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Life-history and Behavioural Adaptations to Flow Regime in Aquatic Insects

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Abstract

Evolutionary history determines how aquatic insects cope with extreme flow events, both natural and anthropogenic. From a macroevolutionary point of view, aquatic insects possess different modes of adaptation (morphological, behavioural, or life history) to cope with flow events. For example, some Ephemeroptera, Plecoptera and Trichoptera are adapted to long-term average cycles of flood and drought via life-history timing, while other groups with aquatic adults (Hemiptera and Coleoptera) may use rain-triggered behavioural responses to escape floods on a per-event basis. From a microevolutionary point of view, populations may also evolve in response to flow regimes at very local scales. Models of life-history and behavioural evolution illustrate how disturbance regime characteristics (timing, frequency, predictability of events) and population structure (course- versus fine-grained, organism lifespan) determine how populations might evolve in response to different flood or drought regimes. All of these factors have implications for the structure of natural lotic insect communities, and for the effective management of dammed rivers and streams using ecological flows.

Introduction

Flood and drought disturbances are a fundamental part of most streams and rivers, and play a central role in the regulation of populations (Hemphill and Cooper, 1983; Holomuzki and Biggs, 2000), the structuring of communities (Fisher *et al.*, 1982; Wootton *et al.*, 1996; Townsend *et al.*, 1997), and the functioning of ecosystems (Grimm and Fisher, 1986; Townsend *et al.*, 1998). Aquatic insects, in particular, occupy the full spectrum of aquatic disturbance regimes, from the most stable headwater spring to the most dynamic desert wash. This diversity of habitats also means that aquatic insects experience a variety of selective pressures, and as such are a model system for understanding how aquatic organisms evolve in response to flood and drought disturbance. From a conservation point of view, as natural flow regimes are altered by human endeavours such as dams and

water diversions (Graf, 1993; Bunn and Arthington, 2002; Nilsson *et al.*, 2005), we need to understand how aquatic organisms might evolve, or fail to evolve, in response to novel disturbance regimes. Some questions come immediately to mind: as flow regimes are changed, will organisms adapt to these novel environments or simply vanish from the system? What are the population-level characteristics that favour adaptation to local flood and drought regimes? To understand these conservation-oriented issues, a basic understanding of how aquatic insects evolve in response to flood and drought is required. This chapter seeks to identify some of the general biological processes that determine how aquatic insects evolve in response to flood and drought.

Most populations of organisms are under selective pressure to evolve in new directions, and at the same time are constrained by their evolutionary past. Aquatic insects are typical in this respect. The variety of general body plans represented by the different insect orders presents an array of evolutionary constraints, while the varied habitats occupied by aquatic insects present a myriad of evolutionary challenges. This chapter will first outline how macroevolutionary patterns imposed by respiratory physiology and general life cycle considerations may favour different modes of adaptation (life history, behavioural or morphological) to flood or drought, with an emphasis on behavioural and life-history adaptations. The focus will then shift to microevolutionary patterns, with an emphasis on predictions derived from current models of life-history and behavioural evolution.

Modes of Adaptation

Major body plans can be a constraining factor on the evolution of strategies for coping with flood, drought, and flow variability in general. For aquatic insects, some a priori predictions about the mode of adaptation (life-history, behavioural, or morphological) can be made based on basic physiology and life cycle (Lytle and Poff, 2004). In general, life-history adaptations are expected in taxa that cannot respond immediately to disturbance events with behavioural avoidance, but may be able to anticipate disturbance from seasonal cues. Behavioural adaptations involve using environmental cues correlated with disturbance (rainfall, for example) as a signal to escape disturbance by moving within a stream or leaving the stream entirely. Movement out of the stream is especially important for mobile, air-breathing taxa that can respond to disturbances on a per-event basis. Morphological adaptations to flood and drought include traits such as streamlining to avoid shear stress during floods and drought-resistant life stages (Townsend and Hildrew, 1994; Poff *et al.*, 2006). This chapter focuses specifically on life-history and behavioural adaptations, and how these relate to flow regime components such as disturbance timing, frequency and predictability.

