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Use of Rainfall Cues by *Abedus herberti* (Hemiptera: Belostomatidae): A Mechanism for Avoiding Flash Floods

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Unlike most aquatic invertebrate taxa in desert streams, adults and juveniles of the giant water bug Abedus herberti *Hidalgo experience low mortality from flash floods (<15%, as opposed to >90%). One explanation is that* A. herberti *use periods of torrential rainfall (>15 cm · hr^{-1}) that often precede flash floods as a cue to abandon streams. "Stream abandonment behavior" consisted of exiting the stream after some threshold duration of torrential rainfall (8.0 min for adults, 29 min for juveniles), moving in a negatively geotactic direction away from the stream, and stopping in a sheltered area away from the active stream channel. Individuals crawled as far as 23 m from the stream, but returned within 24 h. Experiments with simulated rainfall demonstrated that the behavioral cue for stream abandonment behavior is probably related to the impact of rain on the stream surface, and not to other chemical or physical cues associated with inputs of rainwater (i.e., changes in pH, ion concentrations, water temperature, turbidity, or discharge) or approaching thunderstorms (i.e., pressure drops, thunder, lightning, or cloud cover). These other cues may play an auxiliary role in the behavior, however. Stream abandonment behavior can only account for part of the high survival rates observed for* A. herberti *during flash floods, since less than a third of observed individuals responded to either natural or simulated rainfall.*

KEY WORDS: rainfall cues; flooding; disturbance; flash floods; Belostomatidae; *Abedus herberti*.

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INTRODUCTION

Rainfall is used as a cue by many organisms, both terrestrial and aquatic, to initiate specific behaviors or life-history changes. In the deserts of southwestern North America, rainfall during the summer monsoon season brings about new resources and habitats, and many organisms respond to the first rains by breaking dormancy to feed and reproduce. For example, spadefoot toads use the vibrations produced by rain hitting the ground as a cue to crawl to the surface and breed in temporary pools (Dimmitt and Ruibal, 1980). Several ant species respond to rainfall by producing swarms of dispersing winged reproductives (Hölldobler and Wilson, 1990). Diapausing aquatic crustaceans begin feeding and growing as basins and temporary pools fill with water (Pennak, 1953). A large number of plants, shrubs, and trees respond to moisture in the soil with growth in somatic or reproductive tissues (Dick-Peddie, 1993). In each case, rainfall is a useful cue because it is highly correlated with the arrival of favorable habitats or resources, and because it occurs before or concurrent with these environmental enhancements.

For stream organisms, rainfall may also produce negative consequences in the form of flooding. The flash floods that occur in desert streams can be especially sudden and devastating, and numerous researchers have quantified their impact on fish (John, 1963, 1964; Meffe, 1984), invertebrates (Gray, 1981; Gray and Fisher, 1981; Fisher *et al.*, 1982; Molles, 1985; Grimm and Fisher, 1989; Boulton *et al.*, 1992; Stanley *et al.*, 1994), and algae (Fisher *et al.*, 1982; Grimm and Fisher, 1989; Valett *et al.*, 1994). Almost all of these taxa experience significant mortality, and recovery following a flood can involve both rapid population growth within the stream and recolonization from outside the affected area (Williams and Hynes, 1976; Fisher, 1983).

Not all organisms, are negatively impacted during flash floods. Low mortality has been observed in some invertebrate taxa, but the reason for this is not well understood. For example Gray (1981) noted that over the course of nine flash floods spanning 2 years, the average reduction in numbers of both *Abedus herberti* Hidalgo (Hemiptera: Belostomatidae) and adult dytiscid beetles (Coleoptera: Adephaga) in a Sonoran Desert stream was 0%, while the average over all invertebrate taxa was 86%. Mortality rates were similar for a montane Chihuahuan Desert stream, where the loss of *A. herberti* from one flash flood amounted to 15%, while the average across all taxa was greater than 90% (D. A. Lytle, unpublished data). Belostomatids, as well as other aquatic Hemiptera and Coleoptera that possess open spiracles, are capable of abandoning streams to avoid the effects of progressive habitat deterioration such as drying (Hungerford, 1919; Williams and Hynes, 1976; Cushing and Gaines, 1989; Hutchinson, 1993), and it has been suggested that these taxa might also use terrestrial refugia to escape floods (Williams and Hynes, 1976; Gray, 1981). Thus

far, the mechanisms by which these taxa anticipate sudden flash floods have remained obscure.

