Notes and Discussion

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

ABSTRACT.—In tree holes, leaf scraping scirid 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 scirid feeding are a valuable food resource for mosquito larvae [Ochlerotatus triseriatus (Say)] by introducing different amounts of scirid feces to mosquito larvae and measuring mosquito performance. Mosquito larvae survived longer and developed to later instars in treatments with many scirids (and, therefore, a lot of feces) compared to treatments with few or no scirids. This result suggests that scirid 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 coarse 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 scirid 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). Scirid 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, scirid 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 scirids benefit mosquitoes via production of food resources, no one has demonstrated that any of the particles of plant material and feces left behind by scirids are nutritionally valuable to mosquitoes. In this study we document the value of scirid feces as a resource for the tree hole mosquito Ochlerotatus triseriatus (formerly Aedes triseriatus).

METHODS

In early August 1999 we collected scirid larvae (Helodes spp.) from tree holes in Merwin Nature Preserve (approximately 25 km northeast of Normal, Ill.). We did not sort scirids by species because it is
Fig. 1.—Effects of scirid treatment (experimental versus control groups) and number of scirids (covariate) on mosquito performance (larval longevity and final instar attained). Bivariate means (±1 se) for all scirid 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 scirids. MANOVA showed a significant interaction between scirid number and scirid 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 2 liter plastic tub filled with an excess of leaf litter (>50 g of a mixture of white oak (Quercus alba) and sugar maple (Acer saccharum) leaves).

We tested the nutritional value of scirid feces for mosquito larvae by collecting feces from varying numbers of scirids, 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 scirids to climb to the water surface). After 5 d we removed scirids, discarded any containers with dead scirids 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 scirids 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 scirids, but not scirid feces. We recorded the final instar and date of death for mosquito larvae in both experimental and control containers and tested for effects of scirid number (as a continuous variable) and scirid feces on the longevity of mosquito larvae (square root transformed) and the final instar achieved (log10 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 scirids, and none of the control containers appeared to have any fine particles. Scirid feces treatment (Pillai's trace = 17.12, df = 2,100,
P = 0.0001), scritid 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 scritids (Fig. 1). However, in the control treatment, *O. triseriatus* longevity and final instar were uniformly low and showed no clear trend relative to scritid number. Our experiment cannot determine whether *O. triseriatus* derive nutritional benefits from scritid feces *per se*, or from microorganisms that grow on scritid feces. In either case, it is clear that scritid feces contribute to *O. triseriatus* development and survival.

Although our results demonstrate that scritid feces facilitate *Ochlerotatus triseriatus* development and survival, no mosquitoes reached pupation. We used artificially high scritid densities (16 scritids per 50 ml of water is greater than average densities in the field—Daugherty and Juliano, 2001), which would seem to suggest that, although scritid 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 scritids only once and received no additional leaf material, meaning repeated deposition of scritid feces, as would occur in the field if scritids were actively feeding, did not occur. Furthermore, in the field, fine particles derived from scritid 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 scritids 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 scritids 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, scritid 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**


1 Corresponding author: Present address: Department of Integrative Biology, University of California, Berkeley 94720. Telephone (510) 643-3880; FAX (510) 643-6264; e-mail: fezzik@socrates.berkeley.edu