Zoosymposia 5: 269–278 (2011)
www.mapress.com/zoosymposia/

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

Case-repair in three genera of caddisflies (Trichoptera)

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Abstract

Case-building is energetically expensive and case-repair may be a viable alternative to rebuilding for caddisflies when the case is damaged. In this study, we damaged the larval cases of 3 Trichoptera genera: *Lepidostoma* spp.; *Neophylax rickeri* Milne, 1935; and *Onocosmoecus unicolor* (Banks, 1897). We manually damaged the anterior, middle, or posterior portions of the larval case. We measured case lengths before damage, immediately after damage, and after allowing 2 days for repair. Overall, 74.2% of *Lepidostoma* spp. (n=31), 23.5% of *N. rickeri* (n=34), and 50.0% of *O. unicolor* (n=44) repaired their cases. *Lepidostoma* spp. had the highest odds of repair (2.88:1), followed by *O. unicolor* (1:1). *Neophylax rickeri* (0.308:1) was unlikely to repair its case after damage. For all genera, the percentage of the damaged portion repaired by location was not statistically significant. In *Lepidostoma* spp., at all locations, the average percentage of the damaged portion repaired was greater than 100% (larvae repaired the damage fully and continued to add material to the anterior end of the case). The occurrence of repair across the 3 genera at all damage locations suggests that the behavior may be beneficial for protection and more energetically favorable than entirely rebuilding the case, however life history may influence the likelihood of repair.

Key words: case-building, Integripalpia, energetics, case material, silk

Introduction

Caddisfly cases are diverse in their appearance, and vary in the materials used for construction and the shape, structure, and size of the case. All case-building larvae depend on their cases for survival. Specifically, cases provide physical (Otto & Svensson 1980, Nislow & Molles 1993) and camouflage protection (Otto & Svensson 1980, Otto & Johansson 1995, Nislow & Molles 1993) against predators and aid in respiration (Hansell 1974, Wiggins 1996). Cases also reduce aggression and cannibalism in temporary wetland habitats (Wissinger *et al*. 2004), and the presence of predators in the habitat influences preference of case type and material (Boyero *et al*. 2006). Cases offer protection from desiccation in temporary pools and organic cases hold water more efficiently than mineral cases (Zamora-Muñoz & Svensson 1996). Mineral cases have been shown to offer better protection than organic cases, and risk of predation for larvae with cases made of organic materials is higher for damaged cases with decreased length (Otto & Svensson 1980). However, there are tradeoffs between the energetic cost of building a case and predator protection; mineral cases are more energetically expensive to construct than leaf cases (Becker 2001) because silk is energetically expensive and more silk is used in the construction of mineral cases (Stevens *et al*. 1999, Stevens *et al*. 2000). Because of these potential costs, case-repair, in which only damaged portions of cases are

Accepted by K. Majecka, J. Majecki & J. Morse: 6 Dec. 2010; published: 10 Jun. 2011

reconstructed or patched, should be a potential energetic alternative compared to rebuilding a damaged case.

Case-building has been examined from a number of perspectives spanning animal behavior, evolutionary biology, and basic life history features. For example, many studies of caddisfly building behavior were conducted decades ago (e.g., Frankhauser & Reik 1935 and references therein) and case building has contributed to the discussion of early diversification in Trichoptera (e.g., Weaver & Morse 1986). Several studies have extensively examined the specific behavioral sequences for a number of species to infer phylogeny (e.g., Stuart & Currie 2001; Stuart & Currie 2002a, 2002b) and numerous life-history studies have detailed the specific building and case-repair behaviors used by individual species of caddisflies (e.g., Houghton & Stewart 1998, Gupta & Stewart 2000, Norwood & Stewart 2002, Mendez & Resh 2008). Although many studies have focused on construction of completely new cases, few studies have directly examined repair.