Stream Abandonment Behavior

An initial field observation suggested that *A. herberti* are capable of abandoning streams during periods of torrential rainfall that often precede flash floods. During an afternoon thunderstorm at the beginning of the monsoon season in July of 1995 (see Study Site, below), approximately 15 adult and juvenile *A. herberti* were observed abandoning the North Fork of Cave Creek following 5 to 10 min of torrential rainfall (estimated at 5 to 20 cm · hr^{-1}). Individuals crawled out of the active floodplain and into the adjacent riparian areas. During the downpour the stream became turbid with runoff, but discharge did not increase noticeably above baseflow. A flash flood that scoured the stream bottom occurred several hours later.

All individuals traveled perpendicular to the stream channel; none were observed leaving the pool in an upstream or downstream direction. All were negatively geotactic, climbing directly up the 0.5-m near-vertical streambanks. Upon exiting the stream channel and entering the riparian areas individuals continued to travel along the path of highest elevation gain, which resulted in continued movement away from the stream channel. Although none were followed to their final destination, numerous adult and juvenile *A. herberti* were present in the stream 2 days after the flash flood, while nearly all other taxa of aquatic insects had been removed by the flood.

Stream abandonment behavior is clearly one potential explanation for the low mortality rates observed after flash floods in other studies of *A. herberti*. This study elaborates on the initial field observations by reporting data concerning the amount of rainfall necessary to initiate stream abandonment, the nature of the cues that cause stream abandonment, and some of the ecological consequences of this behavior.

METHODS

Abedus herberti

While most belostomatids are pond or lake dwellers (Lauck and Menke, 1961), *A. herberti* are year-round inhabitant of montane streams in the Chihuahuan Desert of the southwestern United States and northern México. Since they brood throughout the year (Smith, 1974), all life stages (five instars, adults, and eggs brooded on the backs of males) are present in streams at any given time. Individual *A. herberti* are known to live for up to a year (Smith, 1974).

Study Site

All observations and experiments were conducted during July of 1997 on the North Fork of Cave Creek and East Turkey Creek, in the Chiricahua Mountains of southeastern Arizona (31.7°N, 109.2°W). Both study sites are situated between 1950 and 2000 m in elevation, where the streams are permanent, spring-fed, first-order drainages. The streams were at baseflow during the study (<1 L $\cdot$ min^{-1}), forming a series of pools. The pools ranged in area from 0.3 to 9 m^2, and their maximum depths were all under 50 cm. Stream substrate consisted of bedrock overlain with cobbles, boulders, and leaf detritus. During the monsoon season of mid-June through August, these streams are subject to intense flash floods capable of scouring the stream bottom (John, 1963, 1964), but flash foods are rare during other times of the year. Because no thunderstorms had occurred for almost a year (August 1996) prior to this study, it is probable that most of the study animals, if not all, were naive to torrential rainfall.

