

Leaf abundance and phenolic concentrations codetermine the selection of case-building materials by *Phylloicus* sp. (Trichoptera, Calamoceratidae)

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Abstract *Phylloicus* sp. larvae live on leaf patches in slow flowing waters and build dorso-ventrally flattened cases from leaf pieces. We hypothesized that *Phylloicus* larvae are selective towards certain leaf species to build a more resistant case. We exposed *Phylloicus* larvae to equal-area leaf discs of three plant species from the Brazilian Cerrado (*Myrcia guyanensis*, *Miconia chartacea* and *Protium brasiliense*) and one non-native species (*Eucalyptus camaldulensis*). *Phylloicus* larvae built cases with discs of all plant species. However, discs of *E. camaldulensis* and *M. guyanensis* were used more (36.4% and 35.7%, respectively) than those of *P. brasiliense* (20.0%). Discs of *M. chartacea* were used in an intermediate proportion (28.6%). Selection was resource density-dependent, i.e. when *P. brasiliense* was offered at higher abundance, it was used more frequently by larvae (ANOVA, $P < 0.001$). Plant

species differed in leaf toughness, phenolic concentration and biomass:area ratio (Kruskal–Wallis, $P < 0.05$). Larvae preferentially used leaves with higher phenolic concentrations ($R_s = 0.907$, $P < 0.001$) independently of toughness and biomass:area ratio. We suggest that *Phylloicus* selects for case-building leaves that are chemically protected against microbial degradation and shredder consumption, and this selection depends on leaf abundance. Our results also reinforce the importance of riparian resources and their diversity to the maintenance of aquatic consumers in tropical shaded streams.

Keywords Shredder behaviour · Brazilian Cerrado · Leaf traits · Tropical streams · *Phylloicus*

Introduction

The Trichoptera (Caddisflies) are one of the most taxonomically rich orders of aquatic insects, with larvae found in nearly all freshwaters (Resh & Rosenberg, 1984; Flint et al., 1999) and occupying diverse microhabitats and trophic niches (de Moor & Ivanov, 2008). Part of this diversity results from variable use of silk secreted by the larvae during net-spinning and case-building (Wiggins, 1996, 2004). Case-building is energetically expensive but protects caddisflies against predators (Otto & Svensson, 1980; Stevens et al., 1999; Otto, 2000; Boyero et al., 2006).

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The Calamoceratidae is a cosmopolitan family of eight extant genera, with over 100 described species (Prather, 2003). The genus *Phylloicus* Müller, 1880, includes 61 known species, and is the largest calamoceratid genus in the New World (Huamantínco et al., 2005). Species are distributed throughout Latin America, but are especially diverse in Brazil, Peru and Venezuela (Prather, 2003). *Phylloicus* larvae are normally found on submerged leaves in stream pools and/or lateral springs (Flint et al., 1999; Wantzen & Wagner, 2006). These larvae are exclusive leaf feeders (shredders), exerting an important role in the conversion of leaf litter into secondary production and promoting the conversion of coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM) in lotic ecosystems (Cummins et al., 1989; Wallace & Webster, 1996; Flint et al., 1999; Rincón & Martínez, 2006).

Phylloicus larvae build dorso-ventrally flattened cases using several leaf pieces (Wiggins, 1996). Since they cut leaf pieces themselves, it is possible that abundance, quality and toughness of available leaves in stream pools determine case-building behaviour. Rincón & Martínez (2006), studying the feeding preferences of *Phylloicus* sp. in Venezuela, observed that these larvae preferred building their cases from leaves with higher levels of phenolics and lignins.

The objective of this investigation was to test whether *Phylloicus* larvae select leaves of particular plant species for case-building. We addressed three questions: (1) Are *Phylloicus* larvae capable of building their cases with leaves of only one plant species? (2) Whenever leaves of more than one species are available, is there a plant species selected preferentially by the larvae for case-building? (3) Is the mechanism of plant species selection (if it exists) dependent on resource density?

Methods

Larvae sampling site and collection

Larvae were collected at Taboões spring (20°03'38" S–44°03'03" W), located inside the Serra do Rola Moça State Park, Minas Gerais State, southeastern Brazil. The spring has a canopy of riparian trees with fallen leaves accumulating in patches within the spring all year. On the sampling

date, abiotic parameters (temperature, pH, electrical conductivity, redox, dissolved oxygen, total dissolved solids and turbidity) were measured in situ using a Horiba multi-probe (Horiba, Irvine, CA, USA). Total nitrogen and total phosphorus concentrations were determined according to APHA (1992). Spring waters were well oxygenated, alkaline with low conductivity and nutrient concentrations (Table 1).

