

A Closer Look at the Behavioral Dynamics of Shredders in Leaf Litter Breakdown

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Abstract

Shredding invertebrates in streams perform extremely important ecological functions. The processing of organic matter by detritivores provides the rest of the lotic system with necessary nutrients (Webster and Benfield 1986). Species richness of shredders has been associated with both increased (Jonsson et al. 2001, Naeem et al. 1994, Schwartz et al. 2000) and decreased (Creed et al. 2009, Malmqvist 1993) decomposition rates depending on how the species present interact with each other and their environments. Little has been done to look at the behavioral mechanisms underlying these differing functional responses. This study uses behavioral analysis to gain definitive insight into shredder interaction dynamics by videotaping the actions of caddisfly species *Pycnopsyche guttifer* and *Lepidostoma sp.* exposed to various leaf type and community composition treatments in controlled artificial streams. It was found that species process significantly less leaf mass when faced with interspecific competition. Further, the interspecific pressure in this study system was found to be interference based and not due to direct physical interaction between shredders. Based on behavioral analyses, this study concludes that detritivore species richness correlates negatively with ecosystem function when a competitively dominant species coexists with a separate functionally dominant species. Behavioral analysis can be a powerful tool in gaining additional insight into the dynamics of ecosystem functioning in streams.

Introduction

The breakdown of allochthonous inputs by invertebrates in lotic environments is something that has fascinated ecologists for years. It is an extremely important process because the activities of shredders result in a processing chain of nutrients down the stream continuum (Webster and Benfield 1986). This serves to maintain the biodiversity of various other functional groups which are dependent on the activity of shredders. This study investigates how species richness and leaf type affects production and behavior of shredders. Although previous studies have provided strong circumstantial evidence for certain invertebrate decomposition dynamics, very few have attempted to gain more definitive understanding of mechanisms by way of behavioral analysis of shredders.

A positive correlation between the richness of shredder species in a given environment and decomposition rates has been demonstrated in multiple studies (Jonsson

et al. 2001, Naeem et al. 1994, Schwartz et al. 2000); however other studies present circumstances under which a negative relationship can occur (Creed et al. 2009, Malmqvist 1993). The conflicting results appear to be dependent upon what types of dominant shredder species are present. Functionally dominant species are those which disproportionately perform important ecosystem functions (Creed et al. 2009), in this case by processing leaf litter at a rate much higher than co-occurring species. On the other hand, competitively dominant species gain access to resources by excluding others.

In cases where a functionally dominant shredder is present, increased biodiversity can greatly speed up decomposition (Schwartz et al. 2000). When a functional dominant such as *Pycnopsyche* is also a competitive dominant that trend is reversed (Creed et al. 2009). These doubly dominant species decrease biodiversity in stream segments by excluding other taxa, but leaf processing rates increase because they decompose litter more efficiently than those whom they exclude.

It is also likely that competitive dominants stake claim on leaf litter of higher quality. The quality of allochthonous input is typically determined by available nutrients, and it has been suggested that increased nitrogen content in leaves can play a role in preference and increased breakdown rates by shredders (Kaushik and Hynes 1969, Herbst 1982).

Work done in the past has looked at *what* ecosystem functions result from given conditions, and just posited as to why it turned out that way. It's been proposed that increased richness leads to mechanical facilitation for dominant species or that maybe intraspecific competition is more prevalent than interspecific competition (Jonsson et al. 2001). The goal of this project is to actually capture behaviors and interactions

throughout leaf breakdown using the caddisflies *Pycnopsyche guttifer* and *Lepidostoma sp.* so that I can analyze what effects are seen with more concrete data as to *why*. My hypotheses are as follows:

H1: Possibly a competitive and functional dominant, *P. guttifer* display more aggressive and interference behaviors when *Lepidostoma sp.* are also present, increasing their own feeding rates when faced with interspecific competition.

H2: The *Lepidostoma sp.* feeding action is at a faster rate on soft green leaves providing facilitation for faster *P. guttifer* consumption, but similar feeding actions on tough senescent leaves provide less facilitation.

H3: Both species spend more time feeding on the nitrogen-rich green leaves than the more nitrogen-depleted senescent ones, displaying a preference for increased nutrient content.

