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Rainfall Cues and Flash-Flood Escape in Desert Stream Insects

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Abstract Desert stream insects may use rainfall cues to anticipate and escape flash floods, but this has been studied in few taxa. We used controlled, replicated experiments to quantify the use of rainfall cues for flood escape in seven common desert stream insects. The hemipterans *Curicta pronotata* and *Aquarius remigis* responded consistently to rainfall cues by crawling vertically away from the water, in such a way that they may escape flash floods in nature. The coleopteran *Gyrinus plicifer* showed no response to rainfall cues. The hemipteran *Ambrysus woodburyi* did not exit the water but sought refuge under submerged rocks. Three taxa (*Ranatra quadridentata*, *Corydalus texanus*, and *Rhantus atricolor*) gave ambiguous results, although the latter apparently responded to environmental cues other than rainfall. We conclude that rainfall cues are a sufficient mechanism for flood escape in some taxa, but other desert stream insects may employ different strategies (behavioral, life history, or morphological) to survive floods.

Keywords Flash flood · rainfall response behavior · natural flow regime

Introduction

Rivers and streams in arid regions of the southwestern United States and northern Mexico are subject to flash floods that cause high mortality in populations, yet these same streams maintain a surprising diversity of aquatic insect taxa (Gray and Fisher 1981; Fisher et al. 1982; Bogan and Lytle 2007). Flash floods arrive with little warning and may scour the stream channel completely, resulting in mortality rates that can exceed 95% for individuals caught in floods (Fisher et al. 1982; Molles

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1985; Lytle 2000). Possibly in response to selection pressures imposed by flash floods, some aquatic insects have evolved behavioral strategies for flood escape. For example, the giant waterbug *Abedus herberti* (Hemiptera: Belostomatidae) uses rainfall response behavior (RRB) to escape streams immediately prior to flash floods: after some critical duration of heavy rainfall, individuals crawl out of the stream to riparian areas where they are safe from floods (Lytle 1999). Individuals later return to the stream post-flood. Experiments have shown that rainfall alone is a sufficient cue to trigger the behavior, although other cues such as ambient light intensity may play a role (Lytle and Smith 2004). If behaviors such as RRB are common among desert stream insects, this could provide a mechanism for the persistence of high diversity in a highly unstable environment.

Aquatic insect strategies for surviving floods encompass several modes of adaptation: life-history, morphological, and behavioral (Lytle and Poff 2004). For any given taxon, a priori predictions about the mode of adaptation can be made based on respiratory physiology and general life cycle. Life-history adaptations include emergence strategies that are synchronized to avoid seasons when floods are likely (Lytle 2002). Life-history adaptations might be observed in insects that require gill respiration as juveniles but have an aerial adult stage (Ephemeroptera, Plecoptera, Trichoptera, Odonata, Megaloptera, and some Diptera). Although larvae of these taxa may experience loss rates near 100% (Lytle 2000), these rates do not include individuals already in the adult stage (Lytle 2003). Morphological adaptations include body shapes that are streamlined to avoid shear stress during floods (Hart and Finelli 1999) and special organs that allow adhesion to substrates (Frutiger 2002). Although morphological adaptations may occur in any taxon, the decoupling of juvenile and adult stages that is characteristic of the holometabolous orders might allow more latitude for morphological specialization 3 of larvae. Finally, behavioral adaptations rely on proximate cues (rainfall, rising hydrograph, etc.) to signal a flood, which is then avoided by moving to safe zones within the stream (Lancaster and Hildrew 1993) or leaving the stream entirely (Lytle 1999; Lytle et al. 2007 in review). Behavioral flood escape might be prevalent in taxa that are air-breathing (Hemiptera and adult Coleoptera) because these are able to persist out of water during floods. Because Hemiptera and Coleoptera often dominate desert streams in terms of both species diversity and abundance (Bogan and Lytle 2007), behavioral adaptations to flash flooding might be commonplace in these systems.

In this study we used controlled, replicated experiments to assess whether seven common desert stream insects use rainfall cues to behaviorally escape flash floods. We focused primarily on aquatic Hemiptera and Coleoptera because these taxa are likeliest to possess behavioral mechanisms for escaping flash floods.

