Exaptation and Flash Flood Escape in the Giant Water Bugs

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Although behaviors may remain highly conserved through evolutionary time, the ecological functions they serve can undergo surprising transformations. We used phylogenetic, correlational, and experimental evidence to show how a >150-million year-old behavior, which originally evolved to facilitate migration, has been co-opted for flash flood escape in two distantly related giant water bug species (Hemiptera: Belostomatidae). Using behavioral experiments with simulated rainfall, we showed that species from flash-flooding as well as non-flash-flooding environments are capable of rainfall response behavior (RRB), the ability to use rainfall as a cue to abandon an aquatic habitat. The results suggest that, in addition to allowing individuals to escape flash floods, RRB is the proximate mechanism generating a well-established ecological pattern: The correlation between rainfall and migration to seasonal breeding habitats that has been documented in 13 species throughout the family. Placing RRB in phylogenetic context reveals that for several taxa the behavior is an exaptation (a trait evolved for one function but later co-opted for another) for escaping flash floods. For Lethocerus medius, *rainfall response behavior is an addition exaptation because the behavior is used to initiate migration to seasonal rain pools (ancestral function) as well as for flash flood escape (co-opted function). In the distantly related* Abedus herberti, *rainfall response behavior is a transfer exaptation because it has been co-opted exclusively for flash flood escape and the ancestral function has been lost. These findings*

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emphasize that a phylogenetic framework is needed to fully understand the origins and ecological significance of behaviors.

INTRODUCTION

Flash floods in desert streams are sudden and severe, often causing mortality in excess of 90% for many aquatic insect species (Gray, 1981; Fisher *et al.*, 1982; Molles, 1985; Lytle, 2000). In contrast, the giant water bug *Abedus herberti* Hidalgo (Hemiptera: Belostomatidae) suffers less than 15% mortality because it uses rainfall that often precedes floods as a cue to abandon streams for higher ground (rainfall response behavior; RRB [Lytle, 1999]). Mortality from floods can be a strong selective pressure, and adaptations to flooding have been identified in fish, aquatic and riparian plants, and other aquatic insects (Lytle and Poff, 2004). However, it is not always a simple matter to determine the origins of a trait from the current selective environment. Most of the ~140 described belostomatid species actually inhabit lentic waters (ponds, lakes, and marshes) or rivers and streams that do not flash flood (Fig. 1). Two species that have successfully invaded flash-flooding streams, *A. herberti* and *Lethocerus medius* (Guerin-Meneville), are very distant relatives; fossil material from the upper Jurassic suggests that these two lineages diverged at least 150 million years ago (M.a.) (Popov, 1971; Smith, 1997). Thus, from an evolutionary point of view it is interesting to know whether *A. herberti* and *L. medius* both possess some form of RRB and whether the behaviors arose independently through convergent evolution or were shared via ancient common ancestry.

Rainfall response behavior may also explain an ecological pattern that is well established in the giant water bugs. A strong rainfall–migration correlation has been documented for 13 belostomatid species spanning most of the genera (Bowden, 1964; Cullen, 1969; Nieser, 1975; Robertson, 1976; Hutchinson, 1993; Lytle, 1999). These studies report a positive correlation between the beginning of seasonal rains and the capture of large numbers of migrating adults at light traps. The pattern is attributed to adults using rainfall as a cue that seasonal rain pools, a food-rich and predator-free environment, are becoming available for breeding (Cullen, 1969; Hutchinson, 1993; Smith and Larsen, 1993). In some cases it has been demonstrated that following migration, histolysis of wing muscles occurs and the resources are shunted toward reproductive tissues (Cullen, 1969), an example of the oogenesis–flight syndrome (Johnson, 1969). The fact that a rainfall–migration correlation is widespread in the Belostomatidae suggests that some form of RRB may
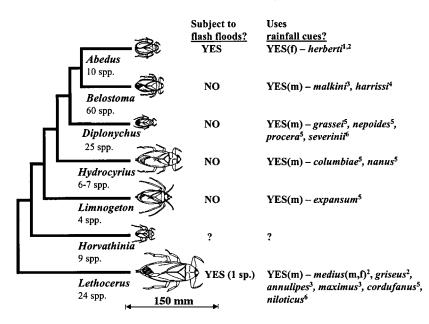
Fig. 1. Phylogenetic relationships, association with flash floods, and use of rainfall cues in the Belostomatidae. Phylogeny follows Lauck and Mencke (1961) and Mahner (1993); redrawn from Smith (1997). m, rainfall cues used for migratory flight; f, cues used for flash flood escape. "Flash flood" refers specifically to flow events where the hydrograph rises instantaneously from base flow to near-maximum discharge. Reference superscripts: (1) Lytle, 1999; (2) this study; (3) Cullen, 1969; (4) Nieser, 1975; (5) Robertson, 1976; (6) Bowden, 1964.