Life-history adaptations

Life-history adaptations include emergence strategies that are synchronized to avoid seasons when disturbances are likely (Gray, 1981; Gray and Fisher, 1981;

Lytle, 2002), or the use of proximate cues such as habitat drying to alter growth and development trajectories (De Block and Stoks, 2004, 2005; Danks, 2006). Life-history adaptations might be expected in taxa that cannot effectively escape disturbances on a per-event basis. In particular, taxa that require gill respiration as juveniles but have an aerial adult stage (Ephemeroptera, Plecoptera, Trichoptera, Odonata, Megaloptera and some Diptera) cannot exit the water immediately to avoid sudden flood events. However, they may be able to synchronize emergence into the adult stage to coincide with the long-term mean expected date of disturbance, thereby avoiding disturbance in most years. Life-history adapted taxa 'play the odds' over long timescales; although the strategy may fail occasionally if a disturbance is early or late (Lytle, 2003), this strategy maximizes long-term expected fitness given the constraints imposed by disturbance (Lytle, 2001).

Unlike floods, the onset of drought is often accompanied by proximate cues such as an increase in temperature and ionic concentrations, and a decrease in flow rate and water level. Particularly in the Trichoptera and Plecoptera, these cues may allow facultative entry into a drought-resistant stage (aerial adults or diapausing juveniles) (Wiggins, 1973; Hynes, 1976; Wiggins *et al.*, 1980; Delucchi and Peckarsky, 1989; Brock *et al.*, 2003), or provide a signal to adjust growth and development rates accordingly (Shama and Robinson, 2006; Robinson and Buser, 2007). In some cases, the transition to a drought-resistant stage occurs constitutively at a particular time, typically in synchrony with the expected date of drought occurrence (Wiggins *et al.*, 1980; Williams, 1996). However, some taxa apparently use asynchronous hatching of eggs as a way of 'bet-hedging' against the uncertainty of drought timing (Frutiger, 1996; Zwick, 1996). The presence or absence of these traits is sometimes responsible for determining species distributions along gradients of disturbance (Wissinger *et al.*, 2003).

Trichoptera may provide the most extreme example of an aquatic insect group that requires much advance notice that a disturbance will occur. The larvae of most Trichoptera species obtain dissolved oxygen via gills, and their aquatic pupal stage may last several weeks, during which time they may be exposed to mortality from flood or drought (Wiggins, 1973). This commitment to an aquatic environment precludes most behavioural strategies involving a temporary escape from flood by leaving the stream and subsequently returning to the water. In this instance a life-history strategy is favoured where emergence into the adult stage is synchronized with the expected occurrence date of flood events (Gray, 1981; Lytle, 2001).

Behavioural adaptations

Behaviours are context-dependent responses to different environmental cues. Although behaviours are often considered more evolutionarily labile than morphology or life history, studies have found a strong phylogenetic component to many insect behaviours such as nest building in Hymenoptera (Wenzel, 1992), web construction in spiders (Bond and Opell, 1998) and case construction in Trichoptera (Wiggins, 2004).

Many behavioural adaptations for disturbance avoidance rely on a proximate cue (rainfall, rising hydrograph, etc.) to signal a disturbance, which is then avoided by moving to safe zones within the stream or leaving the stream entirely. Behavioural strategies tend to take disturbances on a 'case by case' basis, rather than playing the long-run odds as in life-history strategies. For aquatic insects, behaviours may be subdivided into those facilitating within-stream survival during flood or drought, and those allowing escape from the stream during flood or drought. Instances of behavioural flood escape are best known in the Hemiptera and Coleoptera, possibly because their ability to breathe air allows them to persist out of water for relatively long time periods (Lytle and White, 2007). Other taxa that have the ability to persist out of water may possess similar behaviours (e.g. some Trichoptera and Megaloptera: Anderson, 1967; Erman, 1981; Contreras-Ramos, 1998), but more studies are needed to explore this. Within-stream behaviours for avoiding flood disturbance include the utilization of hydraulic refugia occurring in the substrate landscape, as well as adjustments to normal movement patterns that reduce the chance of displacement (Olden *et al.*, 2004; Lancaster *et al.*, 2006).