One hundred and twenty larvae of one undetermined species of *Phylloicus* (Trichoptera: Calamoceratidae) were collected on June 23, 2008, with a hand net. They were taken to the laboratory in an isothermic box with stream water. In the laboratory, they were acclimatized for 24 h in an aquarium (80 cm long, 20 cm wide, 40 cm high) with spring water and a bottom of fine gravel. The aquarium was aerated continuously and some leaves, collected together with the insects in the same pools, were offered as food.

Leaves

In our experiments, we used senescent leaves of three plant species native to the Brazilian Cerrado (*Myrcia guyanensis* Aubl., *Miconia chartacea* Triana and *Protium brasiliense* Engl.) and one non-native species (*Eucalyptus camaldulensis* Dehn.). These leaves were collected from plastic nets (1 m², 10 mm mesh size, approximately 1.5 m height) implanted in the riparian zone (native species) and in a monoculture of *E. camaldulensis* located nearby. All leaves were air dried, sorted by species and stored at room temperature until needed.

Table 1 Water properties of Taboões spring (Serra do Rola Moça State Park, Minas Gerais, Brazil)

Parameters	
Temperature (°C)	20.2
PH	7.9
Electrical conductivity (μS cm ⁻¹) at 25°C	13.0
Redox (mV)	184.0
Dissolved oxygen (mg l ⁻¹)	7.2
Total N (μg l ⁻¹)	35.0
Total P (μg l ⁻¹)	3.0
Total dissolved solids (μg l ⁻¹)	10.0
Turbidity (NTU)	8.0

Values from a single observation

We chose the native species because they are abundant in the riparian forests and present different breakdown rates in Brazilian Cerrado streams. *Myrcia guyanensis* shows the highest breakdown rate ($k = 0.0063 \text{ day}^{-1}$) followed by *M. chartacea* ($k = 0.0033 \text{ day}^{-1}$) and *P. brasiliense* ($k = 0.0020 \text{ day}^{-1}$; Moretti et al., 2007). *Eucalyptus camaldulensis* was used in the experiments because many Cerrado areas have been replanted with eucalyptus monocultures (Klink & Machado, 2005). *Eucalyptus* trees have invaded the riparian forests of some Cerrado streams and the consequences of this change in the litter inputs on invertebrate assemblages are still poorly understood.

Case-building experiments

In the laboratory, the cases were carefully dismantled to remove the larvae. No larva died during this procedure. The individuals were then placed individually in plastic cups (12 cm diameter, 9 cm high) containing burnt fine gravel (4 h at 400°C) and 400 ml of filtered spring water. Plastic cups were aerated and kept at 21°C with a photoperiod of 12 h light and 12 h dark. Leaf discs of 1.8 cm diameter cut with a cork borer were offered as in the three experiments described below. All discs were cut from unconditioned leaves to avoid being eaten. No evidence of larvae feeding was observed during the experiments. In each experiment, we observed the cups over 24 h (different observers), measured the time spent to build a new case and counted the number of discs used by each larva for case-building. One leaf disc was considered as 'used' when the whole disc or part of it was incorporated in the new case. The replicate (plastic cup) was discarded if the individual died after the beginning of the experiments.

In the first experiment, we distributed 40 larvae in individual cups containing 16 discs from only one of the four plant species (*M. guyanensis*, *M. chartacea*, *P. brasiliense* or *E. camaldulensis*) to evaluate the capability of larvae to use the leaf substrates of the four tested plant species (10 replicates per species). In a second experiment, 40 larvae were randomly assigned to individual cups along with 16 leaf discs, four of each plant species, to evaluate whether the larvae would select discs of particular species for case-building.

Finally, in a third experiment, we evaluated whether the abundance of leaf discs could affect their selection. To pursue this question, we prepared two treatments using the most used and the least used plant species observed in the second experiment in different abundances. In the first treatment, we offered in each cup 12 discs of the most used plant species and four discs of the least used one. In the second treatment, we offered four discs of the most used species and 12 of the least used plant species. Larvae (12 replicates per treatment) were randomly distributed in each treatment.