be basal to the entire group, although until now no candidate behavioral mechanism has been proposed.

The goals of this study were to determine whether RRB arose by convergence vs. shared descent in *A. herberti* and *L. medius* and to determine whether RRB might also be the proximate mechanism generating the rainfall–migration correlation observed throughout the Belostomatidae. These goals were accomplished by carrying out controlled behavioral experiments and interpreting the results in phylogenetic context.

Components of Rainfall Response Behavior. One method for assessing the evolutionary history of behaviors is to break them into specific, quantifiable components and then ask which components are identical across taxa and which ones differ. This comparative method is useful for separating behavioral components that have been conserved through evolutionary time (Wenzel, 1992; deQueiroz and Wimberger, 1993; McLennan and Mattern, 2001) from those that are evolutionarily labile (Proctor, 1991, 1992). Eight components of RRB were observed in *A. herberti*, both in the field during natural rainstorms and in experiments using sprayed water to simulate rain

(Lytle, 1999). First, individuals required torrential rainfall ($>15 \text{ cm} \cdot \text{h}^{-1}$ for real rain, $>150 \text{ cm} \cdot \text{h}^{-1}$ for simulated rain) typical of powerful convective thunderstorms to initiate RRB. Second, the duration of torrential rainfall required was fairly consistent among individuals (in field experiments, the average duration was 8 ± 0.6 min). Third, upon receiving a sufficient rainfall cue, individuals immediately began crawling out of the stream. Fourth, movement out of the stream was negatively geotactic—individuals always crawled up the steepest available route, even nearly vertical stream canyon walls. Fifth, startle behavior (rapid return to the water in response to a sudden movement, predator, etc.) was inhibited. Sixth, once the behavior had begun only light rainfall was needed to keep individuals traveling away from the water. Seventh, removing the light rainfall caused individuals to freeze in place momentarily; resuming the rainfall stimulated them to continue crawling until a sheltered area out of the flood channel was reached. Eighth, individuals returned to the water within 24 h. In this study, the eight components were quantified for other belostomatid species to determine the current function (i.e., for flood escape, migration, or both) and the evolutionary origins of RRB.

METHODS

Taxon Selection. Two distantly related belostomatids, *A. herberti* and *L. medius,* occupy perennial mountain streams in southern Arizona (USA) and northern Mexico that are subject to flash floods during the summer monsoon season (July–September). The flightless *A. herberti* (complete wing muscle reduction and slight reduction of exoskeletal features necessary for flight [P. Goodwyn and R. Smith, unpublished data]) is a year-round resident of these streams, while *L. medius* occupies them during all of the year except for the monsoon season. To determine whether they possess similar rainfall response behaviors, individuals of both taxa were exposed to simulated rainfall under identical experimental conditions. Individuals were collected from Cave Creek in the Chiricahua Mountains of southeastern Arizona (USA) during the premonsoon season of May and June 1999. One hundred adult *A. herberti* were exposed to simulated rainfall in $N = 19$ trials (4 or 6 individuals per trial). For *L. medius,* 10 adults in $N = 10$ trials were used. These densities approximate those observed in the field (D. Lytle, personal observation).