Simulated Rainfall Experiments

To test the hypothesis that the direct impact of rainfall on the stream (in the absence of chemical cues from rainwater or physical cues from an approaching storm) is sufficient for the initiation of stream abandonment, monsoon rainfall was simulated by spraying stream water onto natural stream pools containing *A. herberti*. To ensure the absence of storm-related cues, all trials (n = 8) were performed on East Turkey Creek pools during clear, sunny days. Streamwater was drawn from a downstream pool using a Homelite AP520 pump (600 L $\cdot$ min^{-1}) and sprayed into the air with a 5.13-cm firehose fitted with an adjustable spray valve. A steady torrential rain was allowed to fall on a single pool until all individuals had abandoned the stream, or for 40 min. The torrential rain was broadcast over an area of approximately 4 m^2 at an intensity ranging from 12 to 24 cm $\cdot$ h^{-1}; preliminary trials had shown that simulated rainfall of a lower intensity produced no behavioral response. The treatment did not affect water depth since pools were already filled to overflowing, and the temperature is unlikely to have been altered since water was sprayed into the air for only a matter of seconds. For each trial, individuals that abandoned the stream and demonstrated a negatively geotactic response for at least 0.5 m were collected, counted, and categorized to life stage according to Smith (1974). The threshold duration of torrential rainfall required to initiate this behavior was recorded. Adults and instars III through V that remained in the stream were then collected and counted.

To determine the maximum distance adult individuals traveled away from the stream, focal individuals (n = 3) were followed for the entire duration of the stream abandonment behavior. This was accomplished by keeping individuals under a light rainfall as they moved away from the stream, either remotely using

a light spray from the hose or by hand using a 2-gal water bucket with numerous punctures on the bottom. Distance traveled from the stream was recorded.

Nonparametric statistics were used for analysis since the variables of interest were not normally distributed, even after transformations. Observations of threshold duration of torrential rainfall for each individual within a simulated rainfall trial were treated as independent. All error values associated with means were calculated as standard errors.

Tagging

To determine whether *A. herberti* abandon and then return to the stream after torrential rainfall, all adults in one 1.5 × 2.5-m pool in North Fork Cave Creek were tagged and then censused at the onset of the monsoon season and, again, after a natural rainfall event. Tagging was done initially with enamel paint (Testor's) and later with numbered tags (2 × 6 mm) made of Xerox Never Tear plastic paper following the methodology of Freilich (1989). Tagged individuals were counted as they emerged from the pool during torrential rainfall. The pool and adjacent areas (30 m upstream and downstream) were censused 24 h later for returned individuals.

RESULTS

Stream Abandonment Behavior

The qualitative characteristics of stream abandonment behavior were similar for individuals exposed to either natural or simulated rainfall. Individuals that responded required 7 to 45 min of torrential rain of an intensity greater than 1 $cm \cdot h^{-1}$ to initiate the behavior. Upon leaving the stream, individuals consistently showed negative geotaxis as they crawled away from the stream. Travel was maintained in a direction perpendicular to the stream channel. Individuals continued to crawl so long as a light rainfall was kept on them and paused if this stimulus was removed. If the light rainfall was restored, they resumed movement. Movement was terminated when individuals reached a sheltered area that protected them from direct rainfall.

Simulated Rainfall Experiments

Of the eight simulated rainfall trials performed on East Turkey Creek pools containing *A. herberti*, only three produced any stream abandonment response. Within those three trials, a total of 11 (34%) *A. herberti* responded to the simulated rainfall by leaving the stream, while 21 (66%) remained in the stream (Table I). Only adults and instars III and V responded, although all life stages (including encumbered males and instars I, II, and IV) were present in the stream.

Table I. Response of *A. herberti* to Natural and Simulated Rainfall

Life stage	Rainfall type	Intensity ($cm \cdot h^{-1}$)	Number present	Percentage response	Threshold duration (min)
Adult	Natural	5–20	21	29	<8
Adult	Simulated	12–24	12	25	8.0 ± 0.58
Instar V	Simulated	12–24	10	60	28 ± 5.6
Instar IV	Simulated	12–24	6	0	—
Instar III	Simulated	12–24	4	50	30.8 ± 1.75
Instar II	Simulated	12–24	Present	0	—
Instar I	Simulated	12–24	Present	0	—

Adults that responded ($n = 3$) required an average threshold duration of 8.0 min of torrential rainfall, which is significantly less than the 29 min required by $n = 8$ juveniles (Fig. 1; Mann–Whitney U test, $U = 0.50$, $N_1 = 3$, $N_2 = 8$, $P < 0.02$). Three of the five trials that produced no response were performed under exceptionally hot and sunny conditions, which may have inhibited stream abandonment.

