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PITCHER-PLANT MIDGES AND MOSQUITOES: A PROCESSING CHAIN COMMENSALISM[1]

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Abstract. Larvae of the midge *Metriocnemus knabi* and of the mosquito *Wyeomyia smithii* are found only inside the water-filled leaves of the carnivorous pitcher plant, *Sarracenia purpurea,* where they feed on decaying invertebrate carcasses. I examined the interaction between the two species in a natural population in western Newfoundland, Canada.

Experimental manipulations of rates of prey capture by pitcher-plant leaves indicated that both insect species are limited by carcass supply. However, the interaction between them is commensal rather than competitive. Midge growth was unaffected by experimental quadrupling of mosquito density in otherwise unmanipulated leaves. Mosquito growth, on the other hand, increased with midge density in both natural leaves and artificial leaf microcosms.

This interaction is an example of a processing chain commensalism. Although both species feed on carcass material, they use it in different stages of decay: midges feed by chewing on solid material, while mosquitoes filter-feed on particles derived from the decaying matter. Consumption of particles by mosquitoes does not affect resource availability for midges, but feeding by midges does influence particle availability. In artificial leaf microcosms, high bacterial densities occurred sooner in artificial leaves with midges present than in identical leaves without them. Bacteria are a direct food source for mosquitoes, and high bacterial densities also indicate that other organic material is being comminuted, providing particles for mosquitoes and surface area for bacterial growth. Although midges remove some of the carcass resource that also limits mosquitoes, their net effect on mosquitoes is positive because they accelerate conversion of the remaining resource to particles.

Key words: *commensalism, interspecific interactions,* Metriocnemus knabi; *pitcher plant processing chain resource limitation resource processing:* Sarracenia purpurea; Wyeomyia smithii.

INTRODUCTION

Interactions between species are often mediated by the effects of one species on the resources available to another. Interactions mediated by consumer effects on resource quantity have been widely considered. However, there has recently been increasing recognition that consumers have more complicated effects on their resources. Besides reducing resource quantity, consumers may influence resource properties such as defensive chemistry, nutritional quality, decompositional state, particle size, or chemical form (e.g., McNaughton 1976, Faeth 1986, Abrams 1987, Strauss 1991, Masters et al. 1993, Heard 1994*a*). When consumers interact through such effects, understanding population dynamics may require explicit consideration of resource dynamics and changes in resource quality.

One important class of resource quality interactions involves the physical or chemical processing of resources by consumers. In such interactions, termed "processing chains" (Heard 1994*a*), resource material passes through a temporal sequence of two (or more) conditions: it is supplied in an "upstream" condition and processed to a "downstream" condition. A consumer species specializes on resource in each condition. The upstream consumer may influence the rate at which resource is processed as well as simply removing upstream-condition resource. Interactions between consumers in processing chains may be commensal (+, 0) or amensal (−, 0) (Heard 1994*a*, *b*). Many such systems have been described, although in very few have interspecific interactions and their mechanisms been well documented (Heard 1994*a*).

In this paper I examine the processing chain interaction between two detritivorous insects whose larvae live in leaves of the pitcher plant, *Sarracenia purpurea*: the pitcher-plant midge, *Metriocnemus knabi,* and the pitcher-plant mosquito, *Wyeomyia smithii.* Both insects feed on organic material derived from captured invertebrates, and the relevant aspect of resource condition is particle size. *M. knabi* larvae (henceforth "midges") are the upstream consumers, feeding by chewing on sunken, intact carcasses or solid material. *W. smithii* larvae (henceforth "mosquitoes") are the downstream consumers, filter feeding on particles and

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bacteria derived from decomposing carcasses (Buffington 1970, Wiens 1972, Istock et al 1975, Bradshaw 1983).

Although midges reduce potential particle supply by consuming decomposing material, midge feeding is also thought to accelerate resource processing (Buffington 1970, Bradshaw 1983). Midges could accelerate particle formation directly or by providing surface area for bacterial growth on particles produced but not ingested and on particles egested in feces. There have been, however, no experimental tests of this processing role in the pitcher plant system and surprisingly few in other systems where similar assumptions are made (e.g., stream shredders and collectors: Winterbourn et al. 1981, Richardson and Neill 1991, reviewed in Heard 1994*a*).

I examined, experimentally and in natural populations, both the midge–mosquito interaction and the mechanism underlying that interaction. I proceeded in six major steps. First, I used food supplementation experiments to test for resource limitation. Second, I manipulated mosquito density in natural pitchers to test for an effect of mosquitoes on midge growth. Third, I tested for effects of larvae on each other in an artificial pitcher experiment. Fourth, I sought to confirm an experimental effect of midges on mosquitoes with data from unmanipulated pitchers. Fifth, I compared data from unmanipulated and food-supplemented pitchers to establish that the interaction involved food resources. Finally, I examined the role of midges in resource processing with experiments tracking particle counts in artificial pitchers.

Methods

Organisms and study site

The purple pitcher plant, *Sarracenia purpurea* L., is a carnivorous plant widely distributed in eastern and central North America, mostly in bogs and on other wet, infertile soils. Pitcher-plant leaves accumulate rainwater and trap invertebrate prey including ants, flies, snails, and slugs. Capture rates vary with factors such as pitcher size and age (Wolfe 1981, Laird 1988: 363ff, Cresswell 1991, 1993; S. B. Heard, *unpublished data*). Decomposing prey carcasses form the resource base for an assemblage of species that spend part or all of their life cycles in the pitchers. These inquilines include rotifers (Addicott 1974, Bateman 1987), mites (Fashing and O'Connnor 1984), and the larvae of three flies: the pitcher-plant flesh fly, *Blaesoxipha fletcheri* Aldrich (Sarcophagidae); the pitcher-plant midge, *Metriocnemus knabi* Coq. (Chironomidae); and the pitcher-plant mosquito, *Wyeomyia smithii* Coq. (Culicidae). Bacteria (Hepburn and St. John 1927, Prankevicius and Cameron 1991) and protozoa (Addicott 1974, Laird 1988) are also present. The three flies, which dominate the assemblage in terms of biomass, are obligate inhabitants of pitcher-plant leaves.

S. purpurea is not known to produce digestive enzymes (Adams and Smith 1977; with the probable exception of an acid phosphatase, Stauffer 1987). Inquilines play a major role in comminution and digestion of prey (Bradshaw 1983, Bradshaw and Creelman 1984). There is little if any primary production in healthy pitchers (S. B. Heard, *personal observations*; Cameron et al. 1977, but see Dudley 1984), but some bacterial nitrogen fixation may occur (Prankevicius and Cameron 1991). Some dead leaves and twigs also fall into pitchers, but they decay very slowly and their contribution to resource supply is probably minimal.

I examined the interaction between midges and mosquitoes, which are present in pitchers throughout the year. *B. fletcheri* larvae are present only for a few weeks (Forsyth and Robertson 1975; S. B. Heard, *personal observations*), and have no effect on survival or growth of midges or mosquitoes (Heard 1993). Midges and mosquitoes co-occur regionally over most of the range of *S. purpurea* (Bradshaw 1983), although not necessarily in every bog (Heard 1994*c*).

