DROUGHT-ESCAPE BEHAVIORS OF AQUATIC INSECTS MAY BE ADAPTATIONS TO HIGHLY VARIABLE FLOW REGIMES CHARACTERISTIC OF DESERT RIVERS

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Abstract—We document how two species of desert aquatic insects use positive rheotaxis to escape drought in desert rivers. We observed ca. 3,600 adults of the long-toed water beetle *Postelichus immsi* (Coleoptera: Dryopidae) crawling upstream concurrent with upstream recession of surface water in the Santa Maria River, La Paz and Mohave counties, Arizona. At the same time, we observed larvae of the gray sanddragon *Progomphus borealis* (Odonata: Gomphidae) burrowing and swimming upstream in large densities (690 larvae/m^2). Both taxa moved with sufficient speed to arrive at perennial reaches of the river before being overtaken by drought.

Resumen—Se documenta cómo dos especies de insectos acuáticos de zonas desérticas usan el reotaxis positivo para escapar a la sequía. Se observaron alrededor de 3,600 adultos del escarabajo *Postelichus immsi* (Coleoptera: Dryopidae) arrastrándose río arriba mientras que el agua superficial se retrasaba en el río Santa María en los condados de La Paz y Mohave, Arizona. Paralelamente se observaron larvas de

Progomphus borealis (Odonata: Gomphidae) de gran densidad (690 larvas/m^2) desplazándose río arriba por vías subterráneas y nadando. Ambas especies viajaron con suficiente velocidad para alcanzar los tramos perennes del río, evadiendo la sequía.

The dynamic hydrology of desert streams provides a unique opportunity to observe how organisms evolve strategies for surviving floods and droughts. While several examples of behaviors to escape floods have been documented (Meffe, 1984; Lytle and Smith, 2004; Lytle and White, 2007), less is known about behavior to escape drought. This study documents behaviors that allow desert aquatic insects to escape drought by moving to perennial reaches of a river.

On 10 April 2007, we observed aquatic insects in a drying reach of the Santa Maria River, La Paz and Mohave counties, Arizona (34°18′3.8″N, 113°25′27.5″W). About 1500 h on a clear day (high of 31°C recorded at Parker, Arizona), the lower end of a 3–4-km perennial reach was receding upstream at a rate of 0.16 cm/s, presumably due to high evapotranspirative demand from riparian plants, including *Salix gooddingii* (Goodding willow), *Populus fremontii* (Fremont cottonwood), and *Tamarix ramosissima* (salt cedar). Velocity of flow immediately above the recession point was 9.9 cm/s (95% C.I. ± 1.0 cm/s; $n = 5$ observations), whereas downstream of this point the river became hyporheic in deep sand.

Beginning 11 m upstream of the recession point, we observed thousands of adult long-toed water beetles *Postelichus immsi* (Coleoptera: Dryopidae) crawling upstream in a 37 m-long column along the shallow river margins (Fig. 1). We counted an average of 97 individuals/m of stream (±34 individuals; $n = 12$ counts), giving an estimate of 3,600 individuals moving upstream. All showed positive rheotaxis, in that crawling always was oriented in the upstream direction. Individuals moved at a rate of 0.70 cm/s (±0.03 cm/s; $n = 12$), which was four times faster than rate of stream recession, suggesting that the behavior would allow escape from local drought (a deeper, more permanent river reach was 80 m upstream from the recession point). Most individuals traveled along the stream margins in water <1 cm deep, possibly to avoid the faster current. Individuals and small groups (typically 2–3 individuals) occasionally became dislodged by the current and tumbled some distance downstream. The moving column had a fairly abrupt beginning and end, with density of individuals being somewhat uniform along the entire length. Individuals observed immediately upstream of the column showed no evidence of positive rheotaxis but were foraging actively in all directions. We did not observe whether these upstream individuals were eventually incorporated into the column. *Postelichus immsi* occurs on debris and under rocks in streams from western Texas to California (Brown, 1972), and can be the most abundant insect in some desert streams (Evans and Hogue, 2006).

In tandem with the dryopid beetles, we observed larvae of the gray sanddragon *Progomphus borealis* (Odonata: Gomphidae) moving upstream in large numbers (690 larvae/m^2). Sanddragon larvae burrowed to just underneath the surface of the substrate, so most larvae remained hidden beneath sand as they moved. However, numerous burrows left over from this movement were apparent after the water receded (Fig. 1). We observed larvae moving upstream at 0.17 cm/s (±0.06 cm/s; $n = 6$). Although this burrowing rate was slightly greater than the rate of stream recession of 0.16 cm/s, larvae occasionally left the substrate to swim actively in short bursts of ca. 10 cm. This behavior increased their average speed and allowed escape from the recession point. *Progomphus borealis* occurs in sandy shallows of rivers and streams throughout the arid western regions of the United States and Mexico (Needham et al., 2000).