Studies examining caddisfly case-building and repair behavior have had various objectives, including determination of the sensory mechanisms behind case construction and the energetics required for building with different case materials across different species of caddisflies (e.g., Merrill 1965, Rowlands & Hansell 1983, Smart 1974, Tomazewski 1981, Tomazewski *et al*. 1987). However, these studies focused primarily on case-building behavior in terms of complete rebuilding of the case and the repair behavior is only briefly described. For example, Hanna (1960) conducted a general survey of case-building and repair, briefly describing the repair behavior of multiple species that used organic and mineral materials in their cases. Prestidge (1977) observed repairs made to damaged cases of *Pycnocentrodes aeris* Wise, 1958, in a study of case-building behavior of that species.

In this study, we examine case-repair in 3 genera of tube-cased caddisflies at 3 damage locations: the anterior, the middle, and the posterior portions of the cases. We assess (1) whether case-repair is a general behavior found in multiple genera of caddisflies, and (2) for individuals that did repair their cases, whether the extent of repair performed is based on the damage location within each genus. We then summarize general observations of repair strategies at each damage location.

Methods

Case-repair experimental design

We collected caddisfly larvae on February 19, 2007 and March 17, 2007 from Redwood Creek, approximately 1 km upstream of the Hwy 1 road crossing in Marin County, California, U.S.A. (37.8851° N, 122.57683° W). Larvae were collected from both riffles and pools to obtain a variety of case types and taxa. The larvae were primarily 3rd to 5th instars; and, we avoided individuals that were nearing prepupal diapause or pupation (e.g., *N. rickeri* becomes obviously plump). In the laboratory, we sorted caddisflies by case type and composition: leaf and stick; sand; small leaf; stick; and stone cases. Caddisflies were kept separate in plastic containers with mesh siding and these containers were placed in large plastic tubs. Collected individuals were allowed to acclimate to the settings in aerated stream water from the collection site for at least 24 hours before we began experiments.

We experimented with a total of 109 larvae from 3 genera, *Lepidostoma* (31), *Neophylax* (34), and *Onocosmoecus* (44), to test for the frequency and extent of case-repair (Fig. 1). Several species of *Lepidostoma* co-occur at Redwood Creek and we did not distinguish between the species for this study because we were interested in generic-level differences. Cases of *Lepidostoma* (Figs 1A & 1B, Lepidostomatidae) are approximately 7 mm long and have 3 case morphologies which may be species specific: (1) constructed from small leaf or twig fragments arranged irregularly to make a rounded tube case; (2) constructed from quadrate leaf panels to make a quadrate tube case; or (3) constructed from fine, particulate sand arranged into a slender tube case. Cases of *Neophylax rickeri* (Fig. 1C, Uenoidae) are 7-10 mm in length and are constructed from small, rounded mineral particles to form tube cases, often with lateral ballast stones in later instars. Cases of *Onocosmoecus unicolor* (Fig. 1 D, Limnephilidae) are much larger, approximately 12-15 mm long, and are constructed from irregular pieces of wood and leaf fragments.