Characterization of plant species leaves

We estimated leaf toughness with a device that measures the force needed to pierce a leaf disc with a piston of 0.79 mm diameter (see Graça & Zimmer, 2005). In order to determine the toughness of each plant species, we cut leaf discs, avoiding leaf veins, from four leaves using a cork borer of 1.8 cm diameter. Four leaf discs of each plant species were weighed with a 0.1 mg precision balance to determine the biomass:area ratio. We also ground some leaf material for the analyses of total phenolics according to Bärlocher & Graça (2005). Four replicates of each plant species were analyzed.

Statistical analyses

In order to test for significant differences in the plant species use for case-building, we compared the numbers of discs used in Experiment 1 with a one-way ANOVA and in Experiment 2 with Friedman's test, a non-parametric repeated measures comparison test. This test was used because larvae choice was not independent when all plant species were simultaneously offered in Experiment 2 (Roa, 1992). Multiple pairwise comparisons were done by Wilcoxon signed ranks test, with the appropriate Bonferroni correction. In Experiment 3, we compared the numbers of discs used with a two-way ANOVA (log transformed data), using plant species and abundance as factors. ANOVA models used in Experiments 1 and 3 were validated through residual analyses. We used a Kruskal–Wallis test to look for differences in disc toughness values (g), phenolic concentrations ($\% \text{ g}^{-1}$ dry mass) and biomass:area ratios (mg cm^{-2}) among all plant species used in the experiments.

We also calculated Spearman's rank correlation coefficients to evaluate the relationship between the total number of discs used by *Phylloicus* larvae in Experiment 2 with leaf toughness, leaf phenolic concentration and leaf biomass:area ratio of each plant species. All statistical analyses were performed using SYSTAT 10.2 (SYSTAT Software Inc., 2002) and based on Zar (1999).

Results

Phylloicus larvae built cases with leaves of all studied species (Fig. 1) and mortality rates were relatively low (10.8%, across all experiments). When discs of only one plant species were offered (Experiment 1), larvae used a mean number of discs ranging between 5.7 and 7.3, regardless of which plant species was present ($F_{3,32} = 1.661$, $P = 0.194$; Fig. 2A).

When exposed to the four plant species together (Experiment 2), larvae were selective (Friedman's value = 9.439, $df = 3$, $P = 0.024$), using significantly fewer discs of *P. brasiliense* (20.0%) than *E. camaldulensis* (36.4%) and *M. guyanensis* (35.7%). Discs of *M. chartacea* were used in an intermediate proportion (28.6%), not differing from the others (Fig. 2B).

The third experiment revealed that plant species selection was dependent on leaf abundance, i.e. even though *E. camaldulensis* and *M. guyanensis* were more used than *P. brasiliense*, whenever the least preferred species was more abundant in the system, it was more used, independently if combined with discs of *E. camaldulensis* or *M. guyanensis* (Table 2; Fig. 3).

Plant species differed in toughness (Table 3). *Myrcia guyanensis* and *P. brasiliense* were tougher, whereas *E. camaldulensis* and *M. chartacea* were the softest leaves. Phenolic concentrations also differed among plant species and *P. brasiliense* showed the lowest phenolic concentrations (Table 3). Finally, *E. camaldulensis* had thinner leaves than *M. guyanensis* and *M. chartacea*. Leaf selection by *Phylloicus* was correlated with phenolic concentrations ($R_s = 0.907$, $t_{34} = 6.804$, $P < 0.001$) but not with leaf toughness and thickness (toughness: $R_s = -0.294$, $t_{34} = -1.795$, $P > 0.05$; biomass:area ratio: $R_s = -0.134$, $t_{34} = -0.788$, $P > 0.05$).