Other taxa that were present in small numbers, so that we cannot be sure if they were systematically moving upstream, include larvae of the giant water bug *Abedus herberti* (Hemiptera: Belostomatidae), adults of *Berosus* (Coleoptera: Hydrophilidae), tadpoles of the canyon treefrog *Hyla arenicolor* (Hylidae), longfin dace *Rhinichthys chrysogaster* (Cypriniformes: Cyprinidae), and mosquitofish *Gambusia affinis* (Cyprinodontiformes: Poecilidae). Larvae of the American rubyspot damselfly *Hetaerina americana* (Odonata: Calopterygidae) were not observed moving upstream but were seen stranded in drying areas, often underneath mats of algae where they might be protected from desiccation.

Some taxa used positive rheotaxis so long as sufficient water current was available. *Physa* snails

FIG. 1—Left) column of long-toed water beetles (*Postelichus immsi*) moving upstream to avoid drought. Recession point is at top of figure. Burrows of gray sanddragons (*Progomphus borealis*) also are visible near the 11.5-cm tall vial. Right) closeup of *Postelichus* crawling upstream (flow travels from bottom to top of figure).

(Pulmonata: Physidae) in the flowing active channel exhibited positive rheotaxis at a rate of 0.12 cm/s ($\pm$0.06 cm/s; $n = 12$ individuals), but individuals in isolated pools with no flow remained beneath algae mats. Soldier fly larvae (Diptera: Stratiomyidae) and adult hydrophilid beetles exhibited this as well. The directional cue provided by flowing water apparently is necessary for upstream movement, because we never observed individuals of any taxon moving systematically upstream in still-water reaches. This is congruent with the observation of Gray and Fisher (1981) that post-flood, upstream movement of aquatic insects generally is greater during periods of higher discharge, although they noted little upstream movement of either *P. immsi* (=*Helichus immsi*; Nelson, 1989) or *P. borealis*.

The proximate cues used to initiate the observed behavior to escape drought by *P. immsi* and *P. borealis* are not known. Several studies have recorded synchronous emergence of aquatic beetles en masse from drying desert ponds (Zimmerman, 1959; Smith, 1973; Kingsley, 1985). In the dytiscid beetles *Rhantus gutticollis*, *R. binotatis*, and *Eretes sticticus*, mass emigration was preceded by loud, sustained vocalization, which raises the question of whether individuals can communicate a signal to emigrate (Smith, 1973; Kingsley, 1985). Although we did not notice vocalizations during our observations of *Postelichus* and *Progomphus*, underwater vocalization remains a possibility. In the case of *Rhantus* studied by Smith (1973), sound production and emigration were associated with elevated temperatures, high density of individuals, and absence of suitable bottom substrates; i.e., proximate cues associated with drying ponds. During our observations, both rate of flow and water temperature were similar above and below the column, so there apparently was no physical cue to signal that the recession point was approaching. Increased density of conspecifics remains one possible cue, such that individuals are recruited into the dense column as it moves upstream. It also is possible that individuals caught at the drying end of the stream become activated to move upstream. If the latter is occurring, then individuals at the front of the column should have crawled from the furthest distance downstream. Both of these hypotheses are testable by appropriate mark-release of individuals and careful observation in the field.

Drought in desert rivers occurs at multiple timescales: daily, as reaches dry locally due to evapotranspiration of riparian plants; seasonally, as the water table drops due to low rainfall; and episodically following floods, as river margins contract post-flood (Stanley et al., 1997). We have not observed synchronous upstream movement of either taxon during routine benthic sampling or during snorkeling, so it is likely that the behaviors function as a mechanism for avoidance of drought. However, we observed many of these behaviors as water receded following a 28.3 m^3/s experimental flood on the neighboring Bill Williams River, La Paz and Mohave counties, Arizona (9–11 April 2007). As lateral side channels dried during recession of the flood, large numbers of *P. borealis* were observed moving upstream to perennial reaches. Thus, many of these drought-escape behaviors could be interpreted more broadly as adaptations to the highly variable flow regimes characteristic of desert rivers and streams.

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