POLYMORPHIC LARVAL RETREATS IN THE NET-SPINNING CADDISFLY *MACROSTEMUM CAROLINA (*TRICHOPTERA: HYDROPSYCHIDAE): FORM AND PUTATIVE FUNCTION

GORDON R. PLAGUE AND J VAUN MCARTHUR
Savannah River Ecology Laboratory, University of Georgia,
PO Drawer E, Aiken, SC 29802

Larval net-spinning caddisflies of the genus *Macrostemum* Kolenati (Trichoptera: Hydropsychidae) construct their catchnets within protective retreats. This genus is composed of 88 species and is distributed worldwide (Morse 1999). However, the retreat architecture has only been described for three North American species (Wallace & Sherberger 1974, 1975, Wallace 1975) and one South American species (Sattler 1963). The described retreats share a general, rather elaborate architecture (Fig. 1a) with the following characteristics: (i) two chambers, one housing the catchnet and one housing the insect, and (ii) the water entrance hole is at the end of a silken or sand grain tube that leads into the two-chamber area. Here we report an alternate retreat design constructed by some *Macrostemum carolina* (Banks) individuals in the Savannah River, Georgia and South Carolina.

Macrostemum carolina is widely distributed throughout the southeastern United States, and has been recorded west to Texas (Moulton & Stewart 1997) and north to New York (Ross 1944). In coastal plain streams with shifting sand streambeds, *M. carolina* primarily inhabits submerged snags (i.e. fallen trees or branches), gouging the base of their retreats out of the wood and covering the top of the structure with silk. In their original description, Wallace & Sherberger (1974) noted that some *M. carolina* individuals in the Apalachicola River construct a second, slightly different retreat than the one described above. This alternate retreat lacks a silken tube and simply has the entrance hole open into the chamber area (Fig. 1b) (some *Macrostemum zebratum* (Hagen) individuals construct a similar, alternate retreat (see Wallace 1975)). In the Savannah River, *M. carolina* individuals construct the two retreats described above as well as a third type with yet a different entrance hole configuration. The entrance hole of this third retreat also lacks a silken tube and instead has a ~180° silken backstop, with the other ~180° essentially flush with the top of the retreat (Fig. 1c). These backstops vary in size, from 3-8 mm in height, though some of this variation is positively correlated with instar (G. R. P., personal observation). *Macrostemum carolina* is common in the Savannah River (Cudney & Wallace 1980), and each retreat morph is regularly encountered. Individuals of a single morph are often clustered on snags, although the "flush" phenotype is generally the most prevalent (G. R. P., personal observation).

Although these three retreat morphs are discrete behaviors (though see below), the individuals in the Savannah River represent a single, panmictic population (Plague et al., in press). Therefore, retreat construction in *M. carolina* is either: (i) phenotypically plastic, with environmental cues influencing retreat design (e.g. Emlen 1994), (ii) genetically polymorphic, with alternative alleles at a retreat gene (or genes) controlling the design (e.g. Hori 1993), or (iii) partially heritable, i.e., a combination of genetic and plastic control (e.g. Roff 1986). Whichever is the case, natural selection probably plays a role in maintaining the alternative phenotypes (Hartl & Clark 1997, Futuyma 1998). The adaptive value of each design is likely related to the maintenance of adequate water flow through the retreat, and specifically the net. Therefore, each morph may be adapted to a particular microhabitat on the snag. For