Three focal individuals, all unencumbered *A. herberti* adults, crawled total distances of 1.5, 3.0, and 23.5 m away from the stream. For each, negatively geotactic travel at a rate of about 1.5 $m \cdot min^{-1}$ was maintained perpendicular

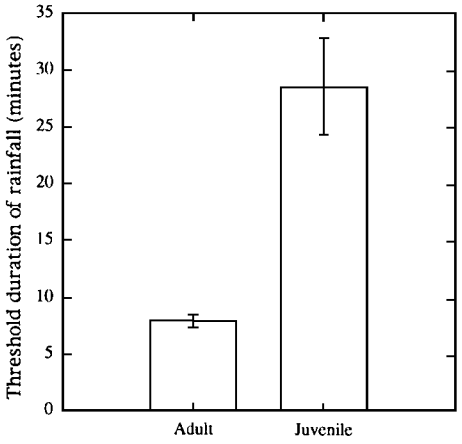

Fig. 1. Threshold duration of simulated rainfall (minutes at 5–24 $cm \cdot h^{-1}$) required to initiate stream abandonment behavior in all adults ($n = 3$) and juveniles ($n = 8$) that exhibited the behavior: Juveniles initiated the behavior significantly later than adults (Mann–Whitney U test: $U = 0.50$, $N_1 = 3$, $N_2 = 8$, $P < 0.02$).

to the stream channel as long as a light rain, from a hand-held bucket, contacted the insect. Momentary removal of this rainfall caused the insect to pause; return of the rainfall reinitiated movement. Individuals were observed to climb directly up vertical rock faces as high as 1.5 m. In each case, travel was terminated when the insect had moved to a spot where it was sheltered from direct rainfall, e.g., a rock ledge, underneath a knot 0.5 m up the trunk of an Arizona white oak (*Quercus arizonica*), and under leaves 1 m high on the trunk of a yucca (*Yucca* sp.). Each of those shelters was situated outside of the active stream channel and, not likely to be disturbed during a flash flood. Water poured into these refugia did not reinitiate movement. Although monitored for nearly an hour, none of these insects were observed to move any farther.

Tagging

Although several thundershowers (<1 cm $\cdot$ h^{-1}) in the preceding weeks had failed to cause stream abandonment, 8 min of hail and torrential rain (5–20 cm $\cdot$ h^{-1}) on 28 July caused at least 6 (29%) tagged adults (3 females, 2 egg-encumbered males, 1 unencumbered male) of 21 present in a North Fork Cave Creek pool to travel 0.5 to 3 m away from the stream (Table I). Individuals stopped moving when the rain slowed, and one (an encumbered male) escaped back to the stream when the observer approached within 2 m. The rain event did not cause a flash flood, and 5 of the 6 tagged individuals (83%) were recovered in the same focal pool the following day, along with 13 others (8 marked, 5 unmarked). The sixth individual that abandoned the stream could not be found within 30 m of similar habitat upstream or downstream of the focal pool.

DISCUSSION

Stream abandonment behavior may enable *A. herberti* to escape the consequences of flash floods in desert streams, since individuals moved into protected areas well away from the portion of the stream channel typically impacted by flooding. The negatively geotactic movement and the direction of travel away from the stream could allow escape from a flood even in streams with steep canyon walls; the clawed tarsi of *A. herberti* allowed individuals to climb vertical rock faces even in torrential rain.

The response to the simulated rainfall experiments indicates that rainfall alone is sufficient for initiating stream abandonment in *A. herberti*. Cues associated with inputs of rainwater (changes in pH, ion concentrations, water temperature, turbidity, and discharge) or approaching storms (pressure drops, thunder, lightning, cloud cover) were not necessary to initiate stream abandonment, although these cues may affect stream abandonment behavior in other ways. For example, shading from cloud cover may play a role in initiation of the behavior,

since any response to simulated rainfall was inhibited on bright, sunny days. In any case, of the trials where *A. herberti* did respond to simulated rainfall, the percentage response was similar to that of a natural rainfall event; 34 and 29%, respectively.