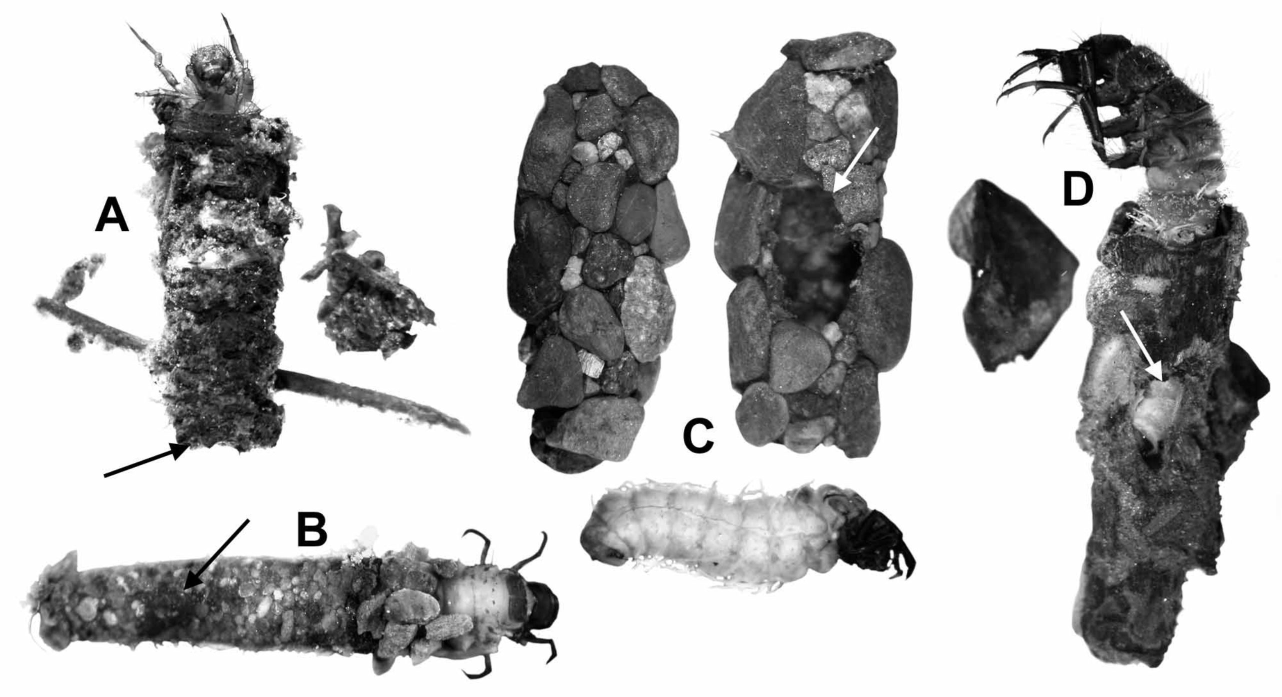

FIGURE 1. Caddisfly genera, case types, damage locations, and repairs. (A) *Lepidostoma* spp. (wood case with posterior damage), (B) *Lepidostoma* spp. (midsection damaged mineral case and silk patching repair, anterior lengthening by adding stones), (C) *Neophylax rickeri* (midsection damaged mineral case (right) and newly built replacement case (left)), (D) *Onocosmoecus unicolor* (wood case with midsection damage). Arrows indicate damage location.

Prior to purposefully damaging the cases, we measured the length of each larval case dorsally along its longest axis using an ocular micrometer (Fig. 2). Each larval case was quickly damaged while the larvae remained inside by using forceps to remove approximately 1/3rd of the anterior, posterior, or middle portions of the case. To damage the anterior and posterior portions of the case, we completely removed a ring from the anterior or the posterior end of the case to shorten the case-length overall (Fig. 1 A). To damage the mid-section, we removed case material from the dorsal side of case with the ventral side remaining intact (Figs 1 B, 1 C & 1 D).

We made different measurements based on damage type using an ocular micrometer. For anterior and posterior damage, we measured the new case length. For mid-section damage, we measured the length and width of the damaged section (Fig. 2). We retained all of the pieces removed from the case and preserved the pieces with the larvae.