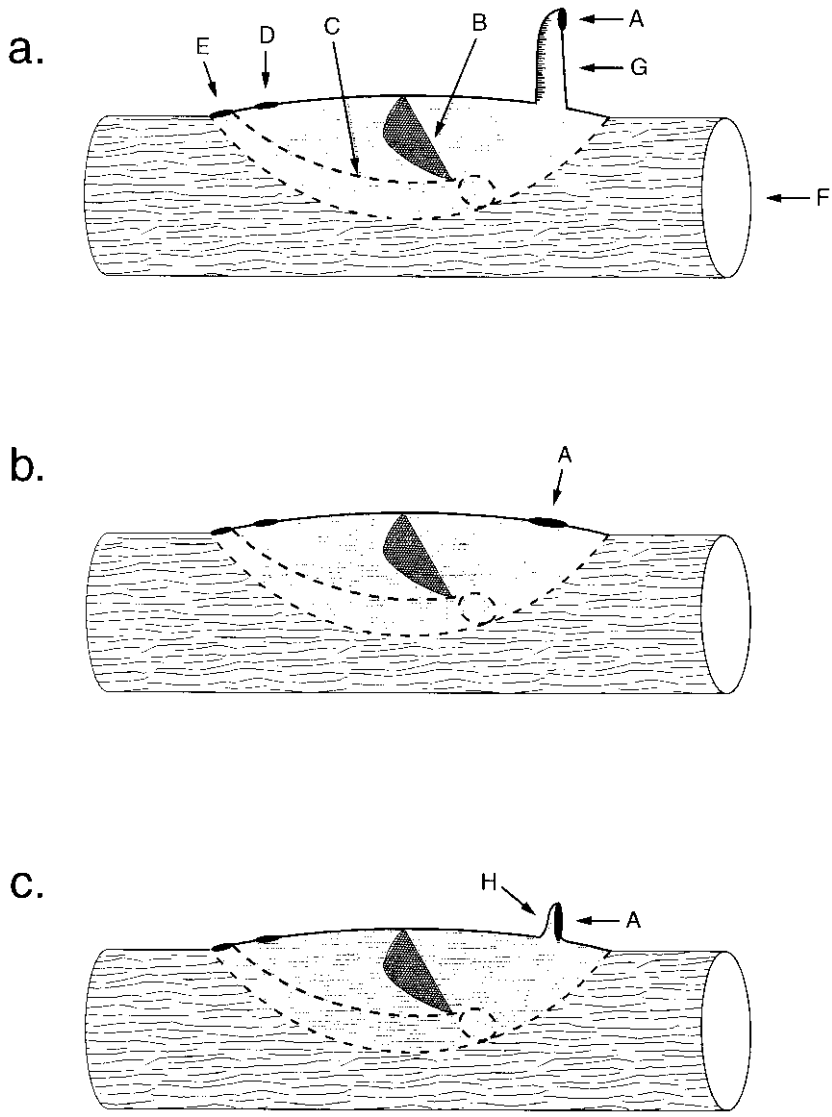

Fig. 1. The larval retreat morphs of *Macrostemum carolina*: (a) "tube retreat", (b) "flush retreat", and (c) "backstop retreat". Abbreviations used in figure: A = water entrance hole; B = net; C = larval chamber; D = net chamber water exit hole; E = larval chamber water exit hole; F = snag; G = silken tube; H = silken backstop. [This figure is modeled after Figure 6 of Wallace (1975).]

example, "flush" retreats may be located primarily on upstream snag locations and therefore receive direct water flow into the retreat; "backstop" retreats may be located on the tops and bottoms of snags (relative to water flow), with the backstop helping to

divert water into the retreat; and "tube" retreats may occur on the downstream side of snags, reaching over the top or bottom of the snag to face into the current. Unfortunately, because snags are generally flexible and often 50 cm or more under water, assessing a retreat's exact *in situ* location and orientation is often difficult. Also, water flow over a snag is undoubtedly extremely complex (Hart et al. 1996), thereby exposing different microhabitats on the snag to similar water flow regimes. Therefore, microflow location, and not simply microhabitat location, is likely a more important selective force in maintaining these alternative morphs.