At the onset of the summer monsoon rains (usually early July [Lytle, 2003]), *L. medius* migrates from flash-flooding streams to temporary rain pools, where they reproduce in a food-rich and relatively predator-free environment (Smith and Larsen, 1993). To test whether *L. medius* exhibit RRB in their non-flash-flooding reproductive environment, 33 adults from Mendoza Canyon (Coyote Mountains, Arizona, USA) were exposed

to simulated rainfall in $N = 8$ trials (3 or 6 individuals per trial). It is not known whether these were adults that recently flew to the pond or newly matured adults that developed within the pond, but the time of year they were captured (7–9 December 1999) suggests the latter. Dissections showed wing muscle development comparable to that of individuals caught flying to light traps in summer (D. Lytle, unpublished data).

To determine whether belostomatids that never inhabit flash-flooding streams are capable of RRB, as suggested by the rainfall–migration correlations, nine adult *Lethocerus griseus* (Say) from the Everglades in Collier County, southern Florida (USA) were exposed to simulated rainfall in $N = 2$ trials. *L. griseus* inhabits non-flash-flooding habitats such as ponds and marshes. Individuals were collected from permanent dry-season habitat (cypress swamp; 5- to 30-cm water depth) in January 2001.

Behavioral Experiments. Giant water bugs were exposed to simulated rainfall under controlled experimental conditions. To create a standardized aquatic/riparian habitat, all trials were conducted using the same behavioral arenas. Two $42 \times 32 \times 23$-cm plastic bins were fitted with 52-cm vertical walls on three of the four sides (one end was left open to allow observation). The bins were lined with fiberglass screening and the walls covered in burlap, providing a rough surface for the insects to climb. The bins contained drain holes to maintain water level at a constant depth of 12 cm.

For each trial, individuals were randomly assigned to one of two behavioral arenas and allowed to acclimate for at least 30 min. To induce RRB, rainfall was simulated by spraying water at 150 cm.h^{-1} from 1.3 m above one of the arenas (randomly selected as the treatment) using a standard spray nozzle (No. WM3501; Raintime, Elyria, OH). A second sprayer supplied the sides of the treatment arena with light rainfall (<1 cm $\cdot$ h^{-1}), which was necessary for individuals to complete the behavior. The unsprayed arena served as a control treatment. We used water pumped directly from the habitat where individuals were originally caught, which is sufficient to induce RRB (Lytle, 1999). Trials were conducted outside in late afternoon to avoid direct sunlight in the arena, which can inhibit RRB (Lytle, 1999). For each individual, the duration of rainfall required to initiate RRB was recorded. For a subset of individuals, all eight RRB components were observed and recorded. Trials were the unit of replication for statistical analyses; when more than one individual was present in a trial the average response time was used. No individual was tested more than once. All individuals were tested within 7 days of capture (most within 48 h) and fed an *ad lib*. diet of wingless crickets.

Phylogenetic Relationships. To interpret the rainfall–migration correlations and the experiment results, species and behaviors were mapped onto

a genus-level phylogeny of the Belostomatidae. The phylogeny is based on the morphological study by Lauck and Menke (1961), which was later corroborated using cladistic methods by Mahner (1993).