Flood escape behaviours include the use of proximate environmental cues as a signal to abandon streams. This has been well documented in the giant water bugs (Hemiptera: Belostomatidae), which use 'rainfall response behaviour' (RRB) to escape flash floods in desert streams. Individuals respond to some characteristic duration of strong rainfall by crawling out of the stream, moving perpendicularly away from the active channel over steep (sometimes vertical) stream banks, and not stopping until they have reached protected riparian areas (Lytle, 1999). The fitness benefit from RRB is substantial: the flightless belostomatid *Abedus herberti* experiences about 15% mortality from flash floods, while many other desert stream taxa endure mortality in excess of 95% (Grimm and Fisher, 1989; Lytle, 2000). Interestingly, RRB in belostomatids turns out to be an ancient, phylogenetically conserved trait that likely evolved to facilitate seasonal migration from perennial dry-season habitats to temporary rainy-season pools (Lytle and Smith, 2004). The co-opted use of RRB to escape flash floods is a more recent evolutionary event that has occurred separately in at least two distinct belostomatid lineages (an 'exaptation' *sensu* Gould and Vrba, 1982). The recent discovery of RRB in other aquatic Hemiptera suggests that flood escape behaviours may be the rule, rather than the exception, at least for taxa inhabiting desert streams where flash floods are commonplace (Lytle and White, 2007). Although rainfall cues are important for many taxa, in principle, other flood-associated cues such as changes in barometric pressure, turbidity, cloud cover or hydraulic pressure waves could be important as well.

For some taxa, behavioural escape from drought can be a viable strategy. Rivers and streams can experience sudden drops in flow caused by diel fluctuations in riparian plant evapotranspiration, lowering of the water table due to low rainfall inputs, and recession to baseflow following flood events (Stanley *et al.*, 1997). Aquatic Coleoptera adults seem particularly adept at drought escape, and the literature contains numerous accounts of beetle adults escaping drying habitats. For example, the dytiscid beetles *Rhantus gutticollis*, *R. binotatis* and *Eretes sticticus*

have been observed taking flight en masse from drying desert ponds, and in some cases the emigration was preceded by loud, sustained vocalization (Zimmerman, 1959; Smith, 1973; Kingsley, 1985). Within-stream movement is also a mechanism for escaping the recession point of rapidly drying streams and rivers. Lytle *et al.* (in press) observed thousands of adults of the long-toed water beetle *Postelichus immsi* (Coleoptera: Dryopidae) crawling upstream concurrent with diel recession of surface water in a desert river. Larvae of the grey sand-dragon *Progomphus borealis* (Odonata: Gomphidae) were also observed burrowing upstream in large densities (690 larvae per m²). Both taxa moved with sufficient speed to reach upstream perennial river reaches before being overtaken by drought. Given the proven ability of many aquatic insects to optimally relocate within streams in response to local fine-scale differences in flow (Lancaster and Hildrew, 1993; Lancaster, 1999; Wellnitz *et al.*, 2001), for many taxa, behavioural drought escape may be a special case of a more generalized ability to track sudden changes in flow.

When do Ecological Conditions Lead to Evolutionary Change?

While macroevolutionary considerations may determine the mode of adaptation to flood and drought, microevolutionary factors, such as ecological context and population structure, may influence the degree to which populations evolve in response to local differences in disturbance regime. From theory of evolution in fluctuating environments (Cohen, 1966; Iwasa and Levin, 1995; Lytle, 2001), we expect that selection for disturbance-escape strategies will be strongest when: (i) per-event mortality is high; (ii) predictability of events is high; (iii) frequency of events is high; (iv) events are 'coarse-grained' (synchronous over larger spatial scales); and (v) the organism's lifespan is long relative to the disturbance return interval. Several more predictions arise from basic population genetic considerations. Selection should be strongest when (vi) population-level additive genetic variance is high, and (vii) gene flow from differently adapted populations is small.