All experiments reported here were conducted in and around Gros Morne National Park, in western Newfoundland, Canada, from 1989 to 1992. The primary study site was a small bog near the park's Visitor Centre, known locally as Long Marsh (49°34′35″ N, 57°52′20″ W, elevation 60 m). Pitcher plants were abundant, and most pitchers harbored both midges and mosquitoes. Larvae needed for experiments were collected from bogs within 10 km of the primary site.

Although further south both midges and mosquitoes can have many generations each year (Paterson and Cameron 1982, Bradshaw and Holzapfel 1990), in Newfoundland both species are univoltine and their phenologies are similar. Eggs are laid in newly opened pitchers in late July and early August. Larvae feed until day length cues signal the approach of winter and then empty their guts (Paterson 1971; in late September in this case) and diapause in the frozen pitcher liquid (Paris and Jenner 1959, Bradshaw and Lounibos 1972, 1977). Feeding and development resume in the spring, with pupation and adult emergence in mid- to late July.

Larval feeding ecologies of the two species differ dramatically. Midge larvae feed by chewing as they crawl over and through the accumulated carcasses at the bottom of the pitcher. Mosquitoes are active swimmers, feeding on particles filtered from the water column or grazed from surfaces. Mosquitoes ingest a variety of particles, including organic debris, protozoa, and bacteria (Istock et al. 1975, Fish and Hall 1978, Bradshaw 1983). Because there is no primary production, these particles can only be derived, directly or indirectly, from the decomposition of prey carcasses.

Larval midges are capable of some movement between pitchers (Paterson and Cameron 1982), but movement away from healthy pitchers appears to be minimal (S. B. Heard, *personal observations*). Larval mosquitoes do not move between pitchers. Individual

TABLE 1. Timing and size of food supplementation experiments, 1990 and 1991.

Experiment	Number of pitchers	Supplemented beginning	Supplemented until	Pitchers harvested
Spring 1990	200	10 June	28 June	4 July
Fall 1990	200	31 July	11 September	23 September
Spring 1991	100	28 May	22 June	29 June
Fall 1991	100	30 July	10 September	21 September

pitchers are therefore natural experimental units and I use them as replicates.

In the northern part of their range, *W. smithii* females do not take blood meals (O'Meara et al. 1981). Although they will feed on sugar solutions or raisins in the laboratory (Price 1958, Istock et al. 1975), they need not do so to produce eggs and they may not feed in nature (Istock et al. 1975, O'Meara et al. 1981). Furthermore, ovarian development in northern populations is largely completed in the pupal stage, and adult feeding does not affect fecundity (Smith and Brust 1971, Moeur and Istock 1980). Adult midges do not feed at all (Wiens 1972). Because all resources for reproduction are accumulated in the larval stage, larval mass is a predictor of lifetime reproductive performance for both mosquitoes (Istock et al. 1975, Moeur and Istock 1980, Farkas and Brust 1985, Bradshaw et al. 1993) and midges (Wiens 1972).

Food supplementation experiments

In 1990 and 1991 I carried out food supplementation experiments to test for limitation of midge and mosquito larval growth by the supply of pitcher prey. In each year I ran two experiments, one with larvae near maturation (spring), and one with the year's new cohort at the beginning of their growth (fall). In each experiment I marked 100 or 200 healthy pitchers (Table 1) with aluminum tags. I excluded pitchers with foul, anoxic fluid, and I used no more than three pitchers from any single rosette.

On every 6th d I added four freeze-killed worker ants (*Formica* sp.) to each odd-numbered pitcher. Even-numbered pitchers were left as unmanipulated controls. Ants are very common prey items for pitcher plants, making up ≈20% of all captures at my study site. All pitchers were allowed to continue normal prey capture during the experiment. Prey capture rates for control pitchers could not be measured, as this would have required constant removal of prey items. However, based on prey capture data from other pitchers (S. B. Heard, *unpublished manuscript*), the treatment was expected to at least quadruple natural prey capture rates.

At the end of each experiment all pitchers were harvested and dissected. Spring experiments were harvested just before larvae would have pupated. Larvae were counted and dried for 3 d at ≈65°C. The total mass of mosquitoes and the total mass of midges from each pitcher were then determined to the nearest 0.1 mg. For each species in each experiment, I compared total per-pitcher masses (henceforth, "total mass") between treatments with an analysis of covariance (ANCOVA). The number of larvae per pitcher (henceforth, "density") was included as a covariate, so that treatment effects would correspond to changes in mass per individual. I log-transformed both density and total mass to linearize responses. When the main effect × covariate interaction was not significant, I repeated the analysis pooling the interaction sum of squares with the error (Zar 1984). A significant and positive treatment effect indicated resource limitation. I discarded any counts of zero in the ANCOVAs, because pitchers containing no larvae provide no information about resource limitation. Discarding zeros could be misleading if they were common and if their occurrence depended on the experimental treatment. When zeroes occurred in >3% of the pitchers, I used G tests of independence to check for this problem (Sokal and Rohlf 1981).

Mosquito density manipulation experiment

In 1992, I manipulated mosquito density in natural pitchers to test for effects of mosquitoes on midge development. I selected 100 healthy pitchers on 14 July, keeping 50 as unmanipulated controls. I added 10 additional first or second instar mosquito larvae to the remaining pitchers. Pitcher contents were not otherwise disturbed. I did not attempt to make a low mosquito treatment by removing larvae because oviposition continued into the experiment and therefore repeated manipulation of the pitchers would have been required. On 2 September, all pitchers were harvested and surviving larvae were sorted, counted, dried, and weighed as described above (see *Food supplementation experiments*). A single pitcher without any midge larvae was discarded. The treatment effect on midge density was assessed by analysis of variance (ANOVA). The treatment effect on total midge mass was assessed by ANCOVA, with midge density as the covariate and both mass and density log transformed. Although mosquito density varied within treatment groups, I ignored this natural variation to allow unambiguous measurement of the effect of the density manipulation, as opposed to other variables that might covary with density in natural pitchers.

Interactions between species can be evaluated using any of several measures of performance (Abrams 1987).

My procedure compared average mass per individual, calculated for each pitcher, among treatments. I assumed that average mass is an estimator of average lifetime reproductive success.

Artificial pitcher larval growth experiment

In 1992 I tested the effect of midges on mosquitoes in artificial pitchers. The artificial pitchers were 50 mL polypropylene centrifuge tubes (Nunc, Naperville, Illinois, USA), painted outside (Interlux Supreme high gloss paint, green #80-CC-5, International Paints [Canada]) to reduce light levels and prevent algal growth. These tubes are similar in volume to large natural pitchers. However, artificial pitchers differ from real ones in thermal (S. B. Heard, *unpublished data*) and chemical (Bradshaw and Creelman 1984) properties. I started each tube on 6 August with 15 mL of distilled water and two drops of natural pitcher fluid as a bacterial, protozoan, and rotifer inoculum. To each tube I added either 8 or 30 first, second, or third instar midge larvae, and either 5 or 15 first or second instar mosquito larvae. Tubes were also designated for low or high food levels, which received 3 and 8 freeze-killed ants during the experiment. Treatments were combined in a fully crossed factorial design, with each combination replicated 8 times (total $n = 64$ tubes). Larval densities were within the range for natural pitchers at the study site. I kept size distributions of larvae as consistent as possible among replicates. I covered the mouth of each tube with bridal tulle ($\approx$1 mm mesh) to prevent further colonization.