Materials and Methods

Site and setup

I utilized a system of closed loop artificial streams which I assembled outdoors on the property of the University of Notre Dame Environmental Research Center (UNDERC) in Land O' Lakes, WI. Each stream had a constantly replenished flow of fresh, cold water because I placed a water supply pipe at the beginning of the loop and a drain pipe at the end. In total, I set up thirty-two streams. I kept flow rates for the streams constant with a system of interconnected paddlewheels. I fitted the top of the streams with light-blocking fabric covers in order to prevent algal colonization. Use of these artificial streams allowed for me to maintain conditions uniformly, and to accurately compare results between all streams.

At the beginning of each stream, I set up two mesocosms to study the shredders. Each mesocosm consisted of a clear plastic cup 4 inches in diameter. The bottoms of the cups were made of 500 μm mesh so that processed leaf litter could fall through and into

the flow of the stream. Into each mesocosm I placed a leaf pack and community of shredders.

Treatments

The two leaf types I used were green and senescent leaves, both of the species *Alnus incana* (Speckled Alder). I put green leaves into the cups in half of the streams and senescent brown leaves into those of the other half. All mesocosms had 1.2g of leaf mass at the onset of the experiment.

I used two species of shredding caddisflies, *Pycnopsyche guttifer* and *Lepidostoma sp.*, as study organisms for this experiment. I used these species because prior surveys showed them to be two of the most abundant shredders in woodland streams surrounding UNDERC (Chris Patrick unpublished). The same surveys show that these two species do indeed coexist, though not commonly, in certain streams. I also preferred to use a species of the genus *Pycnopsyche* because of the findings of Creed et al. (2009) pertaining to *P. gentilis*.

I divided these two species into three treatments: *P. guttifer* and *Lepidostoma sp.* Together or each species alone. For the alone treatments, I put four individuals of *P. guttifer* into one of the mesocosms and fifty-six individuals of *Lepidostoma sp.* into the other. In streams where the two species were to be together, I put two *P. guttifer* and twenty-eight *Lepidostoma sp.* into each of the two mesocosms. These specific numbers were chosen in an effort to standardize biomass across all mesocosms, as it was determined before the experiment by weighing fifty individuals of each species that the *P. guttifer* specimens had an average of fourteen times greater mass than the *Lepidostoma sp.* specimens. Also, the stream surveys done prior to this study (Chris Patrick

unpublished) suggest that this experimental density of 450 *Lepidostoma sp.* and thirty-two *P. guttifer* per m² is comparable to densities seen in nature.

I equally crossed the two leaf types with the three configurations for shredder communities to come up with my array of mesocosm treatments (Appendix A). I set up 4 replicate streams for each treatment and kept shredders absent from the remaining 16 streams to serve as constants for the leaf decomposition portion of the experiment. I stratified the distribution of the treatments in the streams throughout the experimental setup (Appendix B). All mesocosms were inserted into the artificial streams simultaneously, each containing equal biomass.

Data Collection

I ran the experiment for 24 days. I collected behavioral data by way of video footage using a Sony Handycam DCR-DVD digital video camera fitted with a .5x magnification macro scale lens and an additional +4 magnification filter.

Over a span of days 11-17 of the experimental period, I taped for five separate days. I mounted the camera above the stream mesocosms and videotaped the shredders between the hours of 8am and 4pm. One day of taping consisted of me recording 10 min. of footage from each of 24 mesocosms. Eight of the 10 min. sessions were of *Lepidostoma sp.* alone, eight were of *P. guttifer* alone, and eight were of the species together in the same cups. I selected a focal individual to follow for each 10 min. recording session. I then analyzed the films using BEAST Student 2005 behavioral analysis software. Based on observations during filming, I selected several feeding and interaction behaviors to record for each focal organism (Appendix C).

At the conclusion of the 24 day experiment, I collected the total leaf mass left in each mesocosm in order to calculate the amount of leaf mass which was processed in different treatments.

Data Analysis

I treated each day's footage as a pseudo-replicate, and pooled these five pseudo-replicates for each mesocosm to obtain an average value for each of the actions. I used these pooled values as the data points for each true replicate.

I ran a 2-way ANOVA on relevant data points to determine the affects of leaf type (green or senescent) and community type (separate or alone) on the behavior of each of the species. Originally I set .05 as my alpha value for significance, but because I ran a series of multiple ANOVAs for each species, I had to do a procedure-wise correction on that alpha value. I used the Dunn-Sidak correction $(1-(1-\alpha)^{1/t})$ to get a new alpha significance value of .0064. For the singular test comparing the aggressive and defensive behaviors between species, I set .05 as my alpha value.