Mortality, Frequency and Predictability

Factors (i)–(iii) are fairly intuitive. If a lethal event occurs reliably on the same day each year, selection will favour life histories that are synchronized to escape this event. In most models of life-history evolution these three factors are multiplicative, in that a low value of one will cancel out high values of the other two (see fig. 2 in Lytle and Poff, 2004). For example, selection may be weak for high-mortality events that are seasonally predictable but very infrequent, such as freezing events in tropical regions or hurricanes.

The notion of flood or drought 'predictability' deserves some discussion, as this has been defined variously in the literature (Resh *et al.*, 1988; Poff, 1992, 1996). For the purpose of understanding life-history or behavioural evolution, it is useful to define predictability as the degree of correlation between

a disturbance and some environmental cue (*sensu* Lytle and Poff, 2004). For many types of flood and drought, it is possible to determine the mean Julian occurrence date of some flow event exceeding a given magnitude (timing) using long-term hydrograph data. The degree to which this date correlates with the actual date of disturbance across years (the variance) can thus be interpreted as a measure of predictability, in that it describes how reliably that date will predict an actual disturbance event from year to year. Proximately, many aquatic insects use day-length to estimate seasonal timing, and the literature is rich with examples of taxa that adjust growth and development in response to altered day-length (e.g. Johansson and Rowe, 1999; De Blok and Stoks, 2004). In certain cases predictability can be defined without respect to seasonal timing. Some organisms respond to rainfall events as a signal that a flood may soon occur (or a drought may be ending). Desert stream insects such as giant water bugs (Hemiptera: Belostomatidae), other Hemiptera and some Coleoptera use rainfall as a signal to escape flash floods by immediately abandoning the stream and moving into protected riparian areas (Lytle, 1999; Lytle and White, 2007). For these organisms, the degree to which rainfall events (the environmental cue) are correlated with floods (the disturbance) determines the predictability of the flood event. An example of how this kind of predictability can drive the evolution of behaviours in local populations is discussed below.

Coarse-grained versus fine-grained environments

Factor (iv) arises from theory related to measuring fitness in fluctuating environments. In fine-grained environments where disturbances occur independently across patches, and the breeding population is pooled from these patches, the arithmetic mean is the appropriate measure of fitness over time (Cohen, 1966; Gillespie, 1977). This is analogous to the 'patch dynamics' scale in stream ecology studies (Pringle *et al.*, 1988; Townsend, 1989; Downes *et al.*, 1998; Lake, 2000). By contrast, in coarse-grained environments where the entire population experiences the same disturbances in a synchronous manner, the geometric mean is the correct fitness measure. In fluctuating environments, geometric mean fitness is always lower than arithmetic mean fitness, especially when the fluctuations are large. The way this affects trait evolution can be understood heuristically by imagining two different populations of a mayfly, one composed of multiple subpopulations in adjacent streams that flood independently of each other, and another occupying streams that always flood simultaneously. In the former population, each subpopulation experiences the flood regime independently, and then the adults meet in a single swarm to mate and disperse. The population fitness is the arithmetic mean of all subpopulation fitnesses, and the population as a whole is buffered to some degree against a severe disturbance in any single stream (i.e. a zero value in the arithmetic mean will still result in a positive population-wide fitness). In the latter population, a severe flood event affects the entire breeding population simultaneously, producing a low or zero value for the geometric mean fitness. Because of these differences, when per-event

mortality rates are high, selection is much stronger in coarse-grained versus fine-grained environments (Iwasa and Levin, 1995; Lytle, 2001).

Two points arise from this discussion that are important to our understanding of disturbance in aquatic systems. First, larger floods and droughts likely fall into the coarse-grained category as multiple stream reaches are affected simultaneously. Thus from an evolutionary point of view, disturbances that occur at the level of individual substrate particles or reaches are fundamentally different from disturbances that affect entire streams or rivers simultaneously—a point that may affect our interpretation of experiments that focus on disturbance acting at the level of individual rock particles. In other words, patch-dynamic disturbances may not scale up to full-stream flood or drought disturbances, because selection is acting in different ways at these two different scales. Second, the population genetic structure of aquatic insects may have a profound effect on how populations adapt to disturbance regimes, because it may determine whether the environment is coarse- or fine-grained. If a breeding population is drawn from a single stream, or groups of streams that experience simultaneous disturbance events, the coarse-grained fitness measures apply and selection may act more strongly to produce local adaptation. Although the predictions from theory are clear, the effect of environmental grain on aquatic insect evolution has yet to be examined empirically. The genetic structure of aquatic insect populations is an active area of research that should provide many insights concerning how organisms evolve in response to disturbance.