I placed the tubes in the study bog, partially embedded in the *Sphagnum* mat, so that thermal, light, and rainfall regimes resembled natural conditions. I arranged the tubes in four blocks of 16 to minimize risk of loss to moose trampling, and I randomized positions of tubes within blocks. I gave the low food tubes 2 ants on 6 August and 1 on 18 August, and the high food tubes 2 ants on 6 August, 3 on 18 August, and 3 on 24 August. On 3 September, I collected the tubes and counted, dried, and weighed all surviving larvae of each species. I compared surviving mosquito densities and total mosquito masses (both log transformed) among treatments using ANOVAs.

Because I used two mosquito densities, this experiment also allowed a second test of the effect of mosquitoes on midges. I compared surviving midge densities and average per-individual masses (both log transformed) using ANOVAs. Here I examined average per-individual masses, rather than total masses as for mosquitoes, because surviving midge densities differed between mosquito treatments.

Midge mass–mosquito performance correlations

I returned to the food supplementation data to test for an association of midge biomass and mosquito performance in natural, unmanipulated pitchers. I examined residuals from the mosquito ANCOVAs (total mosquito mass vs. mosquito density and food treatment). Each residual represents the deviation of the mass of mosquitoes in a pitcher from the average, corrected for mosquito density and for food treatment. I refer to these residuals as mosquito condition, and they can be thought of as relative indices of mosquito body mass and hence of potential lifetime reproductive success. I plotted mosquito condition against log-transformed total midge mass separately for control and food supplemented treatments within each of the four experiments.

I used similar analyses to examine three other data sets. Two of these were censuses of unmanipulated pitchers, from spring 1989 and spring 1991. The third was a combined data set from spring 1992, involving some unmanipulated pitchers and some pitchers subjected to a *B. fletcheri* manipulation that had no effect on mosquito or midge density or mass (Heard 1993). In these analyses I used residuals from a regression of total mass on density rather than from an ANCOVA, but the logic is otherwise identical.

Any positive effect of midges on mosquitoes should lead to positive correlations of mosquito condition and midge mass for unmanipulated pitchers. Any negative interaction should produce negative correlations. I chose this analysis, rather than the converse analysis of midge residual and mosquito mass, in light of the results of the mosquito density manipulation experiment and the artificial pitcher larval growth experiment. Finally, I compared the correlations between food-supplemented and unmanipulated pitchers. If the mechanism for the midge–mosquito interaction involves food resources, the interaction and therefore the correlations should disappear when resources are not limiting.

Artificial pitcher particle supply experiments

In 1991 I examined the effect of midges on particle levels in artificial pitchers. I set up centrifuge tube pitchers, as described above (see *Artificial pitcher larval growth experiment*), on 15 June. I added 0, 8, or 16 final instar midge larvae and either 2 or 4 ants to each tube. I used 6 replicate tubes per treatment (total $n = 36$), and placed these tubes in the bog in three blocks of 12. On the 6th, 12th, 18th, and 24th d of the experiment, I mixed the fluid in each tube and removed a 2 mL aliquot. This experiment required an artificial pitcher approach because fluid in a real pitcher cannot be well mixed without destroying the pitcher.

I fixed the fluid samples in 4% formalin and refrigerated them for later examination. I stained 100–200 μL subsamples with a DNA-binding fluorescent stain (25 min at 0°C in 5 nmol/L DAPI [4′,6-diamidino-2-phenylindole; Sigma Chemical, St. Louis, Missouri, USA]). I then filtered the subsamples onto black polycarbonate 0.2 μm membrane filters (Nuclepore, Costar, Cambridge, Massachusetts, USA) and examined them by epifluorescence microscopy (excitation wavelength 365 nm, 400× magnification). This technique allows

separate enumeration of bacteria, protozoa, algal cells, and organic detritus (Walker et al. 1988). None of my samples contained algae.

I analyzed counts for bacteria, which were by far the most numerous type of particle. Like most mosquitoes, *W. smithii* likely consumes a mixed diet of bacteria, protozoa, and nonliving organic particles (Istock et al. 1975, Fish and Hall 1978, Bradshaw and Creelman 1984, Dahl et al. 1987, Laird 1988:357, Merritt et al. 1992). While the exact size range of particles filtered by *W. smithii* is unknown, bacteria are likely to be an important diet component, as even the much larger *Culex pipiens* efficiently retains particles <1 μm in size (Dadd 1971). Bacterial counts, then, may be interpreted in two complementary ways: first, as a direct measure of food supply for mosquitoes, and second, as a reflection of increased nonliving particle supply (because comminution of detritus facilitates bacterial growth; Fenchel 1970, Cummins 1974, Hargrave 1976, Meyer and O'Hop 1983, McArthur and Barnes 1988).

For each subsample I counted bacteria in a set area of each of 10 fields spaced systematically across the filter surface. I corrected for the volume of the stained subsample, making counts per unit mixed volume, or equivalently, per unit surface area (in a filling cylindrical tube underwater surface area is a linear function of volume). Because the tubes were allowed to accumulate rain or to lose water by evaporation, patterns in per-volume counts across dates reflect volume changes as well as changes in bacterial populations. I did not attempt to correct for volume to get counts on a per-pitcher or per-bottom-area basis. It is not clear whether a bacterial count per mixed volume, per surface area, per bottom area, or per pitcher is most relevant to filter-feeders that may also graze along surfaces (see Merritt et al. 1992). However, because all artificial pitchers were identical in size and shape, and experienced identical thermal and rainfall regimes, comparisons of counts among treatments within dates are unaffected by the per-volume/per-pitcher distinction or by the volume changes.

I analyzed bacterial counts in two complementary ways. First, I used a repeated measures ANOVA to compare counts between treatments and across dates. The main effect for date is uninteresting because of large volume changes. For within-subjects effects, I report results for multivariate tests based on Wilks' λ. Tests based on Pillai's Trace, Hotelling-Lawley Trace, or univariate statistics did not differ appreciably. In the within-subjects analysis, I did not pool nonsignificant interaction sums of squares (see *Statistical methods*) because I was not interested in testing or estimating the date main effect. Second, where there were significant treatment × date interactions, I examined treatment effects separately at each of the four dates with ordinary ANOVAs. In date-by-date analyses I used an adjusted significance criterion of $\alpha = 0.013$ to maintain experiment-wise $\alpha = 0.05$.

I conducted a second particle supply experiment in fall 1992, with early rather than late instar larvae. Methods were identical to those described above, except that tubes were set up 2 August with 0, 10, or 20 first and second instar midge larvae, all tubes received 4 ants, and each treatment was replicated 9 times.

