Postmolt susceptibility of Ephemerella larvae to predatory stoneflies: constraints on defensive armour

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I examine the effect of molting on predator-prey interactions between larvae of the herbivorous mayfly *Ephemerella subvaria* McDunnough and the predatory larvae of the stonefly *Agnetina capitata* (Pictet). In feeding trials over a range of prey densities (37–225 larvae/tank) *Agnetina* larvae consumed only a small proportion of large *Ephemerella* larvae available to them. Vulnerability of large (8.5–11 mm bodylength) *E. subvaria* larvae to predation by *Agnetina* was found to be dependent on molting condition. In arena experiments, larvae in postmolt condition were killed significantly more often than larvae in an intermolt condition. When offered a choice *Agnetina* larvae almost invariably consumed postmolt larvae first, and in most cases intermolt individuals were not consumed at all. For smaller *Ephemerella* (5.0–7.0 mm bodylength), molt condition had no significant effect on whether a larvae would be consumed by *Agnetina*, however, predator handling time was significantly longer for intermolt individuals. For large *Ephemerella* vulnerability to stoneflies was elevated for at least two hours following a molt. Collection of larval exuviae from the drift indicates that *Ephemerella* larvae molt more frequently during the day, a time when stoneflies are least active. The thick exoskeleton of large *Ephemerella* larvae acts as an effective defense against predaceous stoneflies; however, to grow and develop larvae must occasionally shed their armour and pass through a period of increased susceptibility. Such windows of increased vulnerability may be longer and more important for slow-moving thickly-cuticularized species such as *Ephemerella*, and probably are an important constraint on the evolution of defensive armour.

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Introduction

Most of the interest in behavioral activities that increase vulnerability of prey to predators has centered on the consequences of foraging and mating decisions (Lima and Dill 1990); however, all organisms experience periods where they must trade off increased risk of predation or parasitism against the necessity of undertaking other biological functions (e.g. sleep, defecation, respiration, etc.). The proportion of time spent in some of these activities may be relatively small in terms of annual or even daily measures; however, what happens in these periods may have disproportionate consequences in terms of individual survival (e.g. Kramer et al. 1983).

Activities that increase vulnerability of prey not only have implications for individual survival, they may also have consequences both for prey populations and potentially for the predator populations as well. In such situations, the dynamics of the predator-prey interaction between populations may be largely shaped by what happens during what might be described as rare, infrequent, or transient events. One such event in the lives of all arthropods is the occasional shedding of their exoskeleton in the process known as molting.

To grow and develop all arthropods must undergo this process, which consists of a series of events collectively referred to as the molting cycle. The physiological and cytological events in the molting cycle have been exten-

sively studied in insects and decapod crustaceans and there are numerous ways to classify the various stages of molting cycle (e.g. Neville 1975, Chapman 1982, Skinner 1985). For the purposes of this paper "intermolt" will refer to individuals with fully sclerotized cuticles, "ecdysis" refers to the actual shedding of the old exoskeleton, and "postmolt" refers to the period of expansion and sclerotization (hardening) of the new exoskeleton that immediately follows ecdysis. "Molt" is also used collectively to refer to both ecdysis and the postmolt stage that follows it.

Molting is a traumatic event in the lives of most arthropods, not only because it is physiologically stressful, but also because it may be associated with a period of impaired function for cuticular structures associated with sensory perception, respiration, movement, feeding, and defense (Chapman 1982, Steger and Caldwell 1983, Mill 1985). Despite its universality and potential importance to arthropod populations, there are relatively few quantitative studies that examine the consequences of molting behavior for predator-prey and other types of ecological interactions. Ecological consequences of molting have been most extensively studied in the Crustacea, where it is known to affect feeding, mating behavior, intraspecific aggression and ability to defend territories (e.g. Tamm and Cobb 1978, Lipcius and Herrnkind 1982, Salmon and Hyatt 1983).