Results

Behavioral Tendencies

Frequency counts of specific behaviors for each species revealed differences in actions of the two. Across all treatments, *P. guttifer* performed significantly more acts classified as aggressive than did *Lepidostoma sp.* ($F=4.614$, $P=.042$). The frequency of these aggressive acts were not significantly influenced by community treatment ($F=.072$, $P=.791$) or leaf type ($F=4.238$, $P=.051$). *Lepidostoma sp.* likewise displayed significantly more defensive behaviors than *P. guttifer* ($F=12.05$, $P=.002$). Their defensive tendencies

were also not significantly affected by community treatment ($F=1.339$, $P=.259$) or leaf type ($F=1.929$, $P=.178$).

Time Budget

The basic time budget of focal individuals during this experiment was divided up into four general categories: feeding, moving, interacting and inactivity. The analysis of time spent feeding across the treatments provided the greatest measure of variation. The amount of time that individuals were feeding on the leave was strongly influenced by both species ($F=102.67$, $P<.001$) and community treatment ($F=47.15$, $P<.001$).

Lepidostoma sp. devoted a lot more time to feeding than did *P. guttifer*, averaging over 2 min. more of feeding per 10 min. observation session. Both species budgeted a significantly greater (*Lepidostoma sp.*: $F=37.7$, $P<.001$; *P. guttifer*: $F=11.79$, $P=.005$) amount of time to feeding in the single species treatments than when in the presence of interspecifics (Figs.1 and 2). These analyses of time spent feeding match up to the final calculations of leaf mass lost per treatment, where *Lepidostoma sp.* alone processed the most leaf mass, followed by *P. guttifer* alone, and the two species in the same mesocosm processed the least leaf mass (Fig. 3).

When it comes to leaf preference, neither species devoted significantly more time to feeding on one leaf type or the other. *Lepidostoma sp.* spent minimally more time feeding on senescent leaves ($F=4.14$, $P=.065$) and *P. guttifer* spent minimally more time feeding on green leaves ($F=4.26$, $P=.061$), but neither signal was significant enough to imply actual preference.

There was also no treatment effect observed concerning the amount of individuals' time which was spent interacting, either with conspecifics or interspecifics.

Neither leaf type nor differing community makeup elicited increased direct interaction between caddisfly individuals.

Discussion

Effects of Dominance and Competition

Cross-treatment analysis of overall feeding for the two species leads me to believe that in this system, *Lepidostoma sp.* acts as a functionally dominant shredder. The difference in time spent feeding is clear. In treatments where the shredders were free of interspecific competition *Lepidostoma sp.* devoted 55% of their time to feeding on and therefore breaking down the leaves (Fig. 1), while *P. guttifer* spent a comparatively miniscule 25% of their time doing so (Fig. 2). This time spent feeding is given additional weight by the fact that *Lepidostoma sp.* in treatments alone were in fact able to process significantly more leaf mass than *P. guttifer* in the same amount of time (Fig. 3). And although caddisflies fed for less time when together, *Lepidostoma sp.* still spent 33% of their time feeding compared to 13% by *P. guttifer*. So I believe that *Lepidostoma sp.* processed a much higher portion of the leaf mass in those treatments as well. Qualitative observations throughout the entire experimental process confirm that *Lepidostoma* were much more vigilant in their processing of detritus. Most of the time that they spent moving appeared to be strictly to get to another part of the leaf so that they could begin feeding again. *P. guttifer*, however, were inactive for a good portion of the time (34%). And their movement did not typically appear to be geared towards finding material to feed on. It is because of all these differences, backed up by numerical data and confirmed by numerous observations, that I believe *Lepidostoma sp.* to be a functional

dominant in this experiment, contributing disproportionately more to decomposition function than *P. guttifer*.