Statistical methods

Statistical analyses were performed with SAS Version 6.03 (SAS Institute 1988). Tests were based on type III sums of squares and all treatment effects were considered fixed. Analyses with more than one independent variable were initially performed with full models, but when interactions were not significant I used a pooling procedure to improve estimates of error variance and increase error degrees of freedom (except in the repeated measures ANOVA as noted above, see *Artificial pitcher particle supply experiments*). There is no universally accepted pooling procedure for ANOVA, with recommendations varying from seldom pooling (e.g., Zar 1984) to pooling all nonsignificant interactions (e.g., Bennett and Franklin 1954). However, pooling nonsignificant interactions is the normal procedure in ANCOVAs (Zar 1984). Therefore, for consistency among analyses, in both ANOVA and ANCOVA models I dropped nonsignificant ($P > 0.05$) interactions and pooled those sums of squares with the error. In three- and four-way analyses I pooled sequentially, with the highest level interaction pooled first and the new error variance used to check the next level interactions.

Because I was concerned about test assumptions, I determined some probabilities by comparing test statistics to those calculated for 500 randomizations of the data (Manly 1991). I used randomization for ANOVA/ANCOVA/regression Fs within a factor of ± 3 of the $\alpha = 0.05$ critical value and on correlation coefficients within a factor of ± 1.4 of the $\alpha = 0.05$ critical value. These bounds were arbitrary, but since I found no serious discrepancies between randomization and tabulated probabilities, I considered randomizations unnecessary where test statistics were more extreme.

Results

Food supplementation experiments

In two of the four food supplementation experiments, >3% of the pitchers lacked mosquitoes. In neither case was the occurrence of zeroes associated with experimental treatment (fall 1990, 12 zeroes, $G = 3.77$, $P = 0.052$; fall 1991, 23 zeroes, $G = 0.032$, $P = 0.86$). Midge zeroes were rare. Therefore, discarding zero counts was not problematic.

Both mosquitoes and midges were food limited. Masses of both species responded to food supplementation in 1990 and in 1991 (Table 2). A representative set of data is plotted in Fig. 1. All analyses showed homogeneous slopes and strong food supplementation

TABLE 2. ANCOVA results for food supplementation experiments. Dependent variables are total midge masses (analyses on left) and total mosquito masses (analyses on right). Density is the covariate. Masses and densities were log transformed. All slopes were homogeneous ($P > 0.05$).

Analyses for total midge mass				Analyses for total mosquito mass			
Source	df	MS†	Effect‡	Source	df	MS†	Effect‡
			Spring 1990				
Density	1	70.72	0.67 ± 0.04*	Density	1	33.45	0.59 ± 0.05*
Food	1	33.33	1.18/2.71	Food	1	28.49	0.82/1.77
Error	195	0.26		Error	191	0.27	
			Fall 1990				
Density	1	113.93	0.83 ± 0.06*	Density	1	97.63	0.68 ± 0.04*
Food	1	62.27	0.71/2.34	Food	1	51.00	0.77/2.35
Error	179	0.37		Error	171	0.27	
			Spring 1991				
Density	1	56.01	0.75 ± 0.05*	Density	1	24.83	0.67 ± 0.07*
Food	1	15.57	1.16/2.62	Food	1	25.74	0.59/1.67
Error	94	0.23		Error	95	0.26	
			Fall 1991				
Density	1	60.95	0.85 ± 0.08	Density	1	37.02	0.90 ± 0.08
Food	1	10.45	1.65/3.42	Food	1	11.16	0.44/0.97
Error	91	0.27		Error	69	0.30	

* Slopes significantly less than one ($P < 0.05$).

† All F ratios of these mean squares and associated errors have $P < 0.0001$.

‡ For density, effect columns show slopes of covariate regressions (estimated slopes ± 1 SE); for food, effect columns show predicted values for total mass (mg; back-transformed) calculated for the mean (before transformation) larval density, for control/food-supplemented pitchers

effects. Food limitation and density-dependent growth are also suggested by the fact that slopes were less than one in all covariate regressions (log-transformed total mass vs. log-transformed density; six of eight significantly so, Table 2). Food limitation for both species was consistent, occurring in both seasons and for generations emerging in 1990, 1991, and 1992. In all cases food-supplemented pitchers show at least a 100% mass increase at average larval densities. Unexplained variation (Fig. 1) is at least partly attributable to variation in natural prey capture rates (Wolfe 1981, Cresswell 1991, 1993) and microclimate (Kingsolver 1979, Bradshaw 1980).

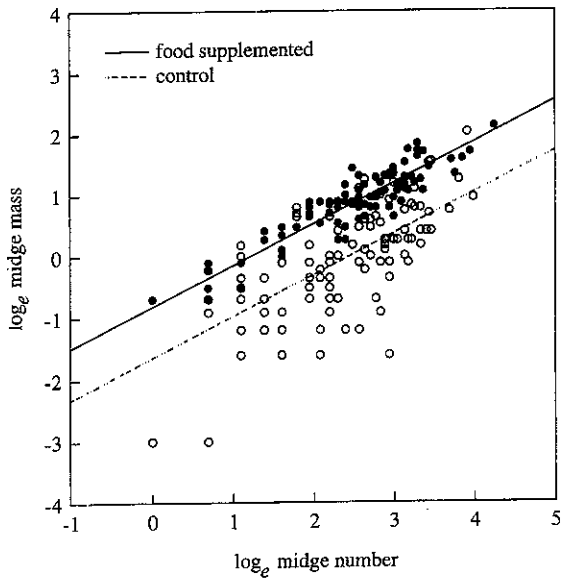

FIG. 1. Representative data for food supplementation experiments (midges, spring 1990). Total midge mass is plotted against midge density (both log transformed); open symbols are for control pitchers and closed symbols for food-supplemented pitchers. Lines are from the ANCOVA analysis after pooling of interaction sum of squares.

Mosquito density manipulation experiment

In natural pitchers given additional mosquito larvae, mosquito densities at harvest were increased about fourfold over controls (means ± 1 SE [n]: control 2.22 ± 0.43 larvae/pitcher [45 pitchers], treatment 8.81 ± 0.63 larvae/pitcher [43 pitchers]). The biomass difference was slightly less (control 0.14 ± 0.03 mg, treatment 0.48 ± 0.06 mg). The densities bracket the grand mean mosquito density for the period 1989–1992 (5.55 ± 0.18 larvae/pitcher [1137 pitchers]). The control values are low, but they are in line with those found in other spring 1992 experiments not reported here (3.76 ± 0.50 larvae/pitcher [80 pitchers] and 2.22 ± 0.28 larvae/pitcher [116 pitchers]).

Mosquito addition had no detectable effect on midge density (ANOVA $F_{1,85} = 3.33$, randomization $P = 0.07$; Fig. 2) or total midge mass (ANCOVA $F_{1,84} = 0.08$, $P = 0.78$ after pooling nonsignificant treatment–covariate interaction; Fig. 2). The lack of response in total mass is particularly striking, because mass should be most sensitive to food availability.