Molting should be especially troublesome for those arthropods that use their exoskeleton either as a structural defense, or depend on cuticular color patterns for camouflage from predators. Such arthropods must periodically face a period of increased vulnerability to predators until pigmentation and sclerotization of their new exoskeleton is complete. For example, Steger and Caldwell (1983) report that newly molted stomatopods are more susceptible to cannibalism by intermolt individuals. In laboratory experiments with crayfish, Stein (1977) found that recently molted crayfish were most susceptible to predation from smallmouth bass, requiring only about 10% of the handling time of intermolt individuals. In field studies, Stein (1977) also found that postmolt crayfish were a preferred prey type of a number of fish species and that individuals normally too large to be consumed by fish could be consumed if in a recently molted condition. Thus, it appears that at least for some crustaceans molting has a cost both in physiological terms and in terms of increased risk from predators.

Unlike crustaceans which molt throughout their lives, most insects have only a limited number of molts (3–5) as larvae and adults usually do not molt at all. This suggests that postmolt vulnerability may be a less significant source of mortality for insects relative to crustaceans; however, some hemimetabolous insects are similar to crustaceans in that they have large numbers of molts during their larval period. For example, Odonata (dragonflies) larvae may molt as many as 15 times (Westfall 1978) and Plecoptera may have from 12 to 24

molts (Harper 1978). Among winged insects (Pterygota) the Ephemeroptera (mayflies) are perhaps the most frequent molters, with as many as 45 larval molts (Edmunds 1978) and with some species exhibiting variable or indeterminate molting behavior (Clifford 1970, Cianciara 1979). If molting behavior does have real costs in terms of risk from predators then a good place to study these costs should be within the Ephemeroptera.

Although most mayfly larvae possess relatively thin cuticles, some species do possess thick, heavily chitinized cuticles that may function in resisting predator attacks. Notable among these are larvae of the genus *Ephemerella* in the family Ephemerellidae, which are a major component of the benthic fauna in streams and rivers in the Holarctic region (Edmunds et al. 1976). *Ephemerella* larvae are slow-moving grazers that prefer to hide or to resist predator attacks rather than to flee them. Interactions between predatory stoneflies (Plecoptera) and *Ephemerella* larvae have been frequently studied (e.g. Peckarsky 1980, Molles and Pietruszka 1983, 1987, Williams 1987, Allan and Flecker 1988, Soluk and Collins 1988a, Peckarsky and Penton 1988). *Ephemerella* larvae can avoid predatory stoneflies by altering their position on stones (Soluk and Collins 1988a), however, their primary defensive mechanism appears to be their armoured exoskeleton (Peckarsky and Penton 1988).

If *Ephemerella* are indeed dependent on a heavily sclerotized cuticle then they will face a period following ecdysis when their slow moving habits will combine with a soft unsclerotized exoskeleton to make them especially vulnerable to predators such as stonefly larvae. In this paper, I examine whether molting by *Ephemerella subvaria* larvae increases their susceptibility to stonefly predators, and explore the consequences of this for behavioral responses such as defense posturing and the timing of ecdysis.

Methods

Larvae of *Ephemerella subvaria* and the stonefly *Agnetina capitata* used in the experiments were obtained from the east fork of the Credit River, in central Ontario, Canada. Larvae of *A. capitata* used throughout this study ranged in size from 12 to 17 mm (total body length exclusive of antennae and cerci) and no food was given to larvae for a 24 h period before the start of experiments. "Small" *E. subvaria* ranged from approximately 5–7 mm in total body length, "large" larvae were approximately 8.5–11 mm long. "Postmolt" is used here in reference to individuals identifiable, by their extremely pale colour, as having molted within the previous 1 or 2 h. "Intermolt" individuals were normally pigmented and although actual duration since last molt was unknown it would have been greater than 4 h given their well developed pigmentation.

Stonefly predation rates

Rate at which larvae of *Agnetina capitata* consumed large *E. subvaria* larvae was assessed for a range of prey densities (37, 75, 150 and 225 larvae/tank) in recirculating stream tanks (Soluk and Collins 1988b). Substrate in the stream tanks consisted of 18 stones (53–110 mm diameter) placed in the bottom of the stream. For each replicate, *Ephemerella* larvae were introduced into the stream tank and 24 h later five *Agnetina* larvae were added. After a further 24 h the stoneflies were removed and then all remaining *Ephemerella* larvae were removed and counted. Missing *Ephemerella* larvae and dead larvae partly eaten by stoneflies were scored as consumed. No control (prey without predator) was used since a previous study (Soluk and Collins 1988b) had indicated that errors introduced in counting or extraction were neglible with this experimental design. Number of replicates varied among the different densities (10, 9, 7 and 5 replicates for densities of 37, 75, 150 and 225 larvae/tank, respectively). Prey densities used in the stream tanks were within the range of densities reported for *Ephemerella* species from field studies (Clifford 1979) and correspond to areal densities of 195, 396, 792, and 1188 larvae m^{-2}.