RESULTS

Both *A. herberti* and *L. medius* from flash-flooding streams had similar rainfall response behaviors. Seven of the eight RRB components were nearly identical between species (Table I). Of the 27 (of 100) *A. herberti* that abandoned the water, the average duration of rainfall required to initiate the behavior was 11 min (SE = 1.7 min). Seven of the 10 *L. medius* responded to rainfall after an average time of 7 min (SE = 1.1 min), which was not significantly different from *A. herberti* (*t*-test, $t = 1.59$, df = 18, $P = 0.129$). A retrospective power analysis showed that this test should have been able to detect differences between the two means of 6 min or greater with a power of 0.8. Most components of the *L. medius* behavior were indistinguishable from those of *A. herberti* (Table I). However, at dusk the quiescent *L. medius* prepared for flight by rapidly pumping their wing muscles for approximately 30–60 min, then took flight. Thus, the RRBs of *A. herberti* and *L. medius* are identical in all respects except for component 8, since *L. medius* initiates flight, while the flightless *A. herberti* returns to the water. None of the control individuals abandoned the water in any of the trials, suggesting that the impact of rainfall on the water is sufficient to initiate RRB. None of the 33 *L. medius* captured in the seasonal breeding habitat exhibited any component of RRB.

Seven of the nine *L. griseus* abandoned the water in response to rainfall, and most components of RRB were identical to those observed in *A. herberti* and *L. medius* (Table I). Unlike the other taxa, *L. griseus* waited until shortly after dusk to exit the water, regardless of the duration of rainfall (Table I). Rainfall in the first trial was started 100 min prior to dusk and three of five individuals abandoned after an average of 114 min. Rainfall in the second trial was started within 30 min of dusk, and all four individuals abandoned after an average of 40 min. No flight or pumping of wing muscles was observed within 1 h following dusk (trials were terminated at this point). One control individual (of four in the arena) climbed 18 cm out of the water at dusk.

DISCUSSION

The RRB of *A. herberti* in the experiments was nearly identical to the field observations of RRB during actual rainstorms reported by Lytle (1999). For this reason the experimental methods appear to provide a reasonable account of the behavior as it occurs in the wild. With a single exception, the

Table I. Summary of Behavioral Responses to Simulated Rainfall Experiments

	Abedus herberti	Lethocerus medius		Lethocerus griseus
		Strong flier		Strong flier
Flight ability	Flightless			
Habitat	Flash-flooding streams (year-round)	Flash-flooding streams (dry-season habitat)[a]	Non-flash-flooding rain pools (reproductive habitat)	Non-flash-flooding marshes (dry-season habitat)
Number of individuals tested	100	10	33	9
Intensity of simulated rainfall	150 cm/h	150 cm/h	150 cm/h	150 cm/h
Duration of simulated rainfall	60 min	60 min	60 min	60 min
Number responding	27	7	0	7
Results				
1. Responds to rainfall cues?	Yes	Yes	No	Yes
2. Duration of rainfall cue required to initiate behavior	~10 min (11 ± 1.7 min, SE)[a]	~10 min (7 ± 1.1 min, SE)[a]	n/a	Unknown
3. Response after receiving rainfall cue	Immediately crawls out of water	Immediately crawls out of water	n/a	Remains until dusk, then crawls out of water
4. Negative geotaxis observed?	Yes	Yes	n/a	Yes
5. Inhibition of startle behavior?	Yes	Yes	n/a	Yes
6. Light rain required to maintain travel once behavior begins?	Yes	Yes	n/a	Yes
7. Removing light rain causes individuals to freeze in place?	Yes	Yes	n/a	Yes
8. Behavior after dusk	Returns to water	Flight	n/a	Flight?
Interpretation of RRB	**Transfer exaptation:** behavior co-opted for flood escape	**Addition exaptation:** behavior used both to initiate migratory flight (ancestral) and for flash flood escape (co-opted)		**Ancestral state:** behavior used only to initiate migratory flight

[a]Not significantly different.

control animals did not respond to rainfall, which suggests that the observed behaviors were triggered by rainfall cues and were not an artifact of the experimental setup.