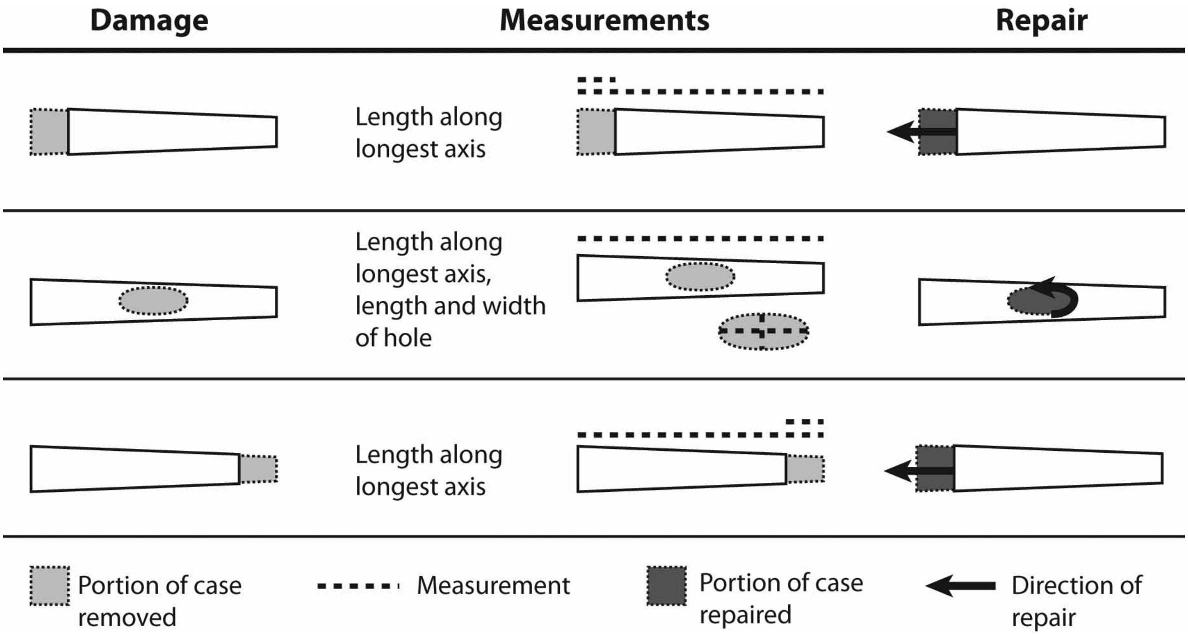

FIGURE 2. Measurements made for each damage location. Grey shading indicates portion of case removed. Measurement dash lines indicate measurements taken. For cases damaged at the posterior end, repair would often occur by extension at the anterior margin of the case.

We observed case-repair for multiple caddisflies at the same time using three 6-well cell culture trays, one for each damage type, immersed in a plastic storage bin with stream water and standard aquarium aeration (Fig. 3). Plastic storage bins were kept in a refrigerator set between 10-15 ºC except during observation periods where they were removed to the laboratory bench for a maximum of 1 hour. Each well contained materials similar to the cases of the test larvae that were collected from the larval habitat at the time of larval collection. We separated each larva in a compartment by damage type and covered the compartment with a fine mesh secured with a rubber band to prevent escape. Individuals were measured once daily and any changes to case structure were noted. Individuals were allowed a total of 2 days to repair based on pilot studies that indicated that repair occurred within 2 days or not at all. After the 2nd day, the caddisflies were preserved in 70% ethanol and were identified to genus. We performed trials until we exhausted the supply of field-collected caddisflies for each of the sampling dates (approximately 1 month after the sampling date).

Data analysis

We calculated 2 metrics to assess case-repair: frequency of repair for each genus and percentage of the damaged portion repaired for each individual. First, we determined the frequency of repair for each genus, calculated as the percentage of larvae that repaired their cases of the total number of individuals examined for each genus. We defined repair as an increase in the damaged case length by at least 2% (to compensate for errors in measurement) for anterior and posterior damaged cases. For mid-section damage, we qualified repair as at least partial sealing the damaged area, or by evidence of material added to the anterior of the case. We used the counts of repair vs. no repair for all 3 genera in a χ^2 test for association to determine statistical significance in repair frequency. We then calculated the odds of repair for each genus, followed by the odds ratios (OR) comparing the genera in pairs using procedure cc in Stata v. 10 (StataCorp 2007). The odds ratios give a statistical estimate of how likely a genus was to repair compared to another genus.

Second, we calculated the percentage of the damaged portion repaired for each of the damage locations by genus. For anterior and posterior damage, we calculated the percentage of the damaged portion repaired as the ratio of the repaired (or new) total case length to the original case length and multiplied the result by 100. For mid-section damage, we calculated the overall percentage of repair as the sum of the percentage change in overall length (e.g., when material was added to the anterior portion of the case) and the percentage of repair to the mid-section (where 100% of mid-section repair was defined as completely sealing the damage hole with added silk; smaller proportions were estimated by the measurements). For all 3 damage types, the percentage of the damaged portion repaired could total more than 100% if it exceeded the size of the pre-damage case (e.g., the larvae fully repaired damage to the mid-section and added material to the anterior of the case, or if the larva added more total length than was removed by anterior or posterior damage). To assess statistical significance of location of repair, we performed a non-parametric Kruskal-Wallis test for each genus to test for differences in the percentage of the damaged portion repaired between damage locations. We included in the Kruskal-Wallis test only caddisflies that repaired their cases.