Postmolt susceptibility

Differential susceptibility of postmolt versus intermolt *E. subvaria* larvae to predation by stoneflies was evaluated in a series of arena experiments designed to maximize encounter rate between mayflies and stoneflies. Each arena consisted of a 355 ml styrofoam cup (bottom diameter 60 mm, top 90 mm) filled with dechlorinated water and vertical circulation of the water was created by bubbling air from the end of a microcatheter air line placed in each cup. No substrate was present in the cups but both *Ephemerella* and *Agnetina* larvae were able to maintain their grip and move about easily on the styrofoam walls of the cup. All experiments were carried out under lighted conditions at a temperature of 13°C.

In the first experiment, to evaluate relative susceptibility of postmolt *Ephemerella* larvae, pairs of larvae (one recently molted and one intermolt, matched for size) were placed in a series of cups. An *Agnetina* larva was then introduced into each cup. Observations of each cup were made under lighted conditions at intervals of 15, 30, 60 and 120 min from introduction of the stonefly larva and the status of the *E. subvaria* larvae (safe, attacked, partially consumed, or consumed) recorded. Some pairs of small larvae were watched continuously for the first hour and the time from initial attack by the stonefly to complete consumption of the *Ephemerella* larva was recorded. Number of cups run on any particular day was determined by the availability of recently molted larvae. Experiments with large *Ephemerella* larvae (36 pairs observed) were conducted in March and April, 1988 and 1989. Experiments

with small larvae (23 pairs were observed) were conducted in November 1988.

To obtain an estimate of the length of the postmolt susceptible period, the experiment conducted above on large *E. subvaria* was repeated with the essential modification that larvae were held in the cup for two hours before the stonefly larva was added to allow some hardening to occur. Data from this experiment was collected in the same way as described above. A total of 35 pairs were observed.

The above experiments with pairs of larvae combine prey selection by the stonefly with absolute vulnerability of the *Ephemerella* larvae and thus they only provide a measure of relative susceptibility. In order to estimate vulnerability of intermolt and postmolt individuals where predator choice was not a factor, the initial experiment was modified so that only a single larva (either post- or intermolt) was placed in the arena with a stonefly larva. Observations were then made in the same manner as with the initial experiment, and the number of cups in which *Ephemerella* larvae were killed by the stonefly was recorded. A total of 110 individual *Ephemerella* larvae (55 postmolt and 55 intermolt) were used.

Timing of molt

To evaluate the hypothesis that molting of *E. subvaria* larvae may be timed on a diel cycle so as to minimize the risk of predation from stoneflies during the postmolt period, frequency of molting in the field was examined. Direct observation of molting in the field in an non-intrusive way is extremely difficult, however, frequency of molting can be indirectly estimated from the number of "articulated" exuviae in the water column at any particular time. The term "articulated" is an arbitrary classification that describes an exuvium with legs and head attached to a thorax. These were assumed to be the most recently shed exoskeletons, since disarticulation of segments and loss of appendages seems to be a consistent feature in the degeneration of exuviae over a period of one or more days (pers. obs.).

Estimates of the number of exuviae in the water column of the east fork of the Credit River were obtained using two drift nets (27 × 39 cm opening, mesh size 750 um). Drift was collected simultaneously in both nets for 15 min at the start of each hour over a 24 h period on 12–13 April, 1989. Samples were preserved in 95% ethanol and subsequently all mayfly larvae and articulated exuviae were removed by picking samples at 6X magnification on a dissecting microscope.