Lifespan

The lifespan of an insect relative to disturbance recurrence interval (v) determines to what degree selection can synchronize a life history with a disturbance regime. At one extreme, univoltine or semivoltine insects must pass through one or several disturbance seasons before emerging into the adult stage. For organisms in flood-prone environments, to use one example, selection might be strong for adult emergence that is synchronous with the expected date of flood disturbance, assuming that floods are sufficiently frequent, severe and predictable. For these taxa, the disturbance season entrains the population by restricting emergence to a specific pre-flood season. Individuals that emerge late risk being removed by floods, and individuals that emerge too early risk placing their offspring in harm's way. This life-history strategy has been observed in univoltine caddisflies inhabiting desert streams where severe flash floods occur during a fairly well-defined season (Lytle, 2002; see example below). At the other end of the spectrum, multivoltine taxa with very short lifespans may or may not face a disturbance season during their lifetime. This kind of multivoltinism has reached an extreme with the desert stream mayfly *Fallceon quilleri* (Ephemeroptera: Baetidae), which matures from egg to adult in an astounding 9–11 days (Gray, 1981). Although this short life cycle prevents the population from becoming synchronized with the seasonal flood regime, it is thought that a rapid life cycle may itself be an adaptation to flooding as it minimizes the time spent as a larva in a flood-prone habitat (Gray and Fisher, 1981).

Life-history strategies and environmental variability

The trade-offs faced by many aquatic insects inhabiting seasonally disturbed environments are typified by the sycamore caddis *Phylloicus mexicanus* (Trichoptera: Calamoceratidae). Sycamore caddis inhabit perennial streams in the desert south-western USA and northern Mexico, which are prone to flash floods during the July–September flash flood season. The flash flood season places limits on *P. mexicanus* emergence; individuals must balance the costs of remaining in the stream (flood mortality) against the benefits (opportunity to continue feeding as larvae and increase fecundity, as adults are non-feeding). Life-history models predict an optimal reaction norm strategy, where individuals are expected to emerge at a smaller body size (and thus lower fitness) as the risk of a flood increases (Rowe and Ludwig, 1991; Johannson and Rowe, 1999; Lytle, 2001).

As with many caddisflies, a large proportion of body mass increase in *P. mexicanus* occurs during the final instar, but the amount of growth varies substantially among individuals. Among-individual variation in body size can be due to genetic differences, environmental factors, or some combination of both. Figure 7.1 shows that fitness, as measured by the number of eggs produced, can vary substantially among females, in this case by a factor of 3 or more. These individuals inhabited a range of food conditions that ranged from scarce to abundant detritus [see Lytle (2002) for background and details]. The lower