The experiments demonstrate that most components of RRB are similar across all three taxa, despite their wide phylogenetic separation and the different habitats they occupy (flash-flooding streams vs. stable marshes). The sharing of specific behavioral components such as negative geotaxis, suppression of startle response, and the necessity of light rainfall to continue movement suggest that these behaviors were acquired by descent rather than by multiple evolutionary origins. Coupled with the near-ubiquity of a rainfall–migration correlation in the Belostomatidae, these findings suggest that some form of RRB is ancestral to the giant water bugs.

Most belostomatid species occupy ponds, marshes, or rivers rather than flash-flooding streams (Lauck and Menke, 1961), and so it is likely that the invasion of flash-flooding habitats occurred secondarily relative to the occupation of non-flash-flooding habitats. In this case it is likely that RRB originally evolved in order to facilitate migration to seasonal breeding habitats, and the use of RRB for avoiding flash floods occurred later. It is not known if flightlessness in *A. herberti* evolved before or after this evolutionary transition. A similar evolutionary transition has occurred in another hemipteran group, the Gerridae, where the use of stable, perennial habitats is the ancestral condition and the invasion of seasonal habitats occurred later (Wagner and Liebherr, 1992; Andersen, 1993). For the two giant water bug species that use it to avoid flash floods, RRB is an exaptation, a character evolved for a particular use and later co-opted for another function (Gould and Vrba, 1982). This is demonstrated most strikingly with *A. herberti,* which has lost the ability to fly and now uses RRB exclusively to escape flash floods. Arnold (1994) refers to this as a transfer exaptation, where a novel function has completely replaced the original function of the trait. *L. medius,* on the other hand, still uses rainfall as a cue to initiate migration, but RRB has been co-opted for flood escape as well, an example of an addition exaptation. Based on this interpretation, we reject the possibility that rainfall response behavior evolved separately in *A. herberti* and *L. medius.*

It is likely, however, that certain components of RRB have undergone adaptation to particular environments. Although not conclusive (since components 2 and 8 remain ambiguous), the experiments with *L. griseus* suggest that the ancestral state of component 3 used by taxa inhabiting non-flash-flooding habitats is to wait until dusk to leave the water—a tactic that avoids visual predators and desiccation in the terrestrial environment. If this is the case, then the fact that *A. herberti* and *L. medius* abandon streams immediately after rainfall, rather than waiting until dusk, may be a more recent adaptation to flash-flooding environments. Selection may have fine-tuned this component of RRB, although even the ancestral behavior would lead to

the escape of at least some floods (those occurring after dusk). Differences in selective environments between the flightless *A. herberti* and the migratory *Lethocerus* species may also explain why a greater percentage of the latter responded to rainfall in the experiments, although this pattern could also be caused by differences among individuals that were not measured (e.g., differences in condition or body mass).

Because there is often a cost to abandoning the water for no reason [terrestrial predators (Smith, 1997), desiccation (Lytle, 1999)], it is not surprising that RRB is suppressed in ecological contexts where it serves no obvious function. None of the *L. medius* taken from their non-flash-flooding breeding habitat showed RRB, which makes intuitive sense because flash flooding is not a risk in ponds and more rainfall would only prolong the pond hydroperiod. It is more likely that these individuals use pond drying as the cue to migrate to perennial mountain streams, a hypothesis that remains to be tested. Conversely, in *A. herberti* the larval stages as well as the adults exhibit RRB (Lytle, 1999), which is congruent with the idea that RRB serves an adaptive flood escape function in this taxon. A prediction that remains to be tested is that juveniles of taxa which do not inhabit flash-flooding waters should not display RRB since there is no adaptive reason to do so.

The findings of this study emphasize that behavioral characters must be carefully examined in order to uncover their evolutionary origins. By identifying specific behavioral components it becomes possible to separate those with deep phylogenetic origins (components related generally to rainfall cues) from those that appear to have evolved in response to recent environments (those specific to avoiding flash floods). Furthermore, this phylogenetic perspective reveals that two seemingly unrelated ecological patterns, flash flood escape and rainfall-related migration, have a single common evolutionary origin.

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