Periods of maximal risk of predation from stoneflies were assessed by combining diel activity data for the two most abundant species of predatory stoneflies (*Agnetina capitata* and *Paragnetina media*) in the east fork of the Credit River. Activity data were originally obtained in the laboratory using infrared sensitive cameras and time lapse video taping methodology (see Soluk
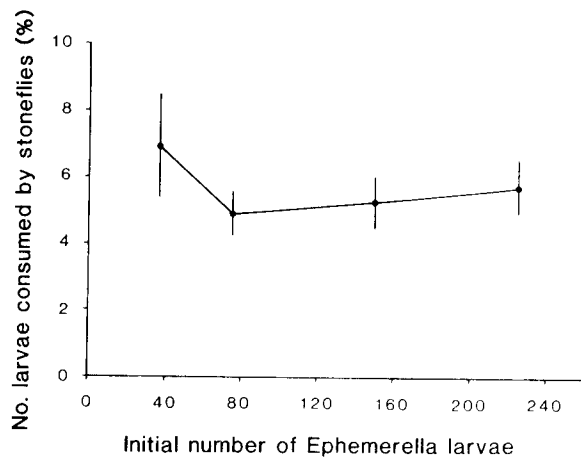
Fig. 1. Mean proportion (± S.E.) of *Ephemerella* consumed by *Agnetina* larvae during a 24 h period, over a range of prey densities. Sample sizes were 10, 9, 7, and 5 respectively, for lowest to highest initial densities of *Ephemerella* larvae.

and Collins 1988c). Data for *Agnetina* were extracted from Soluk and Collins (1988c) and data for *Paragnetina* were extracted from Soluk (1988). Activity is expressed as proportion of time in "major movements" (i.e. movements of more than a bodylength) which are assumed to be indicative of foraging activity.

Results

Stonefly predation rates

Mean predation rate of *Agnetina* larvae on *Ephemerella* larvae remained relatively constant (Fig. 1) ranging between 4.9 and 6.9% per day, despite a six-fold increase in prey density. Statistical analysis (Kruskal-Wallis one-way analysis of variance by ranks, Zar 1984) indicated no significant difference (p = 0.50) between proportions killed by stoneflies at the four densities. Actual number of *Ephemerella* larvae consumed in a 24 h period varied from a mean of 2.6 larvae for the 37 larvae/

Table 1. Numbers of intermolt and postmolt large *Ephemerella subvaria* larvae consumed by larvae of the stonefly *Agnetina capitata* over a two hour period. Separate experiments used either recently molted *Ephemerella* (< 2 h postmolt) or *Ephemerella* that had been held for a two hour period after they had molted (> 2 h postmolt).

	< 2 hours after ecdysis	
	Consumed	Not consumed
Postmolt	18	18
Intermolt	6	30
	> 2 hours after ecdysis	
	Consumed	Not consumed
Postmolt	15	20
Intermolt	7	28

Table 2. Numbers of intermolt and postmolt small *Ephemerella subvaria* larvae consumed by larvae of the stonefly *Agnetina capitata* over a two hour period.

	Consumed	Not consumed
Postmolt	20	3
Intermolt	17	6

tank density up to a mean of 12.8 larvae for the 225 larvae/tank density. It is thus clear that *Argnetina* larvae are able to capture and consume large *Ephemerella* larvae, however, the proportion of the population that they are able to capture is restricted and relatively constant.

Postmolt susceptibility

Large *Ephemerella* larvae in a postmolt condition had a much higher probability of being consumed by the stonefly larvae than intermolt individuals. This was true for freshly molted larvae (Table 1 upper, χ^2 = 9.0, p = 0.003, 2×2 contingency table analysis) and for larvae that were at least 2 h postmolt (Table 1 lower, χ^2 = 4.2, p = 0.039).

Whether or not a small larva had recently molted had no significant effect (Table 2, χ^2 = 1.24, p = 0.264) on whether they would be consumed by stonefly larvae. This was despite the fact that the mean time from capture to consumption by the stonefly was significantly longer for intermolt (4.8 min, n = 11, S.E. = 1.7) than for postmolt (9.5 min, n = 12, S.E. = 1.7) *Ephemerella* larvae (p = 0.01, t-test).