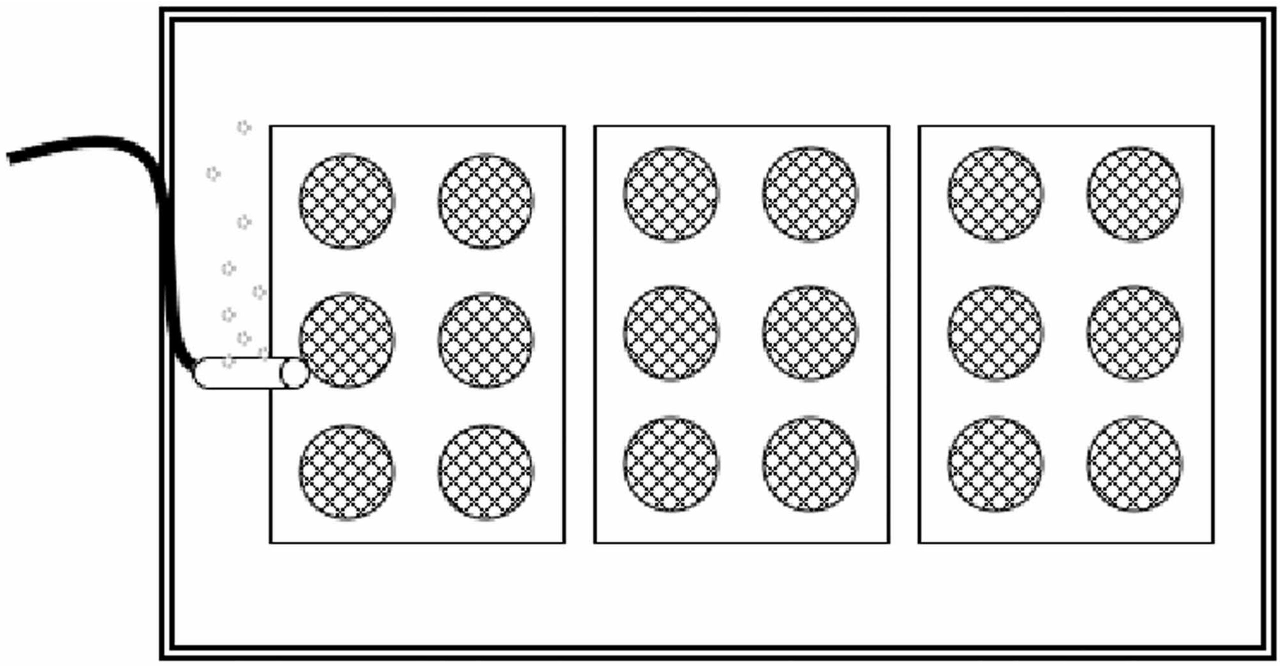

FIGURE 3. Experimental design. Three 6-well cell culture trays were immersed in aerated stream water in a plastic storage bin. One larvae was added per culture cell and each cell was covered with mesh. Damaged anterior, middle, and posterior portions were tested independently in each trial.

Results

Repair experiment

We observed case repair for all 3 genera that we studied: 74.2% of *Lepidostoma*; 23.5% of *Neophylax*; and 50.0% of *Onocosmoecus* exhibited case-repair. The χ^2 test indicated a statistically significant association (χ^2=16.72, P<0.001) for repair between genera (Table 1). Calculations of odds indicated that each genus had different likelihood of repair: *Lepidostoma* was very likely to repair (2.88:1; i.e., 2.88 *Lepidostoma* spp. larvae repaired their cases for every 1 that did not); *N. rickeri* was very unlikely to repair (0.292:1); and likelihood of repair by *O. unicolor* was even (1:1).