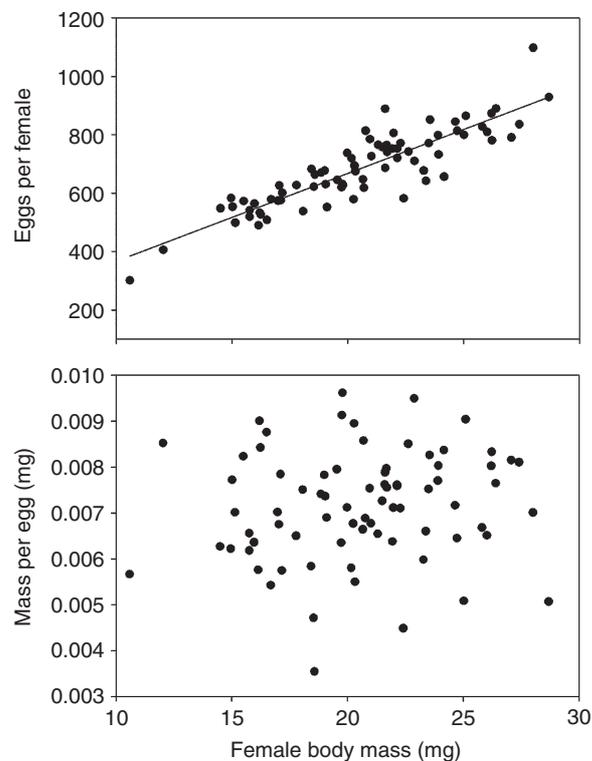


Fig. 7.1. Fitness gradient in a population of the caddisfly *Phylloicus mexicanus*. Fitness is increased by producing more eggs, rather than higher quality eggs. Top panel: larger females produce more eggs than smaller females ($R^2 = 0.78$). Bottom panel: egg mass does not vary systematically with female body mass.

panel of Fig. 7.1 shows that for this species, there is no trade-off between egg quality and quantity, and so egg number is a reasonable predictor of fitness. This population-level variability in potential fitness represents a steep fitness gradient, where realized body mass determines the position of an individual along the gradient. The observed variability, which is typical of many aquatic insects (Statzner *et al.*, 1997), has several implications for life-history evolution in flood-prone environments. First, there exists no single 'one-size-fits-all' optimal body size at emergence; rather, optimal body size at emergence is a reaction norm that changes through time as the costs and benefits of emergence change (in this case, mostly due to the increasing risk of a flood). Indeed, life-history models that incorporate a reaction norm of body size versus time perform substantially better than models that do not (Lytle, 2002). Similarly, the imposition of a disturbance is expected to increase within-population variability in fitness (Rowe and Ludwig, 1991; Lytle, 2001). To visualize this, imagine a population that is free from the time constraint of a disturbance. Even though there might be among-individual differences in growth rate due to genetics or microhabitat, individuals are free to grow until a maximum body size is reached, thereby reducing population-wide variability in egg number. Second, if the among-individual fitness variability is due mainly to environment and not genetics, individuals must be experiencing a large range of ecological conditions. Essentially, there is much latitude in the environment for individuals to do really well or really poorly. These differences could be due to microhabitat differences in ecological conditions (detritus as a food resource, predators, conspecific densities) or legacy effects (oviposition date, growth conditions during early development). If among-individual fitness variability is due to genetics, then fluctuating environmental conditions must maintain a large diversity of phenotypes within the population. In all likelihood, the observed variability is due to some combination of genetics and the environment.

In summary, the large within-population variability in aquatic insect egg production has implications for the evolution of life-history strategies in disturbed environments. A full understanding of these connections will require further studies, such as comparisons of populations of the same species inhabiting disturbed versus non-disturbed streams.

Local Adaptation of Populations

Flood and drought disturbance regimes can vary significantly at multiple spatial scales. Within a catchment, for example, floods may be less common in the headwaters due to small catchment area but commonplace in lower reaches that integrate many smaller drainages. Across catchments, flood and drought frequency, severity and predictability can vary due to differences in catchment area, underlying geology or even land use practices (Allan, 1995; Tague and Grant, 2004). Furthermore, anthropogenic factors such as dams, water diversions, revetments and alteration of flood plains can produce sudden changes (with respect to evolutionary timescales) in flood and drought dynamics (Poff *et al.*, 1997; Bunn and Arthington, 2002). All of these factors raise the issue of the

spatial scale at which aquatic insects can adapt to local differences in flood and drought disturbance regime.