In the experiment in which only a single large *Ephemerella* larva in post- or intermolt condition was placed in the arena with a stonefly larvae, significantly more postmolt larvae were consumed by the stoneflies (Table 3, χ^2 = 4.5, p = 0.034, 2×2 contingency table analysis). This indicates that the higher consumption rate of large postmolt *Ephemerella* is probably a function of absolute vulnerability as well as selection by the stonefly.

Timing of molt

The occurrence of articulated *Ephemerella* exuviae in the water column of the Credit River showed a distinct periodicity, with two to three times as many exuviae being collected from the drift during the day as were

Table 3. Numbers of intermolt and postmolt large *Ephemerella subvaria* larvae consumed in separate trials by larvae of the stonefly *Agnetina capitata* over a two hour period. Each individual stonefly larvae placed with only one intermolt or one postmolt *Ephemerella*.

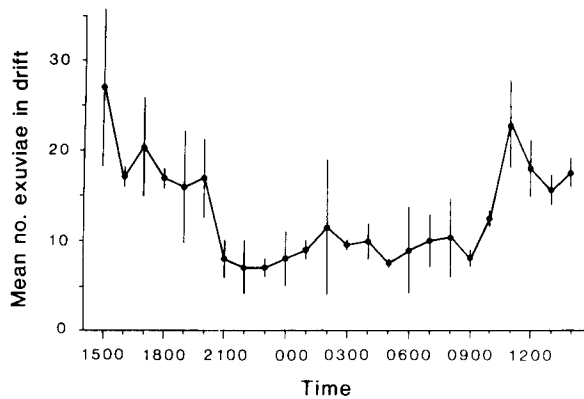|	Consumed	Not consumed
Postmolt	29	26
Intermolt	18	37

Fig. 2. Mean number of *Ephemerella* exuviae collected from the drift in the east fork of the Credit River over a 24 h period. Vertical bars represent the range for the two drift nets used. Dusk and dawn were approximately 1900 and 0700 hours, respectively.

collected at night (Fig. 2). This suggests that molting activity increases during the day relative to the night. Exact degeneration rates of exuviae are unknown, thus their occurrence in the drift at night may represent some base level of retention or resuspension of exuviae shed during previous daylight hours. However, it is probable that some molting does actually occur during the night. Periodicity in occurrence of *Ephemerella* exuviae was not explainable in terms of flow variation since no strong variation in discharge (as measured by height of flow around the drift nets) were noted during the 24 h period.

Activity of larvae of the two predominant species of stoneflies (*Agnetina* and *Paragnetina*) was largely restricted to the dark period of the experiments (Fig. 3). If movement patterns observed in the laboratory are directly correlated with foraging activities in the field, *Ephemerella* larvae should face greatest risk from these predators for a period starting one hour after sundown and ending approximately one hour after sunrise.

Discussion

Large *Ephemerella* larvae appear to do quite well in the evolutionary arms race with their stonefly predators. The low rates of predation observed in the first part of this study (stonefly predation rate experiment) seem typical of interactions between *Ephemerella* and stonefly larvae in general. For example, Peckarsky and Penton (1988, 1989) observed only about 2 to 15% of *Ephemerella* killed in overnight predation experiments. Ability of stoneflies to capture *Ephemerella* can be quite low. Allan and Flecker (1988) present data for encounters between the stonefly *Hesperoperla pacifica* and *Ephemerella infrequens* which indicates that only 2 *Ephemerella* larvae are killed for every 1000 encountered by the stonefly. In comparison, similar data collected for larvae of the mayfly *Baetis* (a very active species with a thin cuticle) indicates that about 18 larvae

are killed for every 1000 encountered by large *Hesperoperla* larvae (Allen et al. 1987).

