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Notes and Discussion

Leaf Scraping Beetle Feces are a Food Resource for Tree Hole Mosquito Larvae

Abstract.—In tree holes, leaf scraping scirtid beetles increase the rate at which leaf litter is converted to fine particles, which may benefit fine particle feeding mosquitoes if these fine particles are valuable to mosquitoes. We tested whether the products of scirtid feeding are a valuable food resource for mosquito larvae [*Ochlerotatus triseriatus* (Say)] by introducing different amounts of scirtid feces to mosquito larvae and measuring mosquito performance. Mosquito larvae survived longer and developed to later instars in treatments with many scirtids (and, therefore, a lot of feces) compared to treatments with few or no scirtids. This result suggests that scirtid feces (and attached microorganisms) constitute a valuable food resource for *O. triseriatus*. Thus, other members of tree hole communities may have complex effects on the population growth of *O. triseriatus*.

Introduction

In streams, feces from leaf shredding macroinvertebrates may be an important source of fine particulate organic matter (FPOM) for downstream collectors (*e.g.*, Wallace *et al.*, 1977). If so, downstream communities should be dominated by fine particle feeding collectors in order to take advantage of the inefficiency ("leakage") of upstream leaf shredders (Vannote *et al.*, 1980). This hypothesis, the river continuum concept, postulates that shredder and collectors populations are coupled via a processing chain, in which upstream consumers affect downstream consumers by converting course particulate organic matter (CPOM) into FPOM (Heard, 1994). In order to determine definitively whether upstream consumers benefit downstream collectors via the conversion of leaf litter into fine particles, it is necessary to show that upstream consumers produce FPOM and that this FPOM is valuable for downstream consumers (Heard and Richardson, 1995). Studies of tree hole insect communities suggest a processing chain may exist between leaf scraping beetle larvae and fine particle feeding mosquito larvae (Paradise, 1999, 2000; Daugherty and Juliano, 2002).

The primary resource for tree hole mosquitoes is microorganisms growing on decomposing plant material (Kaufman *et al.*, 2001, 2002). Plant detritus is largely supplied in the form of whole leaves. As these leaves decay, they are converted to fine particles composed of plant material and microorganisms, which are fed upon by mosquito larvae. Leaf species that decompose more quickly support greater mosquito population growth (Fish and Carpenter, 1982; Yanoviak, 1999) and additions of leaves often increase mosquito population growth, suggesting mosquitoes are resource limited (Walker *et al.*, 1991; Léonard and Juliano, 1995; Macia and Bradshaw, 2000).

Other tree hole insects also feed on leaf material and, therefore, have the potential to reduce (by consumption) or to increase (by production of fine particles or enhancement of microbial growth) resource availability to mosquitoes (Paradise, 1999, 2000; Daugherty and Juliano, 2001, 2002). Larval scirtid beetles (Scirtidae, also known as Helodidae; *Helodes* and *Prionocyphon* spp.) are common inhabitants of water filled tree holes in the Midwestern and Eastern U.S. They are leaf scrapers, or browsers, who consume layers of microbial growth on leaves and leave behind fine particles in the form of degraded plant material and feces (Barrera, 1996). Scirtid beetles can facilitate mosquito survivorship and development (Bradshaw and Holzapfel, 1992; Paradise, 1999, 2000; Daugherty and Juliano, 2002). The most likely mechanism for this benefit is the production of resources via increased conversion rates of whole leaves into fine particles (Paradise, 1999, 2000; Daugherty and Juliano, 2002). By feeding on leaf surfaces, scirtid larvae increase the degradation of coarse leaf material (Paradise, 1999, 2000) and the production of fine particles (Daugherty and Juliano, 2002). Despite these correlational data, and the plausibility of the hypothesis that scirtids benefit mosquitoes via production of food resources, no one has demonstrated that any of the particles of plant material and feces left behind by scirtids are nutritionally valuable to mosquitoes. In this study we document the value of scirtid feces as a resource for the tree hole mosquito *Ochlerotatus triseriatus* (formerly *Aedes triseriatus*).