Phenotypic plasticity versus local adaptation

The 'ideal' aquatic insect should be able to alter its life-history strategy or behavioural repertoire to match a range of disturbance regimes. For example, insects that inhabit streams prone to drought in some years and not others may benefit from a plastic strategy that allows different trajectories of growth and development (Johansson and Rowe, 1999; Johansson *et al.*, 2001; De Block and Stoks, 2004, 2005), assuming that sufficient proximate cues are present to signal the approach of different environmental outcomes (drought versus no drought, for example). For the aquatic insect populations that have been studied across disturbance regime types, phenotypic plasticity does appear to be common. Studies examining the proximate cues associated with the onset of drought (drying of pools, changes in photoperiod that are correlated with drought onset) have generally found evidence for plasticity—that is, individuals adjust rates of growth, development or both to compensate for different environments. In a common garden study of an alpine caddisfly, Shama and Robinson (2006) found that plasticity, rather than local adaptation, accounted for most observed differences between populations obtained from perennial versus temporary streams. Similarly, damselfly larvae from two habitats that differed in permanence showed no evidence for local adaptation in a common garden experiment, but responded to different treatments with phenotypic plasticity (De Block and Stoks, 2004).

Not all among-stream differences in disturbance regime are accompanied by useful proximate cues, however. For example, catchment size may determine the frequency and magnitude of flood events in some stream types (Gordon *et al.*, 1992), but there is no obvious way that an aquatic insect could determine catchment size from proximate cues. Local adaptation may be expected under these ecological conditions. Any population with sufficient heritable trait variation may evolve in response to local conditions, so long as selection is strong enough to counteract gene flow from nearby populations adapted to different optima.

Local adaptation to flood regime in giant water bugs

An example of local adaptation to different flood regimes is seen in populations of the giant water bug *Abedus herberti* that inhabit isolated, perennial streams in the arid south-western USA. Distinct populations of this flightless aquatic insect are confined to catchments that experience a large variety of flood regimes, which is dictated by catchment size. Floods are rare (<1 flood/year) or absent in smaller catchments, while larger catchments can experience multiple floods per year (Lytle, 2003). The predictability of floods from rainfall cues also varies according to catchment size (Fogel, 1969; Osborn and Laursen, 1973): predictability is highest in intermediate-sized catchments, where the correlation between rainfall and floods is strongest, but decreases as watersheds become smaller

(strong rainfall events occur, but catchment area is too small to capture enough water for a flood) or larger (local rainfall is absorbed into alluvial fill, and floods are generated by storms occurring in distant parts of the catchment). The cost of encountering a flash flood is high because mortality rates of most insects caught in floods is near 95% (Grimm and Fisher, 1989; Lytle, 2000). As noted previously, *A. herberti* use flood escape behaviour to survive these events: individuals sense periods of heavy rainfall that often precede floods and use this as a cue to crawl out of the stream to protected riparian areas, then return to the stream post-flood (Lytle, 1999).

The problem faced by individual *A. herberti* is this: if it rains hard for, say, 30 min, does this mean that a flood will occur? How about 40 min? 50? It turns out that this is a classic problem in signal detection theory, a branch of information theory that is useful for understanding how animal behaviours evolve in response to noisy signals (in this case, rainfall events of a given duration that do or do not result in a flood) (Getty and Krebs, 1985; Reeve, 1989; Wiley, 1994; Getty, 2002). Essentially, each *A. herberti* individual must balance the cost of leaving the stream (predators in the terrestrial environment, desiccation) against the cost of remaining in the stream (mortality from a flood), in the context of flood predictability. Two types of mistakes can be made: an individual might abandon the stream when no flood occurs (a 'false alarm'), or an individual might choose to remain when a flood does occur (an 'incorrect rejection'). Rainfall cues provide information about the environment—in general, the longer the rainfall event, the more likely a flood. However, this information profile differs among catchments, because rainfall is a reliable predictor of floods in mid-sized catchments ($\approx 10 \text{ km}^2$), but less so in smaller or larger catchments. Signal detection theory thus predicts that response time (the minutes of rainfall required to trigger RRB) should be fastest in the predictable mid-sized catchments, assuming that costs for incorrect rejections and false alarms are similar across catchments.

Behavioural experiments across 15 *A. herberti* populations inhabiting catchments ranging in size from 4 to $>400 \text{ km}^2$ revealed local adaptation to different local flood regimes: individuals from mid-sized catchments did, in fact, require the shortest durations of rainfall to trigger flood escape behaviour (Lytle *et al.*, 2008). In an extreme case, individuals from the smallest catchment (4 km^2), where floods rarely if ever occur, 'refused' to leave the stream at all—for these individuals, there is simply no benefit to leaving the stream, only a cost.