My first hypothesis regarding increased leaf processing rates in the face of interspecific competition was based on the possibility of *P. guttifer* acting as both a functional and competitive dominant. I believed this might be the case largely because of the work done by Creed et al. (2009) which showed that a different *Pycnopsyche* species, *P. gentalis*, did indeed display both types of dominance. However, that study used a variety of non-caddisfly detritivores as interspecifics. Because caddisflies build cases for themselves out of leaves but other taxa do not, *Pycnopsyche* had additional motivation to process detritus. They not only rely on leaves for consumption, but also for building cases, which could explain why that study showed *Pycnopsyche* to dominate ecosystem function so much. But my study used another caddisfly, which also builds its case out of leaves, as an interspecific. So the *Pycnopsyche* no longer have more uses for the leaves than their competitors. Since *P. guttifer* was not the functional dominant in this experiment, they did not increase feeding rates when combined with interspecifics as I had predicted.

While *P. guttifer* were not dominant functionally, they were able to assert themselves in other ways. At first glance it would be tough to classify them as competitively dominant in this experiment because they did not significantly increase their time spent in direct interaction with interspecifics over conspecifics ($F=1.52$, $P=.241$), nor did they display additional aggression during interspecific interactions. My data and observations give me reason to believe that their competitive advantage does not come from direct or predatory interaction, but is actually derived from interference.

Results of the behavioral frequency portion of this analysis reveal some important information about the general temperament of these two species of caddisfly. *P. guttifer* is the more aggressive species, regardless of whether interactions are intra- or interspecific. *Lepidostoma sp.* are inclined to take a defensive approach to all interactions, not choosing to confront or be the aggressor. In fact, during the course of the experiment it was observed that a large number the aggressive acts performed by *Lepidostoma sp.* consisted of individuals without cases climbing onto the cases of conspecifics. Individuals carrying already established cases appeared to have no reason or desire to confront either species in this study. This dispositional information about the species could serve to explain why *Lepidostoma sp.* reduced their feeding and increased their inactivity so dramatically (Fig. 1) in the presence of *P. guttifer*.

Much has been studied in different ecosystems about a supposed ecology of fear (Brown et al. 1999, Ripple and Beschta 2004). Using some of these basic concepts, I am able to propose a reason for the shift in behavior of *Lepidostoma sp.* in the mixed treatments. Because they behave defensively, *Lepidostoma sp.* may try to avoid interaction with the aggressive *P. guttifer* individuals. When they are freed from this interspecific competition, *Lepidostoma sp.* are able to forage to their full potential with little to no risk of an aggressive encounter. But as soon as *P. guttifer* are introduced to the same community, *Lepidostoma sp.* might increase their inactivity levels as an avoidance tactic. They would possibly rather keep aggression from ever being leveled upon them than have to react to it or defend themselves.

As I have shown, direct competition does not increase in mixed community treatments. But this could be due to the avoidance efforts of the subordinate *Lepidostoma*

sp. So while *P. guttifer* does not directly exert its dominance, it uses interference competition to negatively affect the production of other taxa. Therefore, I think that *P. guttifer* may still be a competitive dominant in this study.

A key difference in the design of my study and that which I based much of my hypotheses off of is that Creed et al. (2009) did not enclose the other detritivores in with the *Pycnopsyche*. They used a semi-permeable barrier which allowed all taxa but the *Pycnopsyche* to come and go in the field. By observing that in most cases *Pycnopsyche* had excluded other detritivores from their territories, Creed et al. were able to come to a conclusion of competitive dominance. But in my experiment, the *Lepidostoma sp.* were not able to leave the shared territory. They reacted simply by reducing their activity levels. Future studies might consider using a mesocosm that allows for different species to move freely in and out. It is very possible that if *Lepidostoma sp.* had been able to leave, they would have. Creed et al. believed that encounter competition played a large role in the exclusion of less dominant species, but by conducting behavioral analysis I am able to say that encounters did not actually increase and it is more likely a case of interference competition.

Effects of Leaf Type on Processing Rates

My second and third hypotheses dealt with the possible differences between processing dynamics on green leaves versus senescent ones. As I found using several different means of comparison, no significant differences were found in the way that either species dealt with the two leaf types. It was expected that detritivores would feed more heavily on soft, nutrient-rich green leaves, but I did not find any preference

displayed for either leaf type. Since there was no increased processing of either leaf, there consequently was no differential facilitation observed.