Methods

In early August 1999 we collected scirtid larvae (*Helodes* spp.) from tree holes in Merwin Nature Preserve (approximately 25 km northeast of Normal, Il.). We did not sort scirtids by species because it is

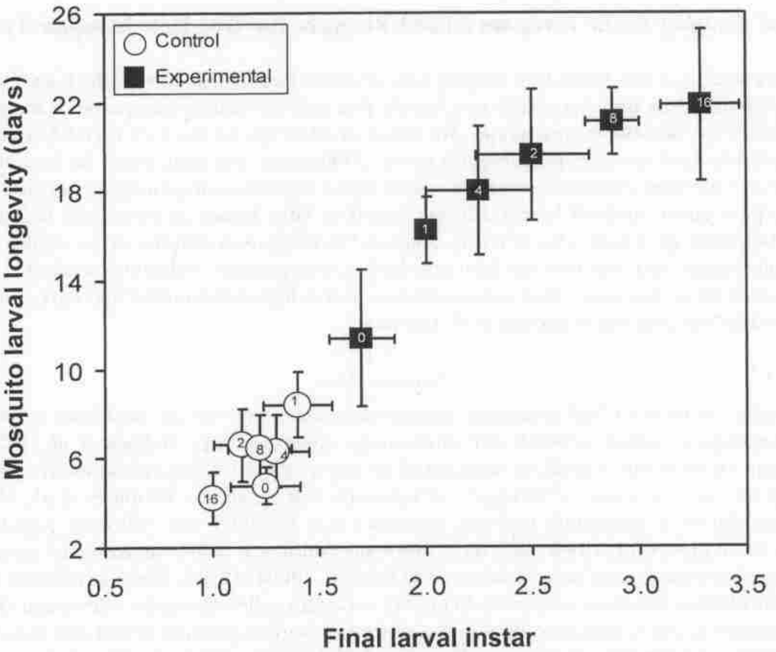

FIG. 1.—Effects of scirtid treatment (experimental versus control groups) and number of scirtids (covariate) on mosquito performance (larval longevity and final instar attained). Bivariate means (±1 SE) for all scirtid treatment-number combinations are shown. Some small error bars are masked by the treatment symbols. Numbers inside of the treatment symbols denote the number of scirtids. MANOVA showed a significant interaction between scirtid number and scirtid treatment

difficult to identify to species living specimens of *Helodes*, which are ecologically similar (Paradise, 1999). We housed these larvae in the lab for the next 3 wk in a 3 liter plastic tub filled with an excess of leaf litter [>50 g of a mixture of white oak (*Quercus alba*) and sugar maple (*Acer saccarum*) leaves].

We tested the nutritional value of scirtid feces for mosquito larvae by collecting feces from varying numbers of scirtids, then rearing individual *Ochlerotatus triseriatus* larvae (F1 progeny from individuals collected at Merwin Preserve) on this substrate. In late August 1999 we placed 0, 1, 2, 4, 8 or 16 similarly sized *Helodes* larvae into 75 ml containers with 50 ml of deionized water and 1 mm screen (to allow the poor swimming scirtids to climb to the water surface). After 5 d we removed scirtids, discarded any containers with dead scirtids and added a 1st instar *O. triseriatus* larva to each container (n ≥ 7 replicates per density). For control containers we dipped (for approximately 1 second) 0, 1, 2, 4, 8 or 16 scirtids into 75 ml containers filled with water and immediately removed them, then added a 1st instar *O. triseriatus* larva to each container (10 replicates per density). Thus, controls received any microorganisms adhering to the scirtids, but not scirtid feces. We recorded the final instar and date of death for mosquito larvae in both experimental and control containers and tested for effects of scirtid number (as a continuous variable) and scirtid feces on the longevity of mosquito larvae (square root transformed) and the final instar achieved ($\log_{10}$ transformed) using multivariate analysis of variance (MANOVA; SAS Institute Inc., 1989).

RESULTS AND DISCUSSION

Although we did not quantify the amount of feces present in containers, there were markedly more fine particles in experimental containers with many versus few scirtids, and none of the control containers appeared to have any fine particles. Scirtid feces treatment (Pillai's trace = 17.12, df = 2,100, P = 0.0001), scirtid number (Pillai's trace = 8.49, df = 2,100, P = 0.0004) and the treatment by number interaction (Pillai's trace = 19.38, df = 2,100, P = 0.0001) all significantly affected the longevity and final instar of *Ochlerotatus triseriatus* larvae. In the experimental treatment there was a strong trend of increased *O. triseriatus* longevity and final instar achieved with more scirtids (Fig. 1). However, in the control treatment, *O. triseriatus* longevity and final instar were uniformly low and showed no clear trend relative to scirtid number. Our experiment cannot determine whether *O. triseriatus* derive nutritional benefits from scirtid feces *per se*, or from microorganisms that grow on scirtid feces. In either case, it is clear that scirtid feces contribute to *O. triseriatus* development and survival.