Stream abandonment behavior in response to rainfall cues, does not account for the high survival rates observed in other studies of *A. herberti* (85–100%), since less than one-third of the individuals in this study responded to either simulated or natural rainfall. It is conceivable that, unlike most other invertebrates, *A. herberti* is capable of surviving flash floods while remaining in the stream. Some stream invertebrates are known to utilize in-stream flow refugia (microhabitats within the stream that are protected from flooding) and dead zones (peripheral areas such as eddies and reverse flows associated with pools and bends) in order to survive floods (Lancaster and Hildrew, 1993). Since over 90% of the stream substrate may be moved during a typical flash flood (Lytle, unpublished data), in-stream flow refugia are rare or nonexistent in these desert streams. Even if flow refugia were available, individuals would need to surface frequently to replenish their subhemelytral airstores, and it is unlikely that individuals could remain in refugia for the several hours required to outlast a flood. Similarly, dead zones are uncommon in these canyon streams because of the highly constrained channel morphology. Thus, it is unlikely that the high survival rates are accounted for by in-stream survivorship, which suggests that some form of stream abandonment it utilized.

Individuals could respond to cues provided by the arriving flood itself. Although flash floods typically occur as a sudden pulse of water and suspended substrates, the arrival of this pulse is heralded by the sound of a "pounding mill of boulders" colliding in the stream channel (John, 1964). *A. herberti* could conceivably use this acoustic cue to abandon streams. The cue would only allow individuals a matter of seconds to climb out of the stream channel, however. This is insufficient time for individuals to crawl free of the active channel, which takes from 1 to 2 min at the measured crawling speed of 1.5 $m \cdot min^{-1}$. Longer periods of rainfall, or heavier rainfall, could also produce stream abandonment in a higher fraction of the population. A maximum rainfall of 24 $cm \cdot h^{-1}$ was used in this study, but downpours in excess of this are known to occur in the region. If some individuals have a higher response threshold, more intense rainfall should cause a greater number of individuals to abandon the stream. Longer periods of rainfall, or more intense rainfall, may also increase turbidity in the water, providing yet another cue. It remains to be determined which of these potential cues, if any, enhance stream abandonment behavior.

While both the simulated rainfall experiments and the field observations were made during daytime, most flash floods in southeastern Arizona actually occur in the late evening or at night. This occurs because of the influence of thermal heating on the production of convective thunderstorms, which is most

pronounced in the late afternoon. Data from a gauging station in Douglas, AZ (75 km SW of the study site), indicate that most monsoon precipitation occurs after 1800 h, suggesting that most flash floods occur at dusk or after nightfall (Sellers and Hill, 1974). It is possible that *A. herberti* are more likely to abandon streams under the cover of darkness, when predation and the risk of desiccation (see below) are less of a concern. Observations and experiments performed at night would certainly answer this question.

Although stream abandonment is a novel behavior that must be unique at least to stream-dwelling insects, the component behaviors of which it is comprised occur more generally. Since rainfall alone was sufficient to initiate stream abandonment in at least some individuals, it is likely that the cue itself is a hydrodynamic one, caused by the impact of water droplets on the stream surface. Many aquatic and semiaquatic insects are sensitive to transverse waves on the water surface (Andersen, 1982) and to longitudinal waves within the water (Aiken, 1985). Adult *A. herberti* are capable of responding to surface and subsurface waves produced during courtship behavior (Smith, 1979, 1997) and, should be sensitive to waves or vibrations produced by falling rain. The use of negative geotaxis for orientation is not unusual either, since the capacity for positive and negative geotaxis is probably common to all freely moving insects (Jander, 1963). The perpendicular travel away from the stream channel that was consistently observed may simply be an epiphenomenon of negative geotaxis, since the steepest topography in the study streams was located on the banks.