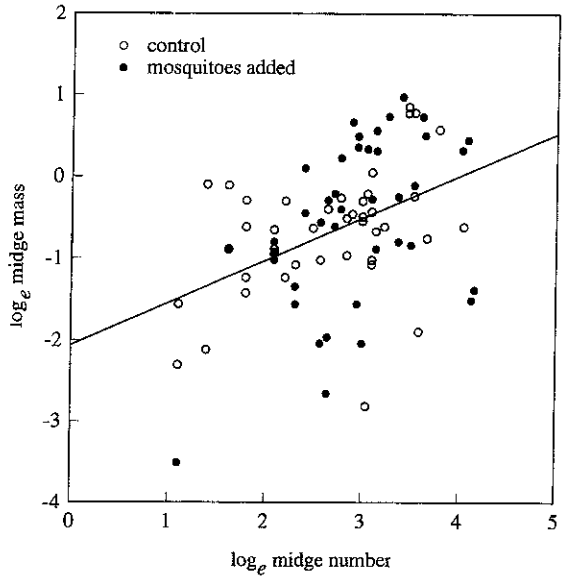

FIG 2. Total midge masses and densities from the mosquito density manipulation experiment Line is the common regression Treatments did not differ significantly in ANCOVA

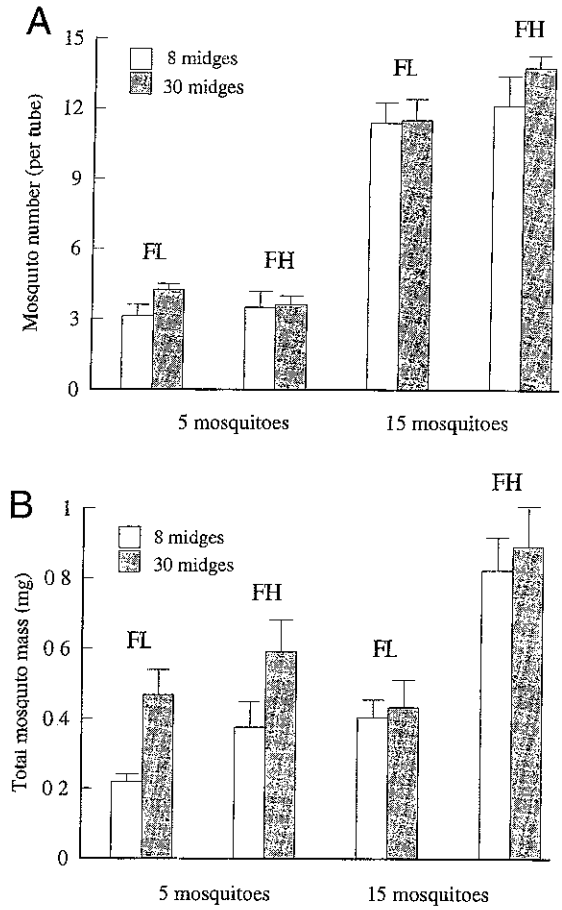

FIG. 3. Mosquito density (A) and total dry mass (B) from artificial pitcher larval growth experiment, averaging over blocks. "FL" and "FH": food treatments, low and high Error bars show 1 SE, from raw data

Artificial pitcher larval growth experiment

There were a variety of treatment effects on larval densities and masses in artificial pitchers. An effect on density in this experiment is equivalent to an effect on survivorship, because starting densities were fixed.

Mosquito survivorship tended to be higher in high midge density tubes, with ≈0.14 more survivors, but the difference was not significant (Table 3, Fig. 3A). Mosquito mass, and therefore growth, was greater in tubes with more midges (Table 3, Fig. 3B) as well as tubes provided with more food. The response to food level was stronger in the high mosquito density treatments, which presumably were more strongly food limited. The mosquito × midge interaction was nearly significant ($P = 0.056$).

Midge survivorship was slightly lower (Table 4, Fig. 4A) in high mosquito density tubes Per-individual midge mass was also lower in these tubes (Table 4, Fig 4B), as well as in the low food treatment tubes The apparent negative effect of mosquitoes on midges in this experiment contrasts with their lack of effect in natural pitchers

Midge mass–mosquito performance correlations

In all seven data sets involving unsupplemented pitchers, mosquito condition was positively correlated with midge mass ($0.28 < \text{Pearson's } r < 0.55$, all $P < 0.012$; Table 5). These correlations were consistent over four generations of larvae The results of the two pre-

TABLE 3. ANOVA results for mosquito density and total mosquito mass (both log transformed) in artificial pitcher larval growth experiment. Interactions not listed were nonsignificant ($P > 0.05$)

Source	Density			Total mass		
	df	MS	P	df	MS	P
Mosquito density treatment	1	18.73	<0.0001	1	0.31	<0.0001
Midge density treatment	1	0.31	0.059*	1	0.14	0.012*
Food treatment	1	0.0075	0.77	1	0.51	<0.0001
Block	3	0.19	0.11*	3	0.037	0.12*
Mosquito × food				1	0.12	0.014*
Mosquito × midge				1	0.074	0.054*
Error	57	0.080		55	0.018	

* Probability determined by comparing test statistics to those calculated for 500 randomizations of the data (Manly 1991).

TABLE 4. ANOVA results for midge density and per-individual midge mass (both log transformed) in artificial pitcher larval growth experiment All interactions were nonsignificant ($P > 0.05$)

Source	Density			Per-individual mass		
	df	MS	P	df	MS	P
Mosquito density treatment	1	0.94	0.04*	1	0.94	0.014*
Midge density treatment	1	16.38	<0.0001	1	3.35	<0.0001
Food treatment	1	0.097	0.49	1	4.99	<0.0001
Block	3	2.52	<0.0001	3	0.77	0.006*
Error	57	0.20		55	0.18	

* Probability determined by comparing test statistic to those calculated for 500 randomizations of the data (Manly 1991)

ceding experiments strongly suggest that the correlations arise from the facilitation of mosquito growth by midges. A positive effect of mosquitoes on midge performance would also produce a positive correlation, but this is ruled out by the absence of such an effect in the mosquito density manipulation or the artificial pitcher larval growth experiment. The correlations, furthermore, cannot be explained by similar responses of both species to variation in prey capture among pitchers. In one set of pitchers, the dry mass of remaining carcass material was recorded, and its inclusion in a partial correlation analysis only strengthened the midge–mosquito correlation (S. B. Heard, *unpublished data*).

In contrast, the four sets of data from food-supplemented pitchers show no correlations between mosquito condition and midge mass ($-0.07 <$ Pearson's $r < 0.16$, all $P > 0.18$; Table 5). Representative data for control and food-supplemented pitchers are shown in Fig. 5.