One explanation for my findings has to do with the selection of leaves for this study. The literature does suggest that nitrogen levels in leaves could determine preference (Kaushik and Hynes 1969, Herbst 1982), and a prior experiment done using a similar setup to this one (Patrick unpublished) showed that senescent leaves were indeed processed at a slower rate than green leaves. These results gave me reason to believe that my study species would preferentially feed on green leaves as well. But for my experiment there was a difference in the senescent leaves that were used. The prior study (Patrick unpublished) used senesced leaves that were collected off of the forest floor. This means they had likely been leached of many of their nutrients over winter. But for my study, more freshly senesced leaves were collected from riparian trees. They were chosen because they are much more representative of the kind of senescent leaves which would fall into natural stream systems. Because they were collected before significant leaching of additional nutrients could take place, they likely contained a nutrient load more similar to green leaves than the older senescent leaves used prior. This more representative allochthonous substrate may not have had enough of a deviation in nitrogen content from green leaves for the detritivores to alter their feeding behavior accordingly.

Another important factor for consideration lies in the experimental design I used. Green leaves and senescent leaf treatments were divided equally among all treatment communities, but in no treatment communities were the detritivores exposed to both leaf types. Individual groups of shredders did not have an option of which leaf to feed on.

Future behavioral studies would absolutely benefit from including treatments where individual shredder communities are in the presence of both leaf types in order to see whether they display a preference under those conditions. This could provide important insight into preference.

Conclusions

At the onset of this study I was looking to investigate questions about leaf preferences as well as interaction dynamics of shredders. Due to possible experimental design oversights and deviations of leaves from previous work, I was not able to determine any effect of leaf type on the behaviors of shredders. I was successfully able to gain insight into the behavioral dynamics of shredder competition and dominance. As analysis proceeded, this became a clear focus.

The additional component of behavioral analysis which I incorporated into this study was conducive to a more definitive understanding of detritivore interaction dynamics. Without considering certain behaviors, I may have expected the processed leaf mass in mixed community treatments to be a sum of those in separated species treatments. And taking into account the processing rates of the individual species, I still may have determined *Lepidostoma sp.* to be a possible functional dominant. But in that case I would have still expected species richness to correlate positively with decomposition (Schwartz et al. 2000). The behavioral component allowed me to pin down the competitive interference of *P. guttifer*. It was this that shed light onto the actual relationships between competition, feeding and decomposition.

In my study system, I found that *Lepidostoma sp.* act as a functionally dominant species while *P. guttifer* act as a competitive dominant through interference. With one species displaying each of these characters, species richness seems to have a negative relationship with ecosystem function. The presence of the competitively dominant species in this case deters the functionally dominant species from performing important ecosystem functions which it normally would. Questions answered by this study are supported by data and backed by definitive behavioral observation. When possible, I believe that there is a great deal of benefit in incorporating behavioral analyses into otherwise circumstantial ecological studies.

