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Examination of the Feeding Behavior of Larval *Tropisternus* (Coleoptera: Hydrophilidae)

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ABSTRACT: Numerous aquatic larval hydrophilid species consume their prey with their heads above the water surface. To determine whether *Tropisternus* sp. exhibit the same behavior, larvae were observed under three conditions: (1) individually with an emergent twig present, (2) in a group with an emergent twig present, and (3) in a group without a twig. All beetles that ate crawled onto the twig and emerged their heads from the water to feed. Several behaviors were observed that do not support some of the hypotheses concerning the adaptive significance of this feeding behavior.

As larvae, most water scavenger beetles (Hydrophilidae) are not scavengers at all, but are voracious predators. Aquatic members of this family feed on a wide variety of aquatic animals, including copepods (Zalom and Grigarick, 1980), mosquito larvae (Nielson and Nielson, 1953; Zalom and Grigarick, 1980), snails (Wilson, 1923a; Balduf, 1935; Miller, 1963), and even conspecifics (Wilson, 1923a; Zalom and Grigarick, 1980; Archangelsky and Durand, 1992). Some aquatic taxa exhibit an interesting feeding behavior wherein the beetle captures a prey item and then raises its head, and sometimes its whole body, out of the water to eat (Table 1).

Several hypotheses have been proposed by others concerning the adaptive significance of this feeding behavior: (1) the potency of the preoral digestive fluids transmitted to the prey through external "blood grooves" on the interior margin of the mandibles could be diluted if larval hydrophilids ate in the water (Miller, 1963; Crowson, 1981); (2) consumption of prey items in the water might attract other hydrophilids to the source of haemolymph or disturbance (L. C. Ferrington, University of Kansas, personal communication), and by emerging, hydrophilids may be avoiding competition; (3) because hydrophilid larvae respire through posterior spiracles (Wilson, 1923a; White et al., 1984), going to the water surface to eat may allow them to respire while feeding (Wilson, 1923b; Balfour-Browne, 1958) (however, some species have been observed feeding at the surface with their heads submerged [Wilson, 1923a], which seems to refute this hypothesis); (4) ingestion of liquid food in a fluid environment may simply be impossible. Another plausible hypothesis not previously addressed is: (5) Removing prey from the water may reduce the risk of prey escape. The objectives of this study were to describe the larval feeding behavior of *Tropisternus* sp., and to consider possible explanations for the adaptive significance of this behavior.

MATERIALS AND METHODS: Twelve *Tropisternus* sp. beetle larvae (identified with the key provided

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Table 1. Hydrophiloidea taxa that have been observed feeding with at least their heads emerging from the water surface. The systematic synopsis is based on Hansen's (1991) cladistic analysis of the superfamily.

Taxa	Reference
Family Helophoridae	
Helophorus spp. Fabricius	Richmond, 1920
Family Hydrophilidae	
Subfamily Hydrophilinae	
Tribe Sperchopsini	
Sperchopsis tessellatus Ziegler	Spangler, 1961
Tribe Berosini	
Derallus angustus Sharp	Archangelsky and Durand, 1992
Tribe Hydrophilini	
Subtribe Acidocerina	
Helochares griseus (=*obscurus* Müller)	Balduf, 1935
Subtribe Hydrobiina	
Hydrobius fuscipes L.	Balfour-Browne, 1910
H. niger Zschach	Balduf, 1935
Subtribe Hydrophilina	
Hydrochara caraboides L.	Balfour-Browne, 1958
Hydrophilus caraboides	Balduf, 1935
Hydrous (=Hydrophilus) piceus L.	Balduf, 1935
Hydrous (=Hydrophilus) triangularis Say	Balduf, 1935
Tropisternus glaber Herbst	Wilson, 1923b
T. lateralis Fabricius	Wilson, 1923b; Balduf, 1935
T. mixtus Leconte	Wilson, 1923b

by White et al., 1984) were collected in April, 1994, from emergent vegetation in an Oconee Forest pond, Greene County, Georgia. They were taken to the laboratory, put into individual vials with water, and kept at 9°C for two days prior to experimentation to minimize respiration rates and subsequent mortality. Larvae were also kept under the above conditions between experimental trials. Feeding trials took place in 6.5 cm diameter finger bowls filled with 24°C water. As the beetles floated head down from the water surface, they were offered either live chironomid or culicid larvae with forceps. The feeding behaviors were observed under three different conditions:

Individual feeding with an emergent twig: On day two (day zero was the day of capture), all 12 larvae were individually placed in separate finger bowls, each with an emergent twig, and were offered food. The beetles were removed from the bowls after either the food was completely eaten or they refused the prey after several offers.

Group feeding with an emergent twig: On day seven, the larvae were randomly divided into four groups. Each group was put into a finger bowl with an emergent twig. One of the beetles was then offered food. The beetles were removed from the bowl after either the food was completely eaten or the food remained unmasticated for 15 min.

Group feeding without an emergent twig: On day eight, the beetles were again randomly divided into four groups. Each group was put into a finger bowl without an emergent twig. Larvae fed in the previous day's experiment were not offered food. The beetles were removed from the bowl after the food remained unmasticated for 15 min.

Individual behaviors of each beetle in all treatments were observed and recorded. Their behaviors were then compared within and among treatments.

RESULTS AND DISCUSSION: *Individual feeding with an emergent twig:* Ten of the 12 larvae accepted the prey. All 10 eventually swam to the twig, crawled up it until their heads surfaced, lifted their heads perpendicularly to the water surface, and began chewing the food. The beetles manipulated the prey with their antennae and maxillary palps, continually turning it around as they ate, which is a behavior observed in other preorally digesting Coleoptera (Richmond, 1920; Evans, 1963). This particular feeding behavior has been noted in only a handful of hydrophilid genera (Balfour-Browne, 1910; Balduf, 1935), which may suggest a lack of observation, not necessarily a lack of occurrence. Nonetheless, it would be valuable to know not only the taxa in which this exact behavior occurs but also the taxa that exhibit various degrees of this behavior, as it could possibly prove to be a useful character in phylogenetic analyses of the family.

Group feeding with an emergent twig: In two of the four groups, the feeding behavior was identical between the beetles offered the prey item and the individually fed beetles. The other two groups, however, behaved differently. In one group, the beetle that was offered the food accepted it, yet never ate. It spent most of the time floating at the water surface with the prey clenched in its mandibles. The other two beetles attempted to steal the food from it, both unsuccessfully. At one point the "owner" emerged from the water onto the twig and held its head up as if it were feeding. However, it never masticated the prey. Why did this beetle take the food but not eat? One possible explanation is that it was not hungry but was saving the food for later. In the final group, the beetle that was offered food behaved as predicted. However, another beetle approached the feeding individual on the twig and stole the prey. This observation suggests that emerging from the water to feed does not necessarily eliminate intrafamilial competitive interactions (hypothesis 2, see above).

Group feeding without an emergent twig: None of these beetles masticated the prey. This observation coincides with Balfour-Browne's (1910) observations of *Hydrobius fuscipes* L. Power struggles between the "owner" and the other beetles occurred in three of the four groups, all resulting in the food being dropped (with none being re-handled by any of the beetles). In two of the groups the prey was dropped <1 min and 3.5 min after receipt, and in both cases the prey was dead at the time. This suggests that reducing the chance of prey escape is not a major selective force affecting this feeding behavior (hypothesis 5, see above). The mechanical force of the grasping mandibles seems an unlikely cause of prey mortality. More likely, death resulted from the toxicity of the preoral digestive enzymes. When the beetle's head is submerged, digestive enzymes may become too dilute to effectively digest prey, possibly the reason none ate, yet the enzymes are still apparently lethal.

The small sample sizes used in this experiment preclude firm conclusions regarding why or how this feeding behavior evolved in hydrophilids. These results are important, however, because they may refute two hypotheses regarding the selective advantage of this behavior (hypotheses 2 and 5), thereby suggesting a need for, and providing a focus for future experimentation.

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