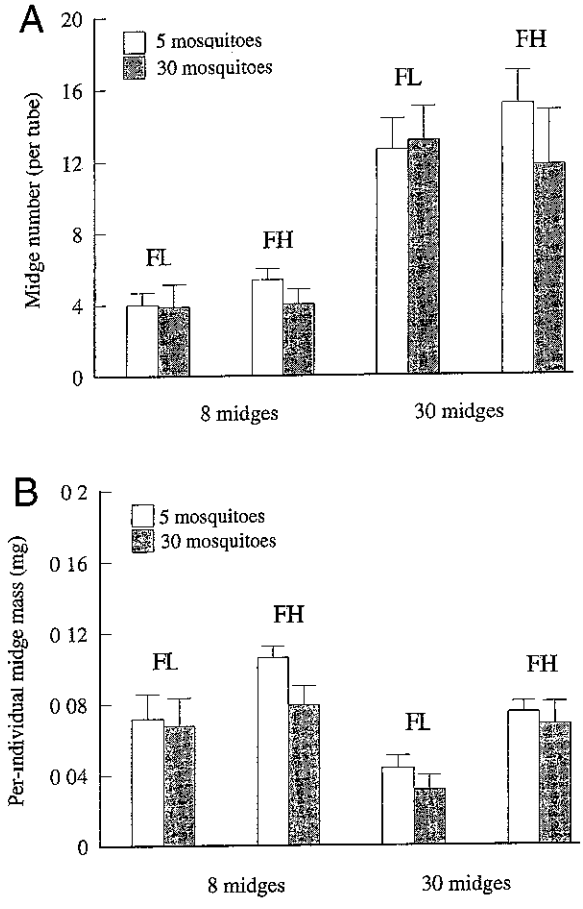

FIG 4. Midge density (A) and per-individual dry mass (B) from artificial pitcher larval growth experiment, averaging over blocks. "FL" and "FH": food treatments, low and high Error bars show 1 SE, from raw data

Artificial pitcher particle supply experiments

Bacterial counts in the particle supply experiment depended on midge treatment and time. The conspicuous decrease over time (Table 6A, Fig. 6) was due at least in part to dilution by rain early in the experiment and is therefore of little biological interest. There was a date × midge interaction, but no date × food interaction. The date-by-date ANOVAs confirm that the date × midge interaction arose from very different time courses for the 0 midge treatment compared to the 8 and 16 midge treatments. For both food treatments, tubes with 8 or 16 midges showed much higher bacterial counts at the first sampling date, but lower counts at the second sampling date (Fig. 6, Table 7). Comparisons among tubes within one date, and therefore these reversals in ranks, are independent of dilution effects. At later sampling dates midge treatments did not differ. The rank reversals are not surprising because no new resource was entering the tubes. Midges can accelerate the breakdown of the carcass material from which particles and bacteria are derived, but they can only decrease the total amount of it.

The tests of between-subjects effects in the repeated measures ANOVA (Table 6B) are equivalent to comparisons among treatments of bacterial counts integrated over the duration of the experiment. Bacterial counts were higher in the high food treatment, but did not differ among midge treatments. Interpretation of these tests may be complicated, however, by the rainwater dilution.

In the fall 1992 experiment, no treatment effects could be detected (Table 8), but the trends resembled the 1991 results. High midge density tubes tended to show higher bacterial counts, although this time there were

TABLE 5. Correlations of mosquito condition (residual after regression of mosquito mass on mosquito density, both log transformed) and log-transformed total midge mass "FS" indicates data from food supplementation experiments

Data set	Unsupplemented			Supplemented		
	r	*n*	*P*	*r*	*n*	*P*
Spring 1989	0.442	115	<0.0001			
Spring 1990 FS	0.304	99	0.0022	0.076	93	0.47
Fall 1990 FS	0.288	90	0.004*	0.159	80	0.18*
Spring 1991	0.367	107	<0.0001			
Spring 1991 FS	0.362	46	0.012*	0.049	48	0.74
Fall 1991 FS	0.541	36	0.0007	−0.062	36	0.72
Spring 1992	0.361	120	<0.0001			

* Probability determined by comparing test statistics to those calculated for 500 randomizations of the data (Manly 1991).

no rank reversals between dates (Fig. 7). The small first and second instar larvae used in this experiment may not have been effective at breaking up ant carcasses, which have more resistant exoskeletons than most other pitcher-plant prey items.

DISCUSSION

Resource limitation

Wyeomyia smithii is known to be generally resource limited in the southern and middle parts of its range (Istock et al. 1976, Bradshaw and Holzapfel 1986, 1990). However, the situation in more northern populations has been unclear. Several authors have maintained that resource limitation is weak or absent in the north (Istock et al. 1976, O'Meara et al. 1981, Lounibos et al. 1982, Bradshaw and Holzapfel 1986, 1990). However, Farkas and Brust (1985) found that adult size and fecundity responded to larval food supplementation at three sites in Manitoba and Ontario (50°–54° N), albeit in an experiment lacking a true control. My food supplementation results echo and extend those of Farkas and Brust (1985) in demonstrating consistent, strong limitation in a northern population. For *Metriocnemus knabi*, my results apparently represent the first demonstration of resource limitation and contrast with Wiens' (1972:16) assumption that food for midges is rarely in short supply.

The midge–mosquito interaction

Although the artificial pitcher experiment suggests inhibition of midges by mosquitoes, in natural pitchers no such effect was detectable. Failure to detect a mosquito treatment effect in natural pitchers is unlikely to have resulted from a lack of statistical power. The manipulation involved a large increase in mean mosquito density, from 2.2 to 8.8, and the higher density exceeds average populations even for high-density years. There was ample time for a response, as on similar time scales

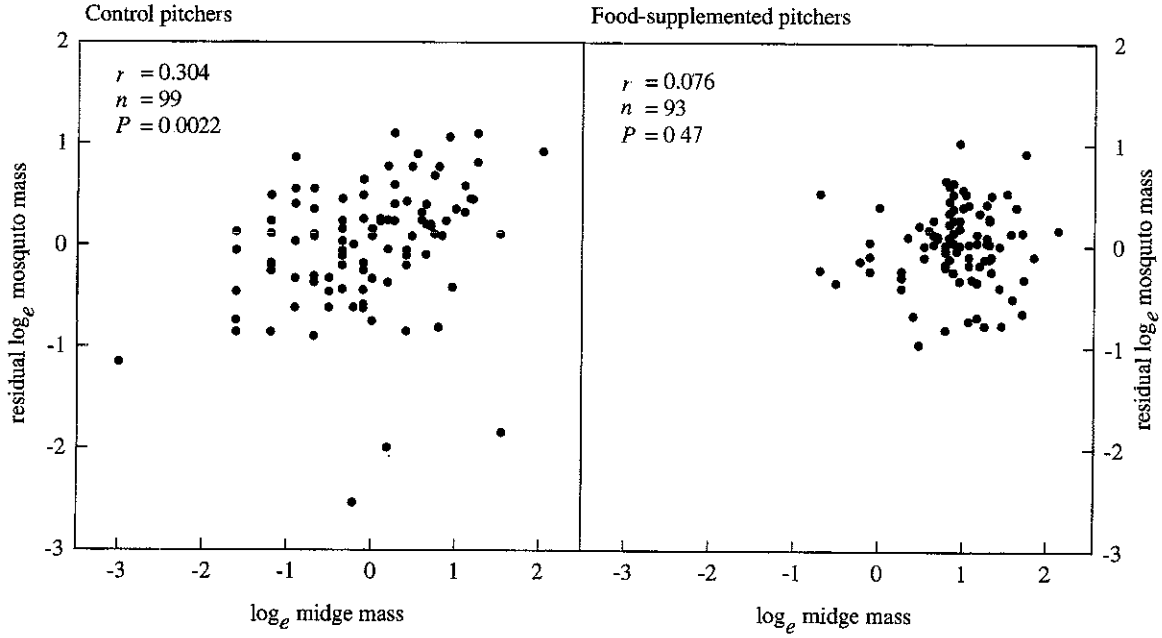

FIG. 5. Representative plots of mosquito condition (residual after regression of total mosquito mass on mosquito density, both log transformed) against total midge mass (log transformed), spring 1990 food supplementation experiment.