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Figures

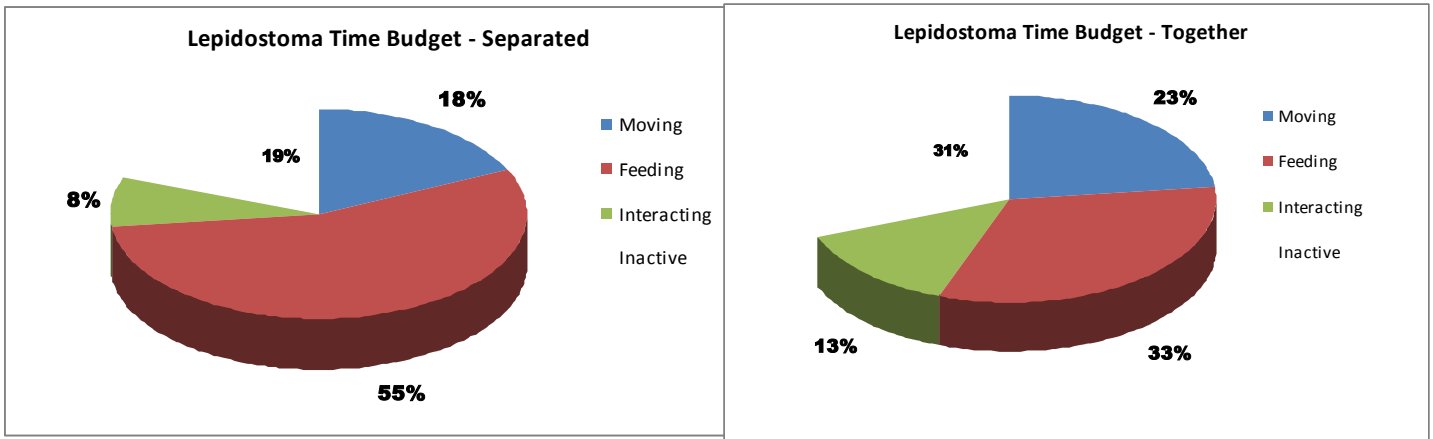


Figure 1 – Average time budget of *Lepidostoma* in two different community treatments. *Lepidostoma* spend significantly more time feeding by themselves than when in treatments together with *P. guttifer* ($F=37.7$, $P<.001$). In the face of interspecific competition, *Lepidostoma* appear to shift time from feeding to inactivity and avoidance. Time spent in interaction does not significantly change between treatments ($F=3.95$, $P=.07$).

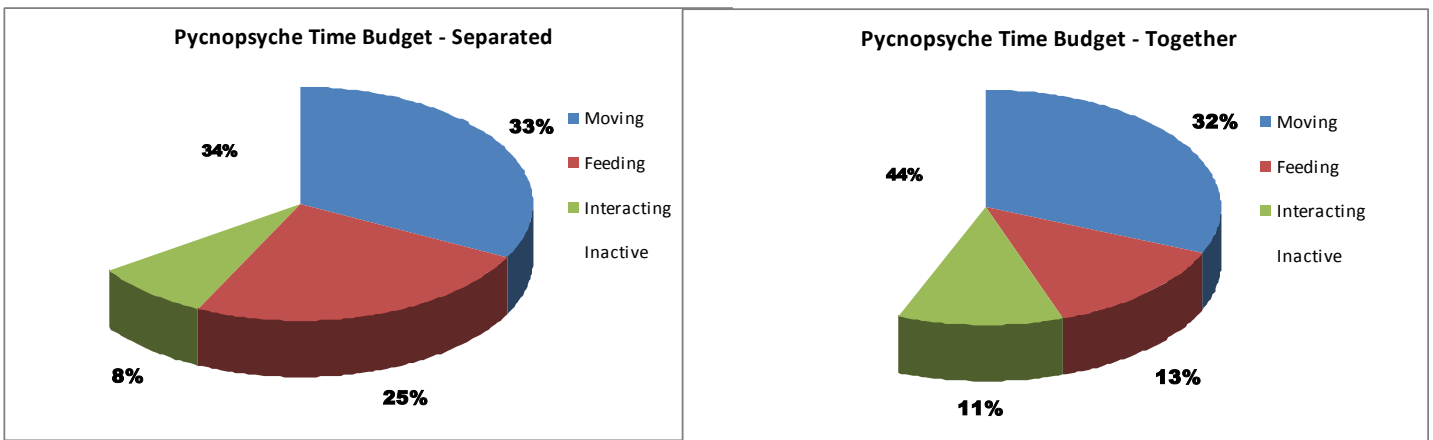


Figure 2 – Average time budget of *Pycnopsyche* in two different community treatments. *Pycnopsyche* spend more time feeding when there are no interspecifics present ($F=11.79$, $P=.005$). Neither interaction time ($F=1.52$, $P=.241$) nor movement differ between treatments.

Figures (continued)