Sattler & Kracht (1963) and Wallace & Sherberger (1975) proposed that the tube retreats in *Macrostemum ulmeri* (Banks) and *Macrostemum transversum* (Walker), respectively, function as Pitot tubes (L-shaped open tubes used to measure fluid velocity), essentially pulling more water (and therefore more food) through the retreat than would flow through passively. This pulling action results from equalizing the pressure differential between the vertical entrance hole (relatively high pressure) and the horizontal exit hole (relatively low pressure). The tube and backstop retreats of *M. carolina* may similarly function as Pitot tubes. If so, these two retreat designs may represent a phenotypic continuum within a single behavior, with the primary fitness differences between them being correlated with the amount of time (which equates to lost feeding time and increased exposure to predators) and energy expended to construct each design; the tube retreat type is presumably more costly on both counts. Therefore, *M. carolina* may actually exhibit only two discrete retreat morphologies: (i) flush entrance hole and (ii) structured entrance hole, with the latter expressing a range of phenotypes.

We thank Gabe Novak for an insightful discussion about the physics of net-spinner retreats, Juanita Blocker and Angela Lindell for helping produce Figure 1, and two anonymous reviewers for improving the manuscript. Manuscript preparation was supported by Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation.

Summary

In the Savannah River, larval *Macrostemum carolina* caddisflies make three different retreats, each with a distinct water entrance hole: (i) flush with the top of the retreat, (ii) at the end of a silken tube, and (iii) with a ~180° silken backstop. Herein we describe the "backstop" retreat (the others have been described previously), and discuss possible selective advantages of each retreat phenotype.

References Cited

Cudney, M. D., and J. B. Wallace. 1980. Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (U.S.A.) river. Holarct. Ecol. 3: 169-182.

Emlen, D. J. 1994. Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Proc. R. Soc. Lond. B 256: 131-136.

Futuyma, D. J. 1998. Evolutionary Biology. Sinauer Associates Sunderland, Massachusetts.

Hart, D. D., B. D. Clark, and A. Jasentuliyana. 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.

Hartl, D. L., and A. G. Clark. 1997. Principles of Population Genetics. Third edition. Sinauer Associates Sunderland, Massachusetts.

HORI, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. Nature 260: 216-219.

MORSE, J. C., editor. 1999. Trichoptera World Checklist. http://entweb.clemson.edu/database/trichopt/index.htm, effective 22 May 1999.

MOULTON, S. R., AND K. W. STEWART. 1997. Preliminary checklist of Texas caddisflies, pp. 349-353 *In:* R. W. Holzenthal and O. S. Flint [eds.] Proc. 8th Internat. Symp. Trichoptera. Ohio Biological Survey, Columbus.

PLAGUE, G. R., M. MULVEY, T. C. Glenn, AND J VAUN MCARTHUR. In press. Moledular genetic markers provide no evidence for reporductive isolation among retreat building phenotypes of the net-spinning caddisfly *Macrostemum carolina*. Molecular Ecology.

ROFF, D. A. 1986. The genetic basis of wing dimorphism in the sand cricket, *Gryllus firmus* and its relevance to the evolution of wing dimorphisms in insects. Heredity 57: 221-231.

ROSS, H. H. 1944. The caddis flies, or Trichoptera, of Illinois. Illinois Natural History Survey Bulletin 23.

SATTLER, W. 1963. Über den Körperbau, die Ökologie und Ethologie der Larve und Puppe von *Macronema* Pict. (Hydropsychidae), ein als Larve sich von 'Mikro-Drift' ernährendes Trichopter aus dem Amazonasgebiet. Arch. Hydrobiol. 59: 26-60.

SATTLER, W., AND A. KRACHT. 1963. Drift-Fang einer Trichopterenlarve unter Ausnutzung der Differenz von Gesamtdruck und statischen Druck des fließenden Wassers. Naturwissenschaften 50: 362.

WALLACE, J. B. 1975. Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona*, and *Macronema zebratum* (Hydropsychidae). Ann. Entomol. Soc. Am. 68: 463-472.

WALLACE, J. B., AND F. F. SHERBERGER. 1974. The larval retreat and feeding net of *Macronema carolina* Banks (Trichoptera: Hydropsychidae). Hydrobiologia 45: 177-184.

WALLACE, J. B., AND F. F. SHERBERGER. 1975. The larval dwelling and feeding structure of *Macronema transversum* (Walker) (Trichoptera: Hydropsychidae). Anim. Behav. 23: 592-596.