TABLE 6. Repeated measures ANOVA results for bacterial counts in spring 1991 artificial pitcher particle supply experiment. Interactions not listed were nonsignificant ($P > 0.05$).

A. Within-subject effects					B. Between-subjects effects			
Source	Wilks' λ	df	F	P	Source	df	MS	P
Date	0.1074	3, 28	77.6	<0.0001	Midge	2	24 220	0.28*
Date × midge	0.3662	6, 56	6.09	<0.0001	Food	1	86 530	0.046*
Date × food	0.8960	3, 28	1.08	0.36*	Block	2	30 790	0.17*
Date × block	0.7683	6, 56	1.31	0.27*	Error	30	17 490	

* Probability determined by comparing test statistics to those calculated for 500 randomizations of the data (Manly 1991).

midges responded strongly to food supplementation and mosquitoes responded to midge treatments.

If the negative effect in artificial pitchers is real, it may be attributable to behavioral interference. Midge larvae aggressively attack other larvae they encounter (Wiens 1972:16), and this behavior presumably has time and energy costs. Real pitchers are trumpet shaped, and midge larvae are found in the narrow part of the trumpet away from swimming and grazing mosquito larvae. Centrifuge tubes are flatter bottomed, and midges in the artificial pitcher experiment were in frequent proximity to grazing mosquitoes. Shape differences could therefore account for the presence of a mosquito density effect in the artificial, but not in natural, pitchers.

Bradshaw (1983) also found a negative effect of mosquitoes on midges: at very high mosquito densities in the laboratory, midge pupation success decreased. However, the effect in that study resulted largely from low midge pupation success at extremely high mosquito densities (80 larvae/pitcher). No mechanism for the decrease was identified, with waste product toxicity or behavioral interference being possibilities at such high densities (Wiens 1972:16, Peters and Barbosa 1977, Carpenter 1983). Densities of 80 larvae per pitcher may occur at the southern limit of *W. smithii*'s range (Bradshaw 1983; but see Bradshaw and Holzapfel 1986), but at my site they exceed the grand mean mosquito density by more than an order of magnitude and the highest single-pitcher density ever recorded (46; of 1137 pitchers) by nearly a factor of 2. Mosquito populations at my site are not unusually low for the region (S. B. Heard, *personal observations*; see also Paterson [1971] for New Brunswick populations).

Whatever the interaction may be at very high densities and in artificial pitchers, midges in natural populations at my study site seem unaffected by mosquitoes. However, a small negative effect cannot be entirely ruled out.

The effect of midges on mosquitoes is clearer. Midges facilitated mosquito growth in the artificial pitcher experiment (Table 3, Fig. 3). This result is consistent with that of Bradshaw (1983), who found earlier mosquito pupation at high midge densities in an experiment using real pitchers in the laboratory. Laboratory experiments and experiments using artificial pitchers allow unambiguous assignment of causality, but they also introduce uncertainty about relevance to natural populations. The correlative evidence (Table 5) confirms that the facilitation of mosquitoes by midges is real and consistently detectable in unmanipulated natural populations.

The repeated absence of a midge–mosquito interaction in food-supplemented pitchers (Table 5) is revealing. Facilitation would be expected under natural conditions but not under food supplementation only if the interaction was resource mediated (and supplementation overcame resource limitation). The midge–

TABLE 7. Date-by-date ANOVA results for bacterial counts in spring 1991 artificial pitcher particle supply experiment. All interactions were nonsignificant ($P > 0.05$). An adjusted significance criterion of $\alpha = 0.013$ gives an experiment-wise $\alpha = 0.05$ for four ANOVAs.

A. Day 6				B. Day 12			
Source	df	MS	P	Source	df	MS	P
Midge	2	424 600	0.0002	Midge	2	99 000	0.0002
Food	1	120 200	0.08*	Food	1	17 520	0.15*
Block	2	27 480	0.49	Block	2	13 010	0.24*
Error	30	37 350		Error	30	8 263	
C. Day 18				D. Day 24			
Source	df	MS	P	Source	df	MS	P
Midge	2	2998	0.49	Midge	2	3142	0.54
Food	1	4838	0.29*	Food	1	1580	0.58
Block	2	4185	0.37	Block	2	3327	0.52
Error	30	4099		Error	30	5035	

* Probability determined by comparing test statistics to those calculated for 500 randomizations of the data (Manly 1991).

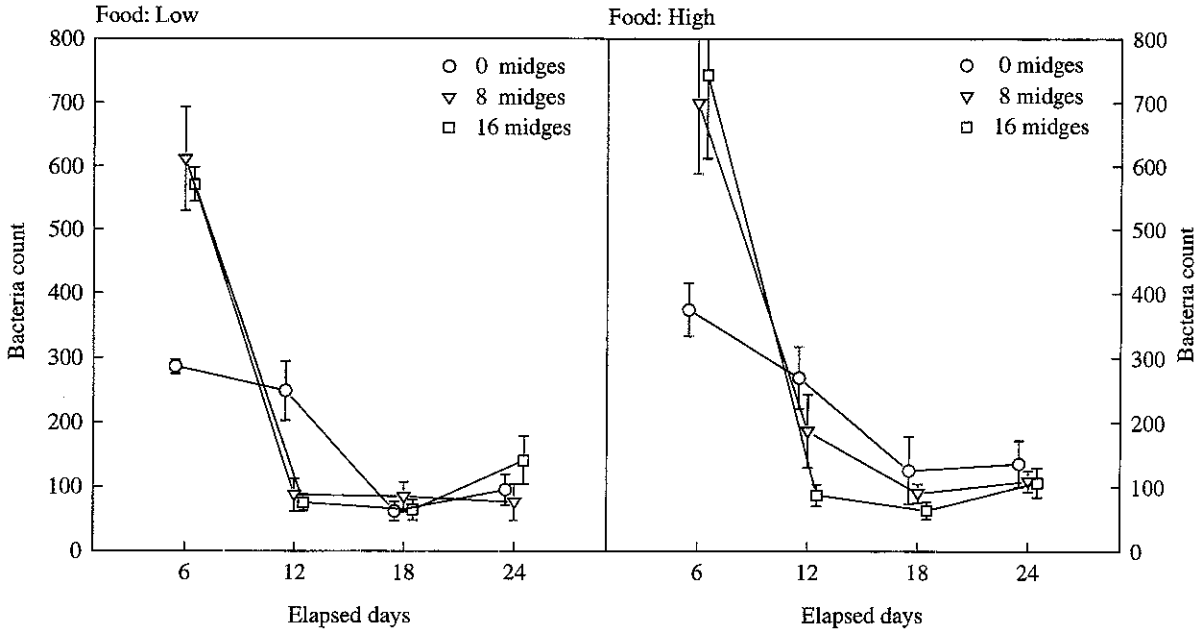

FIG. 6 Bacterial counts and numbers of midges per tube in the three treatments from the spring 1991 artificial pitcher particle supply experiment. Bacterial counts are in arbitrary relative units; symbols show means ± 1 SE

mosquito facilitation, then, must have a trophic mechanism.