Methods

Taxon selection We chose seven taxa that commonly occur in flash-flooding streams of the Madrean Sky Island region of southern Arizona (USA) and northern Sonora (Mexico): the hemipterans *Curicta pronotata* and *Ranatra quadridentata* (Nepidae), *Ambrysus woodburyi* (Naucoridae), and *Aquarius remigis* (Gerridae); the coleopterans *Rhantus atricolor* (Dytiscidae) and *Gyrinus plicifer* (Gyrinidae); and the megalopteran

Corydalus texanus (Corydalidae). All taxa were collected during the pre-monsoon dry season (June and July) and so had not recently experienced heavy rainfall. Individuals were housed in tanks (42×32×23 cm plastic bins) at densities comparable to those observed in streams. Food was not provided since prey is scarce during the dry season (Bogan and Lytle 2007), but individuals were utilized in experiments within days of capture.

Behavioral experiments The response time (minutes of rainfall required to trigger RRB) and response rate (percentage of individuals in the population exhibiting RRB) was quantified for each species using the methodology of Lytle and Smith (2004). For each taxon, individuals were randomly assigned to one of two behavioral arenas, which were 42×32×23 cm plastic bins filled with 12 cm of water and fitted with 0.5 m walls that allow individuals to exit the water by climbing vertically. To provide traction for crawling insects, fiberglass window screen was glued to the plastic bins and burlap cloth was stretched over the vertical walls. Individuals were allowed to acclimate for at least 30 min before trials. One arena was selected at random and exposed to 60 min of simulated rainfall, water sprayed at 150 $cm{\cdot}h^{-1}$ by a recirculating pump from a standard spray nozzle (WM3501; Raintime, Elyria OH) 1.3 above the water surface. Light spray (<10 $cm{\cdot}h^{-1}$) was applied by a second nozzle to individuals that crawled out of the main cone of spray (some taxa are known to stop moving if not contacted by light rainfall; Lytle and Smith 2004). The other arena served as a control. For most taxa, response time was scored as the minutes of rainfall required to trigger RRB (defined as the crossing of a line 35 cm above the water surface). Experiments took place in an open-air, roofed enclosure that blocked direct sunlight and rain. Air temperature, ambient light (lux), barometric pressure, and general weather conditions were recorded at the start of most trials. Trials took place in the afternoon, when natural monsoon thunderstorms typically occur.

Replication and statistics Two replication schemes were possible: use individuals as replicates, or use trials as replicates. We chose trials as the unit of replication because (1) not all taxa were individually numbered which precluded taking means of individuals, and (2) this resulted in a more conservative test because the number of trials was always less than the number of individuals. No individuals were exposed to more than one rainfall trial per day, and individuals were haphazardly reassigned to new groupings each day.

Because of non-normality of data for some of the trials, comparisons of response time (minutes of rainfall required to trigger RRB) and response rate (percent of individuals responding per trial) were made with nonparametric Wilcoxon paired-sample signed-ranks tests (two-sided, $\alpha=0.05$). For descriptive purposes, the figures report the parametric mean and error (±1 S.E.M.) of response time and response rate.

Results

Weather conditions during the experiments constituted typical monsoon season patterns, with either hot, sunny days (maximum air temperature during experiments of up to

36°C, light levels up to 300 lux) or cooler, rainy days (minimum air temperature down 5–21°C, light levels below 25 lux). Barometric pressure averaged 25.6 mm, with deviations associated with changing weather systems and thunderstorms.

Curicta pronotata (Hemiptera: Nepidae)

C. pronotata is a waterscorpion distributed from southern Arizona, USA, into the Sierra Madre Occidental of Mexico (Keffer 1996; Hoekstra and Smith 1998). Although not widespread in the USA, it can be locally abundant along muddy shorelines of spring-fed waters where it blends in cryptically (Sites and Polhemus 1994). We collected 62 adults from stream pools in Ramsey Canyon, Huachuca Mountains (Cochise Co., AZ) on 27 June 2005. Individuals were found clinging to vegetation and rocks just under the water surface. The hemelytron of each was marked with a metallic silver Sharpie pen to increase visibility during experiments. Each treatment and control tank contained seven to nine individuals over a total of $n=23$ rainfall trials.