Although our results demonstrate that scirtid feces facilitate *Ochlerotatus triseriatus* development and survival, no mosquitoes reached pupation. We used artificially high scirtid densities (16 scirtids per 50 ml of water is greater than average densities in the field—Daugherty and Juliano, 2001), which would seem to suggest that, although scirtid feces may provide food for mosquitoes, the supply is not great enough to increase dramatically *O. triseriatus* population growth. However, containers in the experimental treatment were stocked with scirtids only once and received no additional leaf material, meaning repeated deposition of scirtid feces, as would occur in the field if scirtids were actively feeding, did not occur. Furthermore, in the field, fine particles derived from scirtid feeding would consist of both feces produced by incomplete digestion of leaf material and fine leaf fragments produced from the incomplete consumption of leaf material. The relative value of fine fragments produced by the incomplete consumption of leaf material by scirtids is not known, but there is no reason to believe that they are not a suitable substrate for microbial growth and therefore valuable to mosquito larvae. Given that our study allowed only one deposition of feces and that it eliminated the second form of fine particles, our results are likely a conservative estimate of how much resource scirtids provide to *O. triseriatus*.

Processing chain interactions are likely to occur in a variety of ecological systems, especially in cases where there is a high degree of sequential use of a resource by multiple species (Heard, 1994). Understanding how initial consumers affect the availability and value of the resource for subsequent consumers is important for understanding the degree to which one species will benefit or harm other species in these systems. Our results offer evidence that, by feeding on coarse leaf litter and producing feces, scirtid beetles provide a valuable resource for tree hole mosquitoes. Thus, there is potential for processing chain interactions among macroinvertebrates in tree holes.

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LITERATURE CITED

BARRERA, R. 1996. Species concurrence and the structure of a community of aquatic insects in tree holes. *J. Vector Ecol.*, **21**:66–80.

BRADSHAW, W. E. AND C. M. HOLZAPFEL. 1992. Resource limitation, habitat segregation, and species interactions of British tree-hole mosquitoes in nature. *Oecologia*, **90**:227–237.

DAUGHERTY, M. P. AND S. A. JULIANO. 2001. Factors affecting the abundance of scirtid beetles in container habitats. *J. N. Amer. Benth. Soc.*, **20**:109–117.

——— AND ———. 2002. Testing for context-dependence in a processing chain interaction among detritus-feeding aquatic insects. *Ecol. Entom.*, **27**:541–553.

FISH, D. AND S. R. CARPENTER. 1982. Leaf litter and larval mosquito dynamics in tree-hole ecosystems. *Ecology*, **63**:283–288.

HEARD, S. B. 1994. Processing chain ecology: resource condition and interspecific interactions. *J. Anim. Ecol.*, **63**:451–464.

——— AND J. S. RICHARDSON. 1995. Shredder-collector facilitation in stream detrital food webs: is there enough evidence? *Oikos*, **72**:359–366.

KAUFMAN, M. G., S. J. BLAND, M. E. WORTHEN, E. D. WALKER AND M. J. KLUG. 2001. Bacterial and fungal contributions to growth of larval *Aedes triseriatus* (Diptera: Culicidae). *J. Med. Entom.*, **38**: 711–719.

———, W. GOODFRIEND, A. KOHLER-GARRIGAN, E. D. WALKER AND M. J. KLUG. 2002. Soluble nutrient effects on microbial communities and mosquito production in *Ochlerotatus triseriatus* (Say) habitats. *Aquat. Microb. Ecol.*, **29**:73–88.

LEONARD, P. M. AND S. A. JULIANO. 1995. Effect of leaf litter and density on fitness and population performance of the hole mosquito *Aedes triseriatus*. *Ecol. Entom.*, **20**:125–136.

MACIA, A. AND W. E. BRADSHAW. 2000. Seasonal availability of resources and habitat degradation for the western tree-hole mosquito, *Aedes sierrensis*. *Oecologia*, **125**:55–65.

PARADISE, C. J. 1999. Interactive effects of resources and a processing chain interaction in treehole habitats. *Oikos*, **85**:529–535.

———. 2000. Effects of pH and resources on a processing chain interaction in simulated treeholes. *J. Anim. Ecol.*, **69**:651–658.

SAS INSTITUTE INC. 1989. SAS user's guide: statistics. Version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL AND C. E. CUSHING. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.*, **37**:130–137.

WALKER, E. D., D. L. LAWSON, R. W. MERRITT, W. T. MORGAN AND M. J. KLUG. 1991. Nutrient dynamics, bacterial populations, and mosquito productivity in tree hole ecosystems and microcosms. *Ecology*, **72**:1529–1546.

WALLACE, J. B., J. R. WEBSTER AND W. R. WOODALL. 1977. The role of filter feeders in flowing waters. *Archiv fur Hydrobiol.*, **79**:506–532.

YANOVIAK, S. P. 1999. Effects of leaf litter species on macroinvertebrate community properties and mosquito yield in Neotropical tree hole microcosms. *Oecologia*, **120**:147–155.

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