Experimental studies of exploitative competition in a grazing stream insect

D.D. Hart
Academy of Natural Sciences, 19th and the Parkway, Philadelphia, PA 19103, USA

Summary. Field and laboratory experiments were conducted to determine whether intraspecific competition for food occurs during the larval stage of the periphyton-grazing caddisfly Glossosoma nigrior (Trichoptera: Glossosomatidae). Larvae were placed in field enclosures at densities less than, equal to, or greater than their natural densities. Most of these individuals began to pupate after ~3 weeks, whereupon the mass of each individual was determined. Final mass declined significantly as larval densities increased, whereas neither developmental rate nor mortality/emigration rate was significantly affected by density manipulations. A supplemental experiment comparing the final mass of individuals grown at reduced densities in a laboratory stream with individuals from a natural stream bottom confirmed the results of the more extensive field experiment: reductions in density resulted in significant increases in final mass. Periphyton availability in field enclosures declined according to a negative exponential function as larval densities increased. Over the ~25-fold range of larval densities used in these experiments, the final mass of individuals increased linearly with periphyton standing crops. This result suggests that Glossosoma larvae may compete for food even at densities below those employed in this study. Path analysis was used to explore the importance of indirect (i.e., exploitative) and direct (i.e., interference) mechanisms for the observed competitive effects. The analysis indicates that a model based solely on exploitation explains nearly as much of the variance in mass as a model incorporating both interference and exploitation.

Key words: Algal-grazer interactions - Competition - Food depletion - Food limitation - Streams

Field experiments focusing on the importance of competition in diverse natural settings are required before the continuing controversy regarding the role of competitive interactions in populations and communities can be resolved. Schoener's (1983) review makes a compelling plea for increased attention to the mechanisms of competition, since theory (e.g. Fretwell and Lucas 1970; MacArthur 1972; Schoener 1973; Vance 1985) suggests that the effect of competitive interactions on population and community dynamics depends strongly on whether these interactions involve exploitation or interference (sensu Miller 1967). Experimental field studies explicitly focusing on the relationship between resource availability and competition should yield important insights regarding competitive mechanisms, yet recent reviews suggest such studies are scarce (Connell 1983; Schoener 1983).

This study tests the hypothesis that larvae of the grazing stream caddisfly Glossosoma nigrior both reduce, and are limited by, the availability of their food resources. In many streams throughout the world, high densities of larval glossosomatids are commonly found (e.g. Douglas 1958; Coffman 1967; Cummins 1975; Minshall and Minshall 1977; McAuliffe 1983), and are often associated with low standing crops of algae (e.g. Douglas 1958; McAuliffe 1983), raising the possibility that these grazers deplete their food sources. Evidence of food depletion by grazing stream insects is accumulating (e.g. Hart 1981, 1983, 1985a, 1985b; Lamberti and Resh 1983; McAuliffe 1983, 1984), though experimental field studies have rarely tested whether individual fitness components are influenced by such food reductions. This study was motivated in part by a previous investigation with grazing caddisfly larvae, in which the potential rate of periphyton depletion was much greater than its renewal rate, suggesting that larvae compete exploitably (Hart 1981).

Field site and study organism

This study was done in a third order section of Augusta Creek, a hard-water trout stream located in southwestern Michigan, USA (cf. Manny and Wetzel 1973; Ward and Cummins 1978). The larval stage of the caddisfly Glossosoma nigrior lives in a stone case resembling a tortoise shell, and is conspicuous and abundant in this stream. Glossosoma is most common on the upper surfaces of stones in shallow, fast flowing, well-lighted sections of Augusta Creek, where it scrapes periphyton (a microbial assemblage dominated by diatoms, but including green and blue-green algae, bacteria, fungi and detritus) from the substrate (e.g. Chapman and Demory 1963; Coffman et al. 1971; Oemke 1983). Representatives of this genus occur in streams throughout North America (Ross 1956; Wiggins 1977).

In Augusta Creek, Glossosoma completes two generations per year, each with five larval instars (Cummins et al. 1973; Oemke 1983). The summer generation begins when adults emerge in the spring and oviposit. Larvae hatch from these eggs and grow until late summer-early fall, when they pupate. Following pupation, the winter generation commences with oviposition by adults. Individuals hatching
from these eggs remain as larvae until spring, whereupon they pupate, emerge, and oviposit, initiating the next summer generation.

Most aquatic insects (including caddisflies) feed primarily or exclusively during the immature stage of their life cycle. Within this immature stage, most of an individual's adult mass is gained during the last instar (e.g. Waldbauer 1968; Scriber and Slansky 1981). The mass of adults (and pupae in holometabolous insects) might be significantly reduced if food was scarce during this period when immatures are capable of such large increases in mass. Since pupal and adult mass is often strongly correlated with fitness components such as adult longevity (Hawley 1985) and dispersal rate (Roff 1977), female fecundity (Colbo and Porter 1979; Steinwascher 1982; Prout and McChesney 1985; Bernardo et al. 1986) and male mating success (Simmons 1985), competition for food during this critical phase of larval growth may profoundly influence an individual's fitness.