C. pronotata responded reliably and rapidly to rainfall experiments by crawling out of the water and up the sides of the behavioral arena (Fig. 1). Most individuals crawled vertically, and continued crawling as long as light rainfall contacted the dorsum. Individuals froze in place if rainfall ceased. Response rate in the rainfall treatment was significantly greater than in the control (Wilcoxon signed-ranks test, $n=23$, $P<0.00001$).

Ranatra quadridentata (Hemiptera: Nepidae)

R. quadridentata is a widespread waterscorpion commonly found in ponds, lakes, and streams throughout the Madrean Sky Island region and beyond. It is capable of flight and is sometimes found in large numbers in cattle tanks distant from other water sources (Bogan 2005). We collected 30 adults from a large pool in S. Fork Cave Creek, Chiricahua Mountains (Cochise Co., AZ) on 28 June 2006. Individuals were numbered with a metallic silver Sharpie pen, and run in rainfall experiments in groups of 15 (15 treatment and 15 control, then treatment assignment was reversed) over 3 days (all individuals exposed to treatment once daily) for a total of $n=6$ rainfall trials.

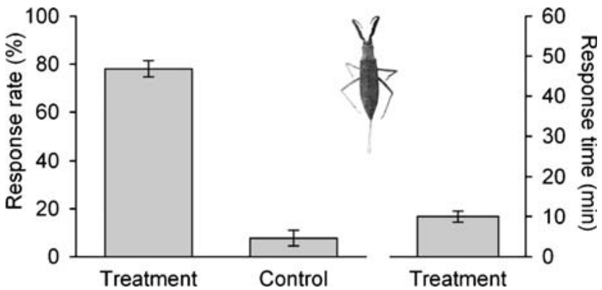

Fig. 1 Rainfall experiment results for the water scorpion *Curicta pronotata*. Individuals exposed to heavy rainfall abandoned the water significantly more frequently than controls.

Treatment response rate was low, with either one or zero responders in any given trial, and not significantly different from the controls where no individuals responded (Wilcoxon signed-ranks test, $n=6$, $P=0.182$; Fig. 2). All treatment responses were in fact due to a single individual that responded in three consecutive trials. This individual crawled vertically to the top of the arena, and did not appear to require light rainfall to continue movement.

Ambrysus woodburyi (Hemiptera: Naucoridae)

A. woodburyi inhabits pools and riffles in perennial Sonoran Desert streams. We collected 21 adults from Middle Fork Cave Creek, Chiricahua Mountains (Cochise Co., AZ) on 11 July 2005, during the pre-monsoon dry season. The hemelytron of each was marked with a metallic silver Sharpie pen to increase visibility during experiments. Each treatment and control tank contained seven or eight individuals over a total of $n=6$ rainfall trials.

No individuals abandoned the water in either the treatment or control tanks, although individuals occasionally broke the water surface to replenish plastron air stores. Many individuals in the treatment tanks did respond by moving underneath rocks, although this was difficult to observe directly or quantify during the rainfall trials.

Aquarius remigis (Hemiptera: Gerridae)

A. remigis is a common water strider found on the surface of interrupted perennial streams throughout the Madrean Sky Island region and beyond. We collected 21 adults from N. Fork Cave Creek, Chiricahua Mountians (Cochise Co., AZ) on 26 July 2005 during the pre-monsoon dry season. Individuals were run in rainfall experiments in groups of seven (seven treatment, seven control) for a total of $n=9$ rainfall trials.

The water striders responded to the rainfall treatment immediately by abandoning the water surface and moving to the vertical sides of the behavioral arena, away from direct rainfall (Fig. 3). The response rate in the treatment tanks was consistently near 100%, and significantly greater than control tank response rate (Wilcoxon signed-ranks test, $n=9$, $P<0.0001$). Upon leaving the water, most individuals froze in place

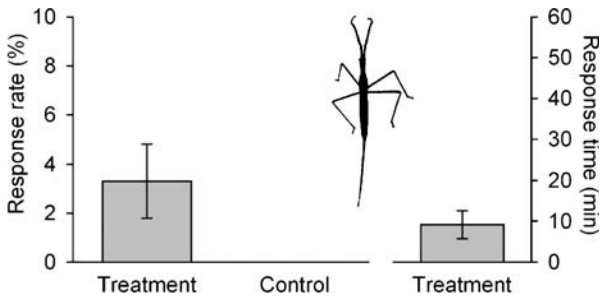

Fig. 2 Rainfall experiment results for the water scorpion *Ranatra quadridentata*. Treatment and control response rates were not significantly different.