Odds ratios indicated that: (a) *O. unicolor* was 3.25 times more likely to repair than *N. rickeri* (OR=3.25, 95% CI=1.10 to 10.07, p=0.0163), (b) *Lepidostoma* spp. were 2.88 times more likely to repair than *O. unicolor* (OR=2.88, 95% CI=0.96 to 9.01, p=0.0172), and (c) *Lepidostoma* spp. were 9.34 times more likely to repair than *N. rickeri* (OR=9.34, 95% CI=2.67 to 33.88, p<0.0001).

TABLE 1. Larval case repair for genera of Trichoptera. Repair was significantly different between genera (χ^2=16.72, P<0.001).

	Lepidostoma	*Neophylax*	*Onocosmoecus*	Total
Repair	23	8	22	54
No Repair	8	26	22	55
Total	31	34	44	109

For the location of repair for the caddisflies that repaired in each genus, the Kruskal-Wallace tests were not statistically significant. For *Lepidostoma* spp., differences in location of repair were not significant (χ^2 (2, n=23)=1.48, p=0.476). Most sections had more than 100% of the damage repaired (anterior portion 112.2±93.3%, n=10; middle portion 107.6±12.6%, n=7; posterior portion 106.0±37.2%, n=6), however the amount of anterior repair was the most variable (Fig. 4A). For *N. rickeri*, there was not a significant difference between the locations of damage (χ^2 (2, n=8)=2.72, p=0.2571, Fig. 4B), however, the sample sizes for each location were small (n=8), especially for the anterior portion (n=2) and mid-section (n=1) of the cases. Posterior-portion repair was highly variable, but the percentage of the damaged portion repaired was much lower (59.6±40.9%, n=5). For *O. unicolor*, differences in repair by location were not statistically significant (χ^2 (2, n=22)=4.34, p=0.1139, Fig. 4C) and mid-section repair was highest with a mean of 91.9±7.2% (n=7). Anterior and posterior damage were repaired only 52.6±34.3% (n=8) and 54.3±39.2% (n=7), respectively. The percent of repair in the anterior and posterior portions were much more variable.

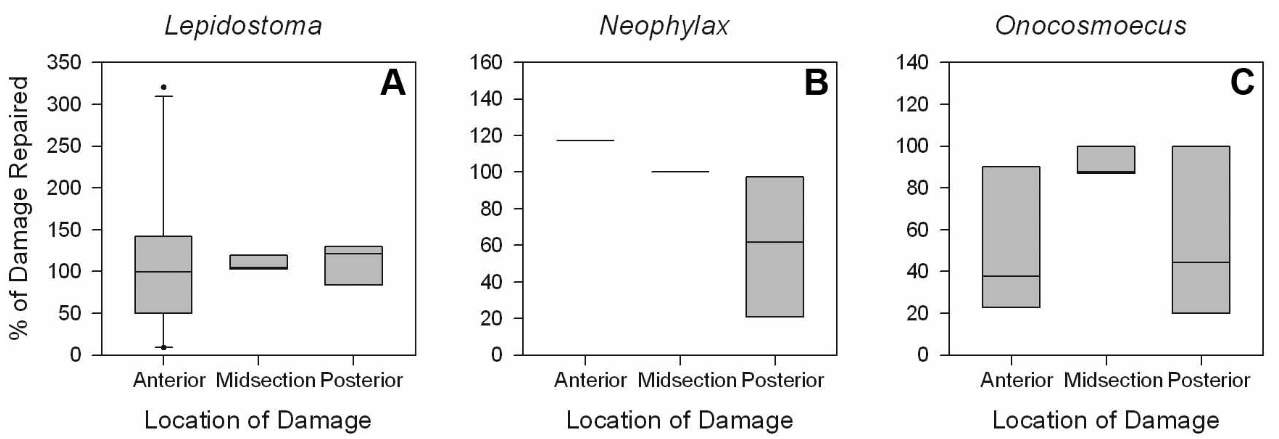

FIGURE 4. Percentage of the damaged portion repaired for each genus by damage location. (A) *Lepidostoma* spp., (B) *Neophylax rickeri*, and (C) *Onocosmoecus unicolor*. The midline of each box represents the median, box extrema are the 25th and 75th percentiles, and whiskers are the 10th and 90th percentiles. Outliers are represented by a dot.

