding results were likely caused by the infection of the two fungal species, *Mucor* sp. and *E. purpascens*, on the control and wood case treatments groups during both years of the experiment. *Epicoccum* species are not documented as pathogenic on animals, although they have been occasionally isolated from clinical samples, and may be opportunistic (Pritchard and Muir 1987). At the very least, the decomposition of the wood cases likely compromised their integrity and may have caused indirect harm to the *Pycnopsyche* larvae. Species of *Mucor* are known opportunistic pathogens in insects, frequently moving from organic matter to living tissue (Ferron 1978, Milner 1997). Other zygomycete fungi, such as those in the order Entomophthorales, are well known for their harmful effects on insects (Chamilos et al. 2008). Specifically, they are able to metabolize insect cuticles from the outside, making them ideal pathogens to spread from case to larva (Freimoser et al. 2003).

Neither of the fungal taxa isolated from our *Pycnopsyche* cases and larvae have been studied for their specific effects on caddisflies and cases. In light of studies of similar taxa, however, it seems plausible that the organic cases of the control and wood case treatment groups constituted more appropriate substrate for the fungus to colonize and then attack the larva (Rayner and Boddy 1988). Both species likely entered the Living Stream environment on the cases of the control treatment and subsequently spread to larvae of the wood case treatment group. Despite the random arrangement of larvae no mineral case was affected, strongly suggesting that such mineral cases provided protection from the opportunistic fungi.

The *in situ* environment did not have any observed fungal infection, nor were there significant differences in emergence success between treatments. Thus, it is likely that the more natural environment was less conducive to fungal infection and that the mineral cases were not advantageous to the larvae. Constructing a non-preferred mineral case, however, did not confer an obvious disadvantage upon the larvae either.

Implications. The ability to change behavior and morphology relative to different environmental stresses is central to natural selection. Strictly behavioral traits, such as drifting to avoid predators, are considered more plastic than morphological traits (West-Eberhard 1989, Relyea 2001, McIntosh et al. 2002). Caddisfly case construction, however, is a behavioral trait that results in morphological change. Thus, it is considered intermediate in plasticity (Boyero et al. 2006). Case material choice has inherent trade-offs for a larva. For example, mineral cases are heavy, composed of more pieces, require more energy to construct, and are difficult to carry through sediment (Stevens et al. 1999, Otto 2000, Dodson et al. 2000). Conversely, they offer greater resistance to predators (Johansson 1991, Nislow and Molles 2006, Otto and Johansson 1995, Boyero et al. 2006) and perhaps also to fungal infection.

Adapting to these trade-offs is crucially important to caddisfly larvae in nature since preferred particles may not always be available and circumstances (e.g., presence of predators or parasites) may differ in different environments. For example, Boyero et al (2006) found that individuals of *Potamophylax latipennis* (Curtis) (Limnephilidae)—a species that constructs both mineral and wood cases in nature—preferred their original wood field case material in laboratory trials, but could be readily induced to switch to minerals in the presence of certain predators. No direct measurement of fitness was made in this experiment, but the authors assumed an increase. They further hypothesized that the mineral case made up for its heavier weight with increased predator protection and that larvae instinctively constructed mineral cases when they could sense such predators.

Conversely, Eggert and Wallace (2003) found that inducing 1st–3rd instar *Pycnopsyche gentilis* (McLachlan) (Limnephilidae) larvae to switch from leaf cases—their preferred material in nature—to mineral cases in the laboratory required total elimination of leaves. The authors also found that *P. gentilis* larvae that did build their cases out of the available minerals had substantially higher mortality due to starvation over a 4-week period. Thus, an induced change in case construction behavior clearly decreased the fitness of the larvae.

Our results suggest a third scenario: an induced change to an obviously non-preferred case construction material actually increased the survival of *P. guttifer*. This increase in emergence success was almost certainly brought about by the protection the mineral cases afforded against fungal infection. Both of the fungi found in our experiment are common in nature. Thus, mineral cases might increase fitness of *P. guttifer* under certain field conditions, such as especially low current flow or high density of the normally gregarious pupae. Our *in situ* experiments, which did not demonstrate such an advantage to mineral cases, were conducted at lower pupal densities than we have observed in the field. Thus, conditions conducive to an increased fitness of larvae with mineral cases may exist in nature.

Further research is needed to investigate these observations. Specifically, treating the Living Stream with a fungicide that does not harm the *Pycnopsyche* larvae would allow for more direct exploration of fungal effects on emergence. Unfortunately, treatment with 10% Tegosept™, an anti-fungal agent commonly used in *Drosophila* cultures (Bahadorani et al. 2008), has thus far led to 100% larval mortality. Conducting case-building experiments in the Living Stream environment in addition to the non-flow and *in situ* environments might help isolate the specific variables (e.g., dissolved oxygen levels, temperature, flow regime) responsible for the increased adaptability in flowing water. Lastly, examining the changes in the survival of larvae with different case types in the presence of various predators or other selection pressures would help to evaluate the relative advantages of the different case types under more real-world conditions.

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