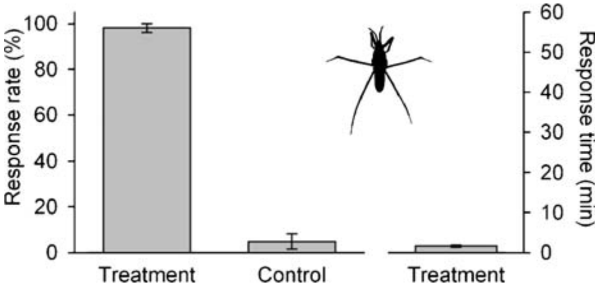

Fig. 3 Rainfall experiment results for the water strider *Aquarius remigis*. Individuals exposed to heavy rainfall abandoned the water by moving to the sides of the behavioral arena significantly more frequently than controls.

within about 10 cm of the water surface. Applying light rainfall caused some individuals to move higher but this was not consistent.

Rhantus atricolor (Coleoptera: Dytiscidae)

R. atricolor is a diving beetle that sometimes occurs in high densities in Madrean Sky Island streams. We collected 56 adults from Ramsey Canyon, Huachuca Mountains (Cochise Co., AZ) on 5 July 2005 during the pre-monsoon dry season. The hemelytron of each was marked with a metallic silver Sharpie pen to increase visibility during experiments. Each treatment and control tank contained from 10 to 28 individuals over a total of $n=6$ rainfall trials.

Individuals were active in both control and treatment tanks, and occasionally broke the surface to replenish air stores. Although some of the treatment individuals abandoned the water by crawling, the control tanks were far more interesting: in three of six trials, as many as 50% of the control individuals climbed out of the water and took flight (Fig. 4). Each of these events was associated with a monsoon thunderstorm occurring in the area, although we did not detect a significant decrease in barometric pressure during trials. While the magnitude of response rate was higher in the control vs. the treatment, this was not significant (Wilcoxon signed-ranks test, $n=6$, $P=0.318$).

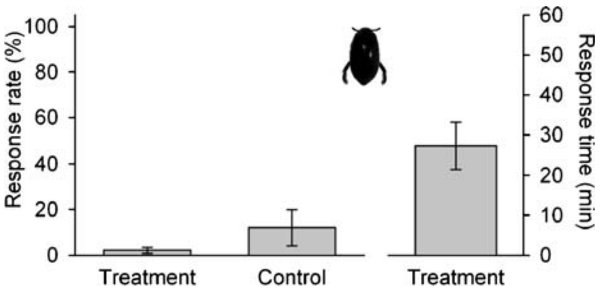

Fig. 4 Rainfall experiment results for the diving beetle *Rhantus atricolor*. Response rate did not differ significantly between treatment and control.

Gyrinus plicifer (Coleoptera: Gyrinidae)

G. plicifer is a small whirligig beetle found in slower-moving areas of streams. We collected 40 adults from the Middle and North Forks of Cave Creek, Chiricahua Mountains (Cochise Co., AZ) on 17 July 2006. Each experiment had 20, 16, or 6 individuals per tank (same number in treatment and control) over the course of three trials.

No individuals were observed abandoning the water during rainfall trials, but treatment individuals were observed clinging to the tank edges during and after trials while control individuals swam actively at the surface. Over the course of two nights, 70% of individuals escaped by flying out of holding tanks. Since no individuals were naive to rainfall when this occurred, we do not know if flight was a delayed response to rainfall.