Observations of case-repair patterns

We observed the same general repair patterns for all 3 genera for the different damage locations (Fig. 2). Larvae that repaired cases with anterior damage added material to the anterior of the case as if the larvae were extending its case between instars. Most of the caddisflies that repaired mid-section damaged cases sealed the damaged area with silk only and did not add building material to the damaged area. However, 3 *Lepidostoma* spp. larvae with mid-section-damaged cases covered the damaged area with building material in addition to adding silk over the damaged area, or they added material to the anterior of the case and cut off the posterior portion of the case at the damage site. In addition, 3 of the mid-section damaged *Lepidostoma* spp. larvae not only attached leaf material to the anterior portion of the case, but also added silk over the mid-section damage (Fig. 1 B). Two *Neophylax* exited their damaged cases and built completely new ones (Fig. 1 C). Most of the larvae that had cases with posterior damage produced a ring of silk around the inside of the posterior end of the case, but did not add leaf or mineral material to the case and were not considered to have repaired their case. Those with posterior damage that did repair their cases added leaf or mineral material to the anterior portion of the case, except for 1 *N. rickeri* larva, which added material to the posterior end.

Discussion

Repair and locations of repair

We observed case-repair behaviors in each of the 3 genera that we studied; however, the likelihood of repair varied with each genus. *Lepidostoma* spp. were the most likely to repair their cases when compared to the other 2 genera and had high levels of repair regardless of damage location. In the case of *Lepidostoma* spp., in-stream habitat and properties of the building material may play a role in the likelihood of repair behaviors. For example, *Lepidostoma* spp. cases in our study had several morphologies, suggesting a level of flexibility in how building materials are used, possibly associated in part with species differences. Cases of most early instars consisted of sand grains and later shifted to detrital materials in the 3rd instar (Anderson 1976). Later instars use larger leaf panels or trimmed thin pieces of wood, customizing or modifying materials encountered in the habitat as needed. In addition, repair behaviors may be required for long-term maintenance of the case. Late instar *Lepidostoma* spp. cases are comprised predominately of leaf panels and other organic materials and may be routinely repaired as leaf panels deteriorate or are consumed by shredding conspecific larvae when food resources are low. In many of our experimental trials, damage was repaired to over 100% at all locations, which indicates that after the caddisfly finished repairing the damage, it continued to build onto the length of its case, perhaps in preparation to remove damaged sections of the case.

Although a few *N. rickeri* individuals were able to repair their damaged cases, this species was least likely to do so. Building material and habitat may have played a role in the tendency of this species to repair its case. Specifically, mineral cases tend to be more energetically expensive to construct than organic cases, but potentially provide better protection from predators (Otto and Svensson 1980) and enough of the damaged case may have remained to achieve satisfactory protection. Larval habitat may be influential. *Neophylax rickeri* larvae prefer riffle habitat with constantly moving water and high dissolved oxygen levels, which were not available in our experimental design. Of the 3 genera, mortality in the pre-experiment holding tanks was the highest for *N. rickeri*. Finally, although the samples of materials provided were collected from the habitat, we may not have provided the same variety of shapes and sizes of materials available in nature, especially the very fine sediment (also apparent in repair by sand-cased *Lepidostoma* spp. (Fig. 1B). *Neophylax rickeri* must select and fit case material (Mendez & Resh 2008) and searching for repair material may be more time consuming and energetically expensive than for construction of a totally new case. The complete case reconstruction that we observed in 2 *N. rickeri* individuals may be the more likely alternative to repair used in nature.