Large *Ephemerella* larvae seem to have developed relatively effective mechanisms to resist consumption by stoneflies; however, it is also clear that these mechanisms are not always effective. Why some *Ephemerella* die when most seem able to resist the attacks of stonefly larvae has been explained by variability, either in the hunger level of the stonefly or in the ability of *Ephemerella* to resist the predator. Hungry stoneflies are known to attack and consume small *Ephemerella* larvae more frequently, whereas satiated stoneflies prefer other prey (Molles and Pietruszka 1983). Although hunger level was controlled (stoneflies were starved for a 24 h period before the start of the experiment) some variation will probably still exist. An especially hungry stonefly larva might be persistent enough to overcome even the most resistant *Ephemerella* larvae. However, if predator hunger were the sole factor controlling number of *Ephemerella* killed, then a significantly higher proportion of prey should be taken at low relative to high prey densities. There is little evidence of this in the relatively linear functional response seen in Fig. 1, suggesting that variation in ability to resist predators may be a better explanation for occasional successful attacks by stoneflies.

It is apparent from the susceptibility experiments that molting condition contributes to variation in the defensive ability of large *Ephemerella* larvae. For a period of at least 2 to 3 h following ecdysis large *Ephemerella* larvae have their defensive capabilities impaired and must suffer increased risk of predation from stoneflies and perhaps from other invertebrate predators as well. Although molt condition was apparently unimportant to small *Ephemerella* when attacked by large *Agnetina*, it would be premature to infer that molting is an important source of increased risk only for large *Ephemerella*. Predator handling time was almost doubled for *Agne-*
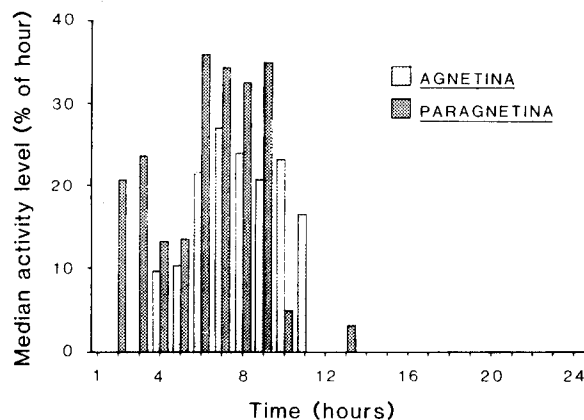

Fig. 3. Median proportion of hour (%) spent actively moving about on the substrate (moves of more than a bodylength) for the larvae of two species of predatory stoneflies common in the east fork of the Credit River. Hours 1 to 12 were night and 13 to 24 were daylight. Data extracted from Soluk and Collins (1988c) and Soluk 1988.

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tina consuming small intermolt larvae relative to small postmolt larvae. Given that handling time of *Ephemerella* increases significantly as predator size decreases in a similar way to that reported for other mayfly prey (Allan and Flecker 1988), smaller *Agnetina* larvae may have difficulty subduing small intermolt *Ephemerella*. Thus although molting by small *Ephemerella* has little effect on their vulnerability to large stoneflies it could potentially increase their vulnerability to smaller stoneflies.

Given that molting is hazardous when stoneflies are present it is not surprising that *Ephemerella* decrease ecdysial activity during the night, when predatory stoneflies are most active in the river. Unfortunately, because the drift data is correlative I cannot resolve whether molting during the day is primarily a way of minimizing risk from predators, or if it has additional selective advantages.

Molting during the day may be advantageous with respect to minimizing risk from stonefly predators, but it could be potentially hazardous if the colour patterning on the exoskeleton of *Ephemerella* larvae serves to make them less detectable to visual predators such as fish. Newly molted *Ephemerella* are not only soft, they are also easily recognized by their white appearance which contrasts sharply with darkly coloured substrates in the streambed. Experimental work suggests that many *Ephemerella* larvae move to the underside of stones in the light (Soluk and Collins 1988a) and in such places risk of a freshly molted individual being detected by a fish may be minimized. However, it should also be noted that substantial numbers of larvae remain on the tops of stones in both the laboratory and the field; so increased risk from fish due to molting cannot be disregarded, especially during the day. It would be quite interesting to determine whether individuals on the upper surfaces of stones move to the undersurface (or vice versa) before shedding their exoskeletons to avoid predators.