Corydalus texanus Banks (Megaloptera: Corydalidae)

C. texanus (recently clarified as distinct from *C. cornutus*; Contreras-Ramos 1998) is a dobsonfly found under large cobbles in flowing reaches of streams and rivers in the Western USA and northern Mexico. Motivated by field observations of larvae abandoning a river during a monsoon thunderstorm (C. Olson, personal communication), preliminary rainfall experiments using a prototype of the current experimental setup were conducted with 40 larvae from Oak Creek near Sedona (Coconino Co., AZ) in early June of 2001. Three size classes were present, possibly indicating the presence of first-, second-, and third-year larvae. These experiments found a response rate of nearly 50%, but results were inconclusive since no controls were used, replication was low (three trials), and larvae showed signs of oxygen stress.

To repeat these experiments, we collected ten larvae (all size classes) from Middle Fork Cave Creek, Chiricahua Mountains (Cochise Co., AZ) on 13 July 2006. Five small cobbles (ca. 10-cm diameter) were submerged in each tank to provide cover. Unlike the other taxa we investigated, *C. texanus* larvae use gills rather than surface air for respiration, so we placed an airstone in each tank to ensure adequate oxygenation. Treatment and control tanks contained from three to five larvae over n=6 trials. *C. texanus* behavior was qualitatively different from the other taxa (larvae moved

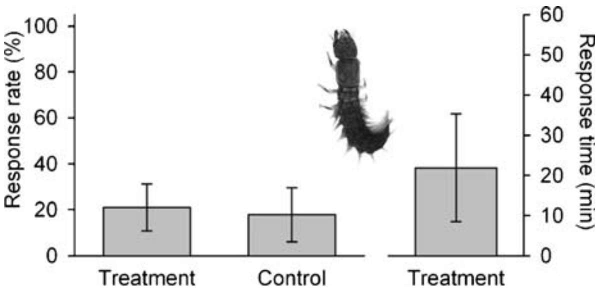

Fig. 5 Rainfall experiment results for the dobsonfly *Corydalus texanus*. Response rate did not differ significantly between treatment and control.

laterally rather than vertically after exiting the water) so we counted all individuals that exited the water as responders.

During rainfall trials, larvae in the treatment tanks, and to some degree the control tanks, became very active by crawling around the tank edges. In some instances larvae remained several centimeters out of the water, not moving, for many minutes at a time, particularly in the treatment tanks where splashing water kept the arena walls damp. All three size classes were observed leaving the water. Antagonistic encounters between larvae were noted, although none resulted in injury (larvae were cannibalized in holding tanks, however). No significant difference in response rate was observed between treatment and control (Fig. 5; Wilcoxon signed-ranks test, $n=6$, $P\leq0.924$).

Conclusions

Our experiments found conclusive evidence for rainfall response behavior in two of the seven taxa examined. Both *Curicta pronotata* and *Aquarius remigis* responded reliably to rainfall cues in such a way that they would likely avoid flash floods. Gerrid water striders experience loss rates of 70% from flash floods, which is lower than veliid water striders (100% loss) but not nearly as low as the giant waterbug *Abedus herberti* (14% loss) which uses RRB to avoid floods (Lytle 2000). No data on flood survival are available for *C. pronotata*, but our results would predict a loss rate substantially lower than the high rates (near 100%) observed for some taxa. Along with the belostomatids *A. herberti* and *Lethocerus medius*, there are now four clear examples of rainfall cues being used for flood escape, all of them Hemiptera.

The fact that we found RRB in *C. pronotata* but not in *Ranatra quadradentata* has implications for the phylogenetic origins of RRB. Qualitatively, the response of *C. pronotata* was similar to behavior observed in belostomatids which inhabit the same streams: individuals respond after some specific duration of rainfall, exit the stream by climbing vertically, and continue crawling so long as light rainfall contacts the dorsum. These behavioral components typify RRB throughout the Belostomatidae and provide evidence that RRB is ancestral to the entire family (Lytle and Smith 2004). It is possible that *C. pronotata* shares RRB with the belostomatids via common ancestry, since the sister-group relationship of nepids and belostomatids is strongly supported (Mahner 1993). *R. quadridentata* gave inconclusive evidence for RRB, however, since only a single individual responded in experiments. If future experiments provide more conclusive evidence for RRB in *Ranatra*, this would suggest that RRB might be basal to the entire Nepoidea (Belostomatidae + Nepidae).