Not all life stages of *A. herberti* responded equally to rainfall. It is not clear why no instar IV individuals abandoned the stream, since both instars III and V showed this behavior. This may be an artifact of low sample size ($n = 6$ instar IV tested). While adults treated with either natural or simulated rainfall required a threshold duration of torrential rainfall of about 8 min, juveniles of instars III through V abandoned the stream only after more than three times this amount of torrential rain (Fig. 1). Adults may be better suited to the terrestrial environment than juveniles and, quicker to abandon the stream. Adults are often observed out of the water, since males must occasionally expose eggs to the air for them to remain viable (Smith, 1976), and adults are occasionally seen drying themselves on sun-exposed rocks near the stream (Smith, 1997; D. A. Lytle, personal observation). Juveniles are never seen out of the water, except during stream abandonment behavior. The cuticle of adults is also more rigid than the cuticle of juveniles, as evidenced by the shriveling of pinned juvenile specimens but not adults. This difference could translate into unequal abilities to avoid dessication. If juveniles are not as physiologically equipped for terrestrial life as are adults, then the large threshold duration of torrential rainfall required by the juveniles may represent a trade-off between flood avoidance and the hazards of moving to a nonaquatic environment. This is especially true of instars I and II, which, though frequently seen in the streams, were never observed to

leave the water. Their small body sizes [8- and 11-mm body length, respectively (Smith, 1974)] make them especially prone to dessication, in addition to being susceptible to the heavy runoff and hailstones produced by thunderstorms.

Rainfall is not a perfect cue for flash floods, as evidenced by the abandonment of a stream that did not flood. It is not known what the consequences are for individuals that abandon streams unnecessarily, but *A. herberti* is known to be preyed upon by terrestrial mammals and birds (R. L. Smith, personal communication). In some circumstances the rainfall cue may also fail to warn belostomatids of a flood. Rainfall from the convective thunderstorms of the summer monsoon season can be extremely localized, and it is possible for a downstream reach of stream to experience a flash flood caused entirely by precipitation several kilometers distant (Sellers and Hill, 1974).

Although stream abandonment behavior explains, at least in part, why flood-related mortality is low for *A. herberti*, it remains to be seen if a similar use of rainfall cues accounts for the low mortality observed by Gray (1981) for adult dytiscid beetles. It is also possible that similar cues are utilized by other aquatic and semiaquatic Hemiptera that inhabit flood-prone streams, since all of those taxa are capable of moving to terrestrial environments for at least short periods of time. Few data are available on flood-related mortalities in those Hemipteran taxa, however. Stout (1982) reported decreases in postflood recapture rates for marked naucorids in a Costa Rican stream, but those decreases may have been caused by lowered sampling efficiency in the flood stream.

Besides facilitating the survival of flash floods, stream abandonment behavior may have other ramifications for populations of *A. herberti*. Although flight is common in the Belostomatidae, it is unusual in the genus *Abedus* (Menke, 1977). With the exception of Gray and Fisher's (1981) report of flight in *A. herberti*, where it is possible that *Lethocerus medius* was actually observed (L. J. Gray, *in. litt.*, 1997), flight has never been documented in *A. herberti*. It is possible that the apparently flightless *A. herberti* uses periods of stream abandonment to move upstream within a drainage or to colonize adjacent drainages. The negatively geotactic movement of individuals could result in a net-upstream diplacement of a population during stream abandonment or even the migration of individuals over low ridges that separate drainages near their headwaters. The fact that egg-encumbered males are capable of abandoning streams suggests that new habitats can be colonized by a single migrating individual. Periods of rainfall also provide an opportunity for encumbered males to disperse without risking the dessication of their eggs (Smith, 1976).

Rainfall cues may play a different role in those belostomatid taxa that do have the ability to fly. A correlation between rainfall and the dispersal of aerial adults has been reported for 12 belostomatid species, none of which live in habitats prone to flash floods (Bowden, 1964; Cullen, 1969; Robertson, 1976). It remains to be seen if those taxa use rainfall as a cue for dispersal and, if so,

whether the behavior is similar to the stream abandonment behavior observed in *A. herberti*.

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