During the summer of 1980, Glossosoma larvae occurred at high densities in several Augusta Creek riffles. I used a combination of field and laboratory experiments to test the hypothesis that at such densities, Glossosoma reduces the availability of periphyton and is consequently food limited.

Methods

Field experiments

I manipulated larval densities using in situ enclosures. The enclosures were shallow (~3-cm deep), square (~15 x 15 cm), open-topped boxes constructed from 3-mm cast acrylic, covered at the top with a large mesh (mesh size ~3 mm) nylon fabric. Artificial substrates (15 x 15 x 0.5 cm unglazed quarry tiles), which provide a suitable surface for both grazing insects and periphton (e.g. Hart 1981), were placed on the stream bottom about one month before the experiment and allowed to develop periphyton standing crops that were similar to those on nearby natural substrates (see Results). At the outset of the experiment, one tile was placed within each enclosure.

Animals were added to the enclosures to create larval density levels above, equal to, and below those found in the field. Several days before the experiment began, field densities were quantified by haphazardly tossing a metal ring sampler (area=23 cm²) onto the stream bottom in several microhabitats preferred by Glossosoma (i.e. sites characterized by moderate (> 25 cm s⁻¹) current velocities measured ~3 cm above the substrate, shallow (<35 cm) depths, and pebble-cobble substrates). The number of larvae (predominantly fourth-instar) within the area enclosed by the ring was counted. The average number of larvae per sample was 2.9 ±0.3 (Note: the mean ± one standard error are presented throughout) (N= 58), which is equivalent to ~29 larvae per tile (upper surface area = 225 cm²).

Accordingly, the three density levels established were FIELD (30 larvae/tile), ABOVE (60 larvae/tile) and BELOW (5 larvae/tile). A fourth density level in which larvae were absent (ZERO) was created to monitor the growth of periphyton in the absence of Glossosoma. The number of replicate enclosures for the ZERO, BELOW, FIELD, and ABOVE density treatments were 2, 30, 6, and 4, respectively.

The field experiment began on 30–31 July and terminated on 21 August 1980. The enclosures were seeded with fourth instar Glossosoma larvae, which molted and spent the fifth instar feeding until pupation. The mesh size of the enclosure covering was small enough to retain most Glossosoma larvae, and other species of grazers were rarely found in the enclosures. Dry mass determinations were obtained for a randomly chosen subsample of these larvae to provide an estimate of larval mass at the experiment's outset.

Individual larvae were randomly assigned to enclosures. To reduce variation in environmental conditions between enclosures, I fastened them with rubber bands to anchored wooden platforms that were raised ~20 cm off the stream bottom. Larvae moved and grazed within the enclosures much as they do on the stream bottom. The enclosure's area was ~50% greater than Cummins' (1975) estimate of the area within which a larva moves during a 24-h period. Current velocity ~3 cm above the enclosures (41 ±4 cm s⁻¹, N=6) was nearly identical to that ~3 cm above the adjacent stream bottom (43 ±5 cm s⁻¹, N=4) where Glossosoma occurred, and turbulence within the enclosures was sufficient to prevent silt or fine sand from accumulating. The enclosures' mesh coverings were cleaned once or twice per day during the study to remove any snagged debris (e.g. leaves). Fourth instar larvae molted to the fifth instar while inside the enclosures, and because Glossosoma larvae often abandon their cases and build new ones at each molt (e.g. Anderson and Bourne 1974; Cummins et al. 1973), a small amount of sand and gravel was added to each enclosure regularly to provide materials for case construction.

I censused larval densities in the enclosures twice during the experiment. Some reduction in densities occurred, particularly in the ABOVE enclosures, and immediately following the first census (on day 6 of the experiment) I replaced missing individuals with fourth instar larvae from the stream bottom. I did not add larvae to compensate for losses after the first week of the experiment.

On day 14, I collected periphyton samples with a syringe sampler modified from Loeb (1981) to assess food quantity (i.e. particulate carbon and nitrogen) and food quality (as reflected by the C:N ratio). Four 314 mm² randomly selected samples per tile were collected from each of the ZERO, ABOVE and FIELD density tiles, and from nine randomly chosen BELOW tiles. Samples were transferred to vials and stored on ice. Within hours, the samples were filtered through precombusted Whatman GF/F 13-mm diameter glass fiber filters at a vacuum <0.5 atm. Samples were then dried at 60°C, acid-fumed for ~15 min to remove inorganic carbon (Wetzel 1965), and stored in a desiccator until determinations of particulate carbon and nitrogen were made with a Carlo-Erba CHN analyzer (Stainton et al. 1977).

Although all the individuals had not pupated by the termination of the experiment, some had pupated ~one week earlier. Individuals were collected from each tile and briefly plunged into near-boiling water to reduce the likelihood of gut content regurgitation. They were then immediately placed in a 1% formalin solution and stored at ~1°C to minimize loss of mass. Within several days, each individual was categorized as either a larva, prepupa, or pupa (male or female) according to the criteria of Ross (1944), Anderson and Bourne (1974), and Wiggins (1977). Pupae and prepupae were then dried at 60°C in a drying oven.