Ambrysus woodburyi showed no evidence of RRB as observed in other taxa, but individuals did move underneath rock substrates during rainfall trials. Thus, it is possible that this species seeks shelter from floods within the stream channel. Although it is hard to imagine individuals surviving an actual flash flood, where there is often scouring of substrate down to bedrock, naucorids are generally good swimmers and may be able to locate instream refugia or slower areas in stream margins that are less prone to bed scouring (Sites and Willig 1991; Herrmann et al. 1993).

Our preliminary observations of the coleopterans *Rhantus atricolor* and *Gyrinus plicifer* suggest that they may rely on other cues associated with monsoon thunderstorms, such as drops in barometric pressure or reductions in light intensity. It is interesting that *R. atricolor* flight coincided with occurrence of actual thunderstorms, and that only individuals in control tanks responded with flight. It is possible that individuals in the control tank were able to sense lowered barometric pressure (or some other thunderstorm cue) while at the surface replenishing air stores, and that treatment individuals were not able to do this because of water turbulence. Our observations of *G. plicifer* also suggest that rainfall cues were not sufficient to allow flood escape, since individuals flew from holding tanks long after the experiments were finished. These flights may have had nothing to do with flood escape (unsatisfactory conditions in holding tanks, for example). In any case our experiments were not conclusive concerning these taxa, and further study of RRB in Coleoptera is needed.

Experiments with *Corydalus texanus* larvae found that individuals are certainly capable of leaving the water for at least short distances, but that rainfall is not always required to induce this behavior. Despite the addition of large cobbles and oxygenation to our holding tanks and experimental tanks, larvae were active and aggressive during most experiments, and cannibalism occurred in the holding tanks (even with only two to three individuals per tank). Thus, our experimental conditions may not have provided an adequate setting for natural behaviors to take place, and it is possible that some of the responses observed were due to inter-individual conflict rather than rainfall cues. Our observations did reveal the potential for flood escape in this taxon, however. Larvae were quite comfortable out of the water, especially in damp areas receiving spray from the artificial rainfall. Other *Corydalus* species are able to persist terrestrially for weeks at a time by breathing through spiracles (Contreras-Ramos 1998). It is not difficult to imagine *C. texanus* larvae moving actively on land that is saturated with water from heavy rainstorms, thereby avoiding flash floods. Megaloptera also pupate on land, so it is conceivable that rainfall might be a cue for third-year larvae to leave the water for pupation. A testable prediction arising from this hypothesis is that third-year larvae that respond to rainfall will use this as a cue to escape floods and begin pupation, while first- and second-year larvae leave and then return to the stream (flood escape only). The fact that most *C. texanus* adults fly during June and July in the USA (Contreras-Ramos 1998) supports this hypothesis, because this corresponds to the first part of the rainy monsoon season in the Southwestern deserts of the USA.

Other studies have found strong differences in RRB among genetically isolated populations of the same species. In the giant water bug *Abedus herberti*, populations from catchments where floods and rainfall are not well-correlated (small catchments where floods are rare, or large catchments where distant storms produce floods) respond very poorly to rainfall (Lytle et al. 2007 in review). In this study, all individuals came from midsized watersheds (10–20 km^2) where rainfall is known to be a robust predictor of floods. Thus, it is unlikely that the lack of response to rainfall cues we observed in some taxa is simply a local, population-level phenomena.

The prevalence of taxa that use rainfall cues for flood avoidance has implications for river management as well. A number of projects have used floods from dam releases to manage downstream habitats, with the intent of enhancing habitat for flood-dependent plants and animals (Patten et al. 2001; Shafroth and Beauchamp

2006). Because dam releases will often occur without prior rainfall cues, taxa that could use rainfall cues to avoid rainfall-generated floods might suffer excess mortality from artificial floods, which occur without warning.

In conclusion, our study adds to evidence from previous reports that rainfall cues are an important mechanism for avoiding flash floods in desert streams. Along with life-history and morphological adaptations, these behavioral adaptations may be important for maintaining high species diversity in flood-disturbed environments.

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