Larvae of *O. unicolor* were capable of repairing their cases, but the frequency of repair was statistically inconclusive, with only half of the larvae repairing the damage. The cases of *O. unicolor* have a mix of hardnesses in the detrital materials used, with hard pieces of wood and leaf matter interlocked in a way similar to the stones of the cases of *Neophylax*. *Onocosmoecus' unicolor*'s flexibility for repair may be somewhat intermediate between those of *N. rickeri* and *Lepidostoma* spp. Repair of anterior and posterior damage was highly variable, which may have resulted from a lack of a full range of materials normally available in the natural habitat. Repair of mid-section damage was less variable than damage at other sections and, like *Lepidostoma* spp., showed about 100% likelihood to repair their cases, suggesting that an intact case mid-section is important, whether for structural reasons or for protection.

Although all 3 genera demonstrated the ability to repair their cases, they did not all repair with equal frequency or at all damage locations; life history may have been influential in the likelihood to repair cases. For example, age may contribute an energetic factor, because repair may result in a change in resource allocation as the larvae prepares to develop into an adult (Stevens *et al*. 1999). Case-building activity has also been shown to decrease in 4th and 5th instars as focus shifts to gathering resources for pupation (Li & Gregory 1989). *Lepidostoma* spp. were least likely to have been influenced by pupation pressures because many species emerge in summer and had enough time to repair and gather resources (multiple species in Oregon: e.g., *L. unicolor* (Banks, 1911) in July, *L. cascadense* (Milne, 1936) in late summer-autumn; Anderson 1976, Grafius & Anderson 1980) *Onocosmoecus unicolor* emerges primarily in late summer to autumn, however some begin a resting period as early as March in Oregon (Wisseman & Anderson 1991). *Neophylax rickeri* emerges in autumn (Mendez & Resh 2008; Mendez *et al*. 2007) in Redwood Creek, however in February and March at the time of our study, many *N. rickeri* shifted from the 4th to the 5th instar in preparation for a 6–month, prepupal diapause. This need to maximize resources toward development may have reduced the likelihood of repairing cases, however predation risks during diapause and pupation (Mendez & Resh 2008; Rutherford & Mackay 1986) may be reduced with an intact case. Because we did not restrict our study to a single instar or consider instars in our analysis, it is unclear if energetic considerations based on age had an effect on repair behavior.

Case-repair patterns

For a number of Integripalpian caddiflies, the process of the initial building and constructing a replacement case has been well documented (e.g., Hanna 1960, Stuart & Currie 2001, Stuart & Currie 2002b) and a number of behavior patterns used in case-building reported in the literature were similar to those we observed for case-repair. For example, in both case-rebuilding and case elongation between instars, building behaviors are largely a directional building process. Pieces of material are either cut or selected, and are attached to the anterior margin of the case in a ring. As the case elongates, it is pushed further down the abdomen until the desired case length is achieved and any extra length of material is removed. In our study, we found that larvae in the 3 genera used these same building strategies for repair, especially for both anterior and posterior damage. Anterior damage was addressed by simply adding onto the anterior end of the case. Posterior damage was often inspected by the larvae (flipping in the case), but case material was not added to the posterior end; instead material was added to the anterior end of the case. This behavior differs from the repair behaviors observed by Hanna (1960) and Prestidge (1977) who removed a portion of the posterior of the case to form a hole in the side of the posterior of the case, similar to our mid-section damage treatment, resulting in a patching of the hole with silk or ignoring the damage. In our study, we removed an entire ring of the posterior portion of the case and the repair we observed was an anterior elongation. Because posterior portion material is often removed by the caddisfly after the case elongation phase during normal growth, it is not clear if this anterior elongation in response to posterior damage also accommodates for future growth or if anterior repair is simply the most effective strategy.

Damage to the mid-section resulted in a different suite of behaviors that were not anteriorly directional such as those employed in case building. For example, all 3 of the genera examined in this study repaired mid-section damage by patching the damaged area with silk, similar to patches made by the sand-cased limnephilid caddisfly *Pycnocentrodes aeris* (Prestidge 1977) and observed by Hanna (1960). However, for *Lepidostoma* spp., new building material was also integrated. After patching the damage, material was often added to the anterior of the case so that the damaged portion could be removed once the extended case reached the appropriate length. Repair behaviors clearly exist for mid-section damage to cases.

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