In a sense, the *A. herberti* populations encompass the ideal conditions for local adaptation to different flood regimes. They are flightless and so local adaptation is not counteracted by gene flow from differently adapted populations, i.e. factor (vi) in the section above is satisfied. Phylogeographic analysis of mitochondrial data suggests that at least some of these populations may have been isolated since the Pleistocene (Finn *et al.*, 2007), allowing plenty of time for natural selection to adapt populations to local flood regime characteristics. Furthermore, high haplotype diversity in many populations suggests that there may be, or have recently been, much heritable trait variation on which selection can act [factor (vii) in the section above]. Flash floods are also a very strong selective pressure, as the cost of making a mistake approaches 100%. Thus, the *Abedus herberti* system provides a baseline against which we can evaluate local adaptation

to flood or drought in other aquatic insect taxa. We now know that given sufficient time, sufficient isolation of populations and sufficiently strong selective pressures, that aquatic insect populations can adapt locally to a range of disturbance regimes.

Further Research and Management Implications

The examples given above show that aquatic insect populations can evolve in response to local flow regimes, at least under conditions where isolated populations are experiencing strong local selection. Next, we need to determine how common local adaptation is: Do most aquatic insect populations show some degree of local adaptation to flood or drought regime, or does this only happen in 'extreme' cases (i.e. fragmented populations with strong, divergent local selective pressures)? Also, many of the empirical examples come from desert systems where flood and drought are significant in both magnitude and frequency, and thus strong selective pressures—are adaptations to flood and drought as common in temperate and tropical systems? General disturbance theory predicts that traits such as life histories will evolve most quickly when disturbances are sufficiently frequent, strong in magnitude, and predictable (e.g. Lytle and Poff, 2004). The answers to these questions await further studies across different stream types.

Human-caused alteration of natural disturbance regimes is becoming ubiquitous in fluvial ecosystems, especially in the larger rivers (Nilsson *et al.*, 2005), and so an understanding of how organisms might evolve in response to this, or fail to evolve, is needed immediately. For example, anthropogenic changes to flow timing, magnitude, and frequency have increased disturbance predictability in some cases, e.g. by homogenizing flow regimes below hydropower dams (Poff *et al.*, 1997), and decreased disturbance predictability in other cases, e.g. irregular drought occurrence due to water diversion (Rader and Belish, 1999). Some aquatic populations have been observed to adapt rapidly to novel conditions if heritable genetic variation is available for selection (Hendry *et al.*, 2000), so it is possible that aquatic insect populations may respond rapidly to novel changes in flow regime.

A growing body of research is demonstrating that behavioural adaptations to flooding and drought involving rainfall cues may be commonplace, and this has implications for the management of regulated rivers and streams. A number of river restoration projects are employing ecological flows from dam releases to manage downstream habitats, with the intent of enhancing habitat for flood-dependent organisms (Patten *et al.*, 2001; Richter *et al.*, 2003; Shafroth and Beauchamp, 2006). Because dam releases will often occur without prior rainfall or other cues associated with natural flood events (increased turbidity, cloud cover, lowered barometric pressure), aquatic insects that rely on these cues might suffer excess mortality from artificial floods that occur without warning.

In summary, macroevolutionary patterns appear to determine the mode of adaptation (behavioural, life history, morphological) that aquatic insects may possess to cope with floods or droughts. In certain aquatic insect groups, respiratory requirements and life cycle constraints cause some modes to be favoured over others. As behavioural adaptations involving rainfall cues are widespread in

some taxonomic groups, the implications of this for ecological flow events (which seldom have appropriate rainfall cues) needs to be explored. At microevolutionary scales, populations may adapt locally to natural differences in disturbance regime, especially when certain evolutionary criteria are met (factors pertaining to disturbance mortality, frequency and predictability; organism lifespan; environmental grain; heritable variation for trait; population isolation). Whether populations are evolving in response to anthropogenic changes to flood and drought regimes remains an open question.

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