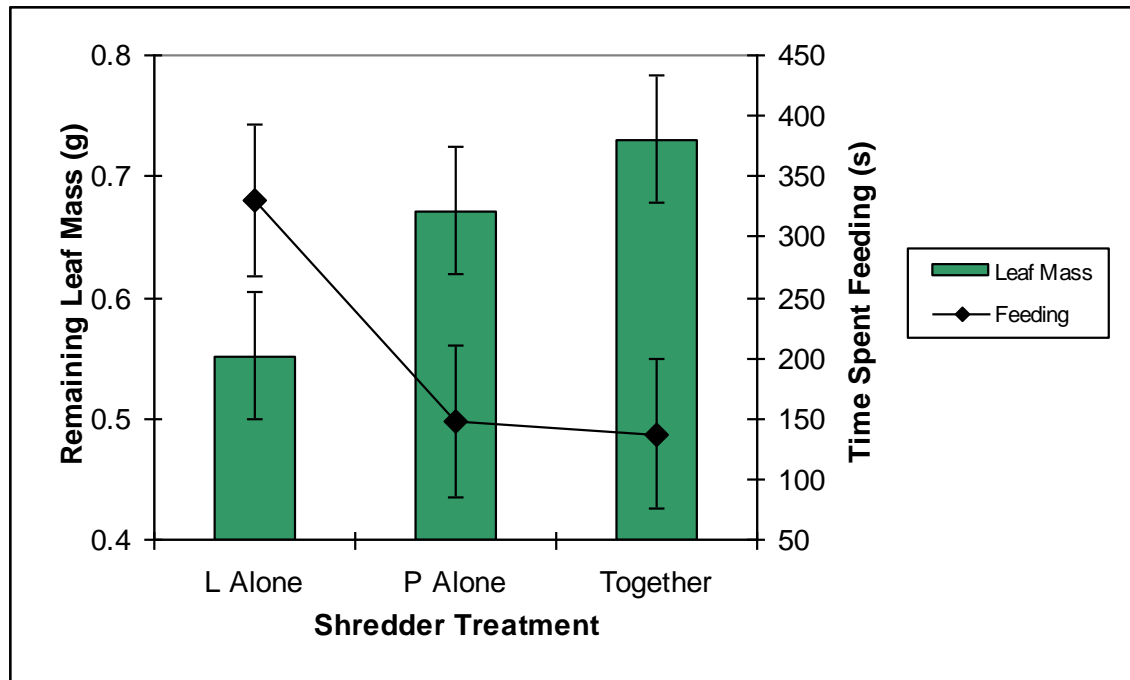


Figure 3 – Comparison of decomposition and time devoted to feeding. As more time is spent feeding in the treatments, more leaf mass is processed. The leaf mass processed by a mixed community is not a sum of individual processing rates, but it actually decreases as a result of the decreased feeding effort when the two species are together. This is a byproduct of interference competition.

Appendix A – *List of Different Mesocosm Treatments*

	Leaf	Shredder	Community Treatment	# of Replicates
1	Brown	Pycnopsyche	Separate	4
2	Green	Pycnopsyche	Separate	4
3	Brown	Lepidostoma	Separate	4
4	Green	Lepidostoma	Separate	4
5	Brown	Pycnopsyche and Lepidostoma	Together	4
6	Green	Pycnopsyche and Lepidostoma	Together	4
7	Brown	None	None	4
8	Green	None	None	4
9	None	None	None	4

Appendix B - *Layout of Treatments in Artificial Streams*

Stream Bank 4	GS1	GT1	GA1	BS1	BT1	BA1	GS2	GT2
Stream Bank 3	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Stream Bank 2	GA2	BS2	BT2	BA2	GS3	GT3	GA3	BS3
Stream Bank 1	BT3	BA3	GS4	GT4	GA4	BS4	BT4	BA4

1st letter = Leaf Treatment (G= green, B= brown or senescent)

2nd letter = Community Treatment (S= separated, T= together, A= shredders absent)

= replicate number

Appendix C – Behaviors Recorded During Video Analysis

Type of Data Collected	Behavioral Category	Specific Behavior Recorded	Description of Recorded Behavior	
Scored for Duration	Feeding	Feed on Stem	Number of seconds spent feeding on stem of leaves	
		Feed on Lamina	Number of seconds spent feeding on lamina of leaves	
		Feed Total	Sum of time spent feeding on stem and lamina of leaves	
	Moving		Number of seconds spent crawling around with head up, not feeding	
	Interacting	Conspecific Interaction		Number of seconds engaged in direct interaction with the same species
		Interspecific Interaction		Number of seconds engaged in direct interaction with other species
		Total Interaction		Sum of time spent in direct interaction with either species
		Climb On		Number of times a focal individual climbs onto another individual's case
	Scored for Frequency	Aggressive Behavior	Grab	Number of times a focal individual grabs another individual, face to face
			Bite	Number of times a focal individual bites another individual, face to face
Case Wave			With a competitor grabbing case, Number of times a focal individual waves its case in a circular motion	
Defensive Behavior		Flee/Turn	Number of times a focal individual turns or crawls away from a bout of interaction	
		Interspecific Bout	Number of isolated interaction events with individuals of other species	
Bouts of Interaction		Intraspecific Bout	Number of isolated interaction events with individuals of same species	