Resource processing by midges

In addition to consuming carcass material, midges can also play an important role in processing it, as reflected in the higher short-term bacterial counts in artificial pitchers with midge larvae (Figs. 6 and 7). Earlier appearance of bacteria in the presence of midges means improved food availability for mosquitoes, both directly and as a sign of increased comminution. In real pitchers midge effects would be stronger than in my short-term experiments, as new prey items are continually being captured. The accelerated provision of particles likely underlies the facilitative effect of midges on mosquitoes.

Several studies have demonstrated analogous processing effects of shredding invertebrates in streams (e.g., Short and Maslin 1977, Wallace et al. 1982, Mulholland et al. 1985). Effects of processing by shredders on stream collectors, however, have rarely been tested (Winterbourn et al. 1981, Richardson and Neill 1991, Heard 1994*a*). Processing by consumers has been suggested in many other systems and is probably common (reviewed in Heard 1994*a*).

Processing chains and the midge–mosquito interaction

The pitcher-plant midge–mosquito commensalism makes clear the importance of explicit consideration of resource dynamics. In isolation, the results of the food supplementation experiments paradoxically suggest a competitive interaction. Both species were limited by carcass supply, and such joint limitation by a single resource is often considered typical of competitive interactions, or even as defining them (e.g., Begon et al. 1986:199, Ehrlich and Roughgarden 1987:247). Indeed, discussions of pitcher-plant inquilines have often been couched either in terms of detecting competition (e.g., Bradshaw 1983) or in terms of accounting for the coexistence of presumably competing species (e.g., Fish and Hall 1978, Barton and Smith 1984).

Closer examination reveals that the picture of joint resource limitation of pitcher-plant inquilines is incomplete. The system is better viewed as a processing chain (Heard 1994*a*, *b*), where midges are limited by solid carcass material and mosquitoes by particles, and midges both consume and process carcasses. The joint limitation of midges and mosquitoes by carcass supply can then be reconciled with the commensal (+, 0) interaction between them.

I previously (Heard 1994*a*, *b*) developed simple theoretical models of processing chain interactions. While these models were not intended as precise descriptors of midges and mosquitoes, the major conclusions drawn from them are robust to model details and they provide some insights. The two key elements of these systems are (1) the unidirectional flow of resource between conditions (here, from solids to particles), and (2) the dual role of the upstream consumers (here, midges) as consumers and as processors.

The probable lack of an effect of mosquitoes on midges corresponds to a general feature of processing chains: because resource flow is unidirectional, down-

TABLE 8. Repeated measures ANOVA results for bacterial counts in fall 1992 artificial pitcher particle supply experiment. Interactions not listed were nonsignificant ($P > 0.05$)

A. Within-subjects effects					B. Between-subjects effects			
Source	Wilks' λ	df	F	P	Source	df	MS	P
Date	0.1036	3, 20	57.7	<0.0001	Midge	2	19 790	0.26*
Date × midge	0.7786	6, 40	0.89	0.53*	Block	2	44 250	0.042*
Date × block	0.7016	6, 40	1.29	0.25*	Error	22	14 580	

* Probability determined by comparing test statistics to those calculated for 500 randomizations of the data (Manly 1991)

stream consumers cannot influence upstream consumers through trophic interactions. Processing chain interactions can be either amensal or commensal, depending on whether or not the benefit to the downstream consumer of increased processing by the upstream consumer outweighs the loss of resource to consumption. My experiments indicate that resource processing by midges in pitcher-plant leaves provides a net benefit to mosquitoes.

The two most important determinants of processing chain interactions involve processing rates and time horizons (Heard 1994*a*, *b*). Commensalism is likely when there is substantial loss of unprocessed resource from the system and when processing in the absence of the upstream consumer is slow. Commensalism is also likely, regardless of processing rates, when effects are evaluated at a time horizon short of equilibrium—in fact, all processing chain interactions are commensal at sufficiently short time horizons (Heard 1994*b*). For pitcher-plant midges and mosquitoes I cannot discriminate unambiguously between these alternatives, but some discussion is possible.

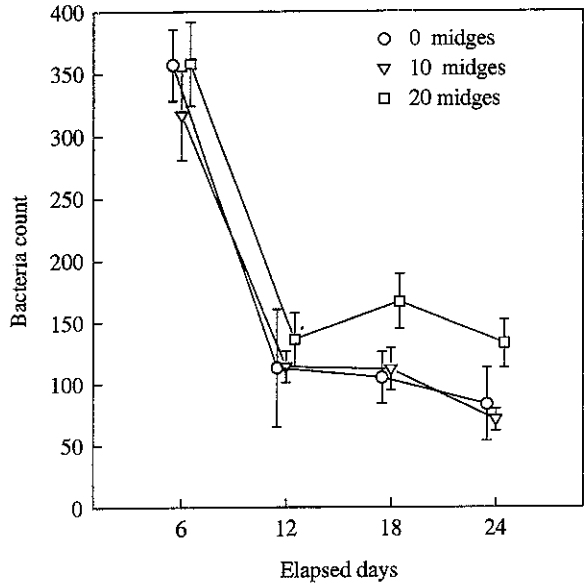

FIG. 7. Bacterial counts and midge number per tube from the fall 1992 artificial pitcher particle supply experiment. Bacterial counts are in arbitrary relative units; data show means ± 1 SE.

Rapid resource loss seems unlikely to account for the midge–mosquito commensalism. Export of solid material from pitchers is negligible, so consumption by midges represents a real loss to mosquitoes of resource which would eventually appear in particulate form. The commensalism may instead be due to the relatively short time horizon that is relevant to the growth of larvae in a pitcher. Pitcher assemblages probably never reach equilibria, where combined maintenance costs for a pitcher's inhabitants balance prey input, and neither growth nor further resource accumulation is possible. Larvae pupate and leave pitchers on seasonal cues (Paris and Jenner 1959, Bradshaw and Lounibos 1972), and prey capture rates remain high enough to support further growth very late in the season despite a decline in old pitchers (Fish and Hall 1978; S. B. Heard, *unpublished data*).

If the midge–mosquito–prey system did reach an equilibrium it is possible that the interaction would be reversed—mosquitoes in pitchers *without* midges might actually do better because they would eventually have access to all the nutrients in the prey. Such temporal reversals in interactions are general features of equilibrium-amensal processing chains (Heard 1994*b*). For this reason it is critical that a putatively commensal processing chain interaction be assessed at the time horizon that is relevant in nature. In my spring experiments and correlations larvae were weighed at or near the completion of larval growth, so we can be sure that the midge–mosquito commensalism is not an artifact of an experimentally imposed short time horizon.

Whatever the immediate reason, it is clear that pitcher-plant mosquitoes benefit from midge-mediated resource processing, and this benefit is substantial enough to outweigh consumption by midges of the carcass material whose supply ultimately limits mosquito growth. The process of untangling this complex interaction illustrates the utility of models which explicitly consider resource, as well as consumer, dynamics.

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