There is probably an interesting evolutionary tradeoff in the Ephemeroptera between thickness of exoskeleton and degree to which molting increases vulnerability to predators. In contrast to *Ephemerella*, many mayflies with thin exoskeletons (e.g. *Baetis*) depend on rapid swimming or crawling to escape potential predators. Possessing a thick exoskeleton and the appropriate musculature to move it about limits the speed and flexibility of *Ephemerella* larvae so that they are slow crawlers and poor swimmers. In the postmolt period, both *Baetis* and *Ephemerella* are able to move about in an apparently normal fashion before sclerotization of exocuticle is complete (the cuticle is still white and unpigmented). Regaining the ability to move in the postmolt period restores the ability of *Baetis* to escape predators, however, being able to move is of little benefit to a soft postmolt *Ephemerella* larvae, which is still constrained to be slow-moving by virtue of its body plan.

Since *Ephemerella* cannot effectively flee from a predatory stonefly larvae, the duration of time in which it is vulnerable to predation will be determined by the speed of the processes that strengthen the cuticle (e.g. sclerotization and deposition of new cuticle). A problem for a thickly cuticularized species is that the sclerotization process is partly dependent on diffusion of substances into the exocuticle (Locke 1974), thus thick cuticles should take relatively longer to harden than thin ones. A relative measure of this time differential exists in the observation that *Ephemerella* larvae are recognizably in a postmolt condition for at least 2 h following ecdysis, whereas postmolt *Baetis* are indistinguishable from intermolt larvae in less than an hour after ecdysis. Although I have no specific information on the vulnerability of postmolt *Baetis*, it seems likely that the cost of molting in such thinly cuticularized species is low relative to that experienced by *Ephemerella*.

Consideration of the importance of postmolt susceptibility may give us a more complete understanding of behavioral interactions between stonefly larvae and *Ephemerella*. For example, when in close proximity to predatory stoneflies, both post- and intermolt *Ephemerella* larvae usually exhibit a posturing behavior (scorpion posture) which consists of bending the tip of the abdomen upward and bringing the caudal filaments up and over the body (see Peckarsky 1980). This behavior has generally been interpreted as having a defensive function, however, this view has been challenged by Peckarsky and Penton (1988) who found that *Ephemerella* larvae with cerci intact had the same probability of being killed by stoneflies as those with cerci removed. They considered the scorpion posture to be an example of the "ghost of predation past" in that it had arisen at an earlier stage in the coevolutionary arms race between *Ephemerella* and stoneflies and no longer served an adaptive function. Knowledge of the postmolt vulnerability of *Ephemerella* enables me to suggest that although scorpion posturing had no effect on whether intermolt larvae were consumed by stoneflies (intermolt larvae generally have low vulnerability to stonefly attack), it might be of importance to softer postmolt individuals who may benefit from any behavior that slows or discourages attacks by stoneflies.

One problem with suggesting that scorpion posturing serves an adaptive function for soft postmolt *Ephemerella* is that it does not explain why well-sclerotized intermolt larvae continue to exhibit this behavior, although they gain no apparent benefit in terms of reduced mortality. However, consideration of the way in which insect cuticle is laid down and strengthened may provide an answer. Insects continue to lay down cuticle not only within the postmolt period but also throughout the intermolt period (Chapman 1982), thus it may be difficult for an individual *Ephemerella* larva to determine its vulnerability to stonefly attack at any particular time. In contrast to Peckarsky and Penton's (1988) reference to the "ghost of predation past" (evolutionary past), this might be described as "the ghost of predation

just past" (developmental past), where the larva continues to respond as if it was vulnerable because it cannot accurately determine when its period of increased vulnerability has ended. Alternatively, it is not clear that intermolt *Ephemerella* larvae do not benefit in other ways from discouraging stonefly attacks, since even well sclerotized individuals may sustain sublethal injuries while being variously bitten and trod upon by a large predatory stonefly.

There is a vast literature on the physiology of molting and the biochemistry of the arthropod cuticle; however, there has been little interest in anything other than metabolic costs of molting behavior. Molting is no less important to insect growth and development then is feeding or any other essential physiological process. I have indicated that, at least for heavily cuticularized species such as the larvae of mayfly *Ephemerella*, molting significantly increases potential risk of being consumed by predators and this may explain unusual aspects of their behavior. A more complete understanding of the consequences of molting can give us potentially valuable insights into both ecological and co-evolutionary relationships of many species of arthropods.

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