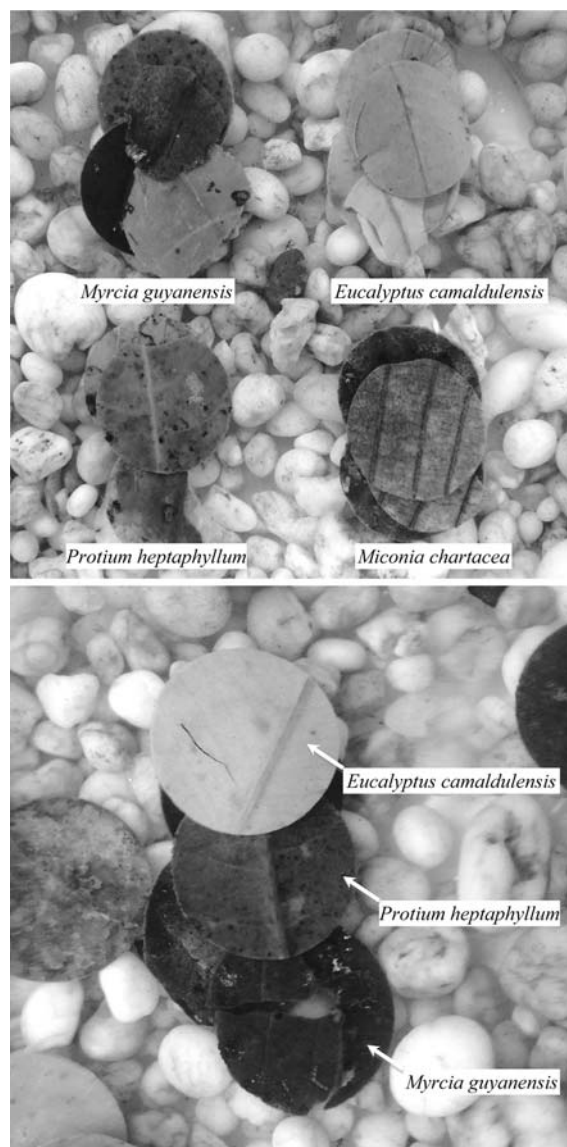


Fig. 1 Cases built by *Phylloicus* larvae with monospecific (top) and multispecies (bottom) plant leaf discs

Discussion

Phylloicus larvae built cases with all plant species offered. After removal from their original cases and placement in the plastic cups, each larva immediately took shelter under the leaf discs and started to cut some of them. Larvae spent less than 24 h to build new cases, and in 11 cups, new cases were observed only 3 h after the beginning of the experiments. The behaviour exhibited by the larvae and the time

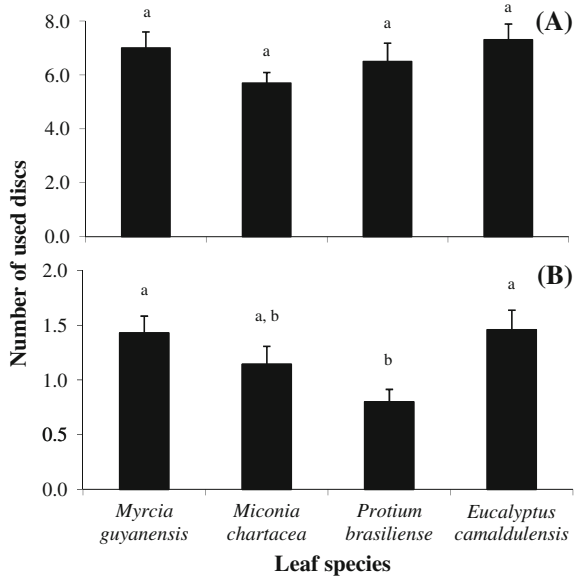


Fig. 2 Number of discs used by *Phylloicus* larvae (mean \pm SE) when plant species were offered individually (A) and combined (B). Values sharing superscript letters are not statistically different ($P > 0.05$)

Table 2 Results from a two-way ANOVA of general differences in number of discs used on the two plant species combinations in Experiment 3

Leaf combination	Factor	F	df	P
<i>E. camaldulensis</i> and <i>P. brasiliense</i>	Leaf	4.031	1	0.053
	Abundance	27.780	1	<0.001
	Leaf \times Abundance	0.000	1	1.000
<i>M. guyanensis</i> and <i>P. brasiliense</i>	Leaf	5.175	1	0.029
	Abundance	19.725	1	<0.001
	Leaf \times Abundance	0.106	1	0.747

Data are from Fig. 3

needed to build their cases were similar to those observed by Norwood & Stewart (2002) for the North American *Phylloicus ornatus*.

The preference of *Phylloicus* larvae for *E. camaldulensis* and *M. guyanensis* was positively correlated with leaf phenolic concentrations, suggesting that *Phylloicus* larvae preferred to build cases with less palatable leaf pieces (Graça, 2001; Bärlocher & Graça, 2005). Given that *Phylloicus* cases present a relatively large surface area (Wantzen & Wagner, 2006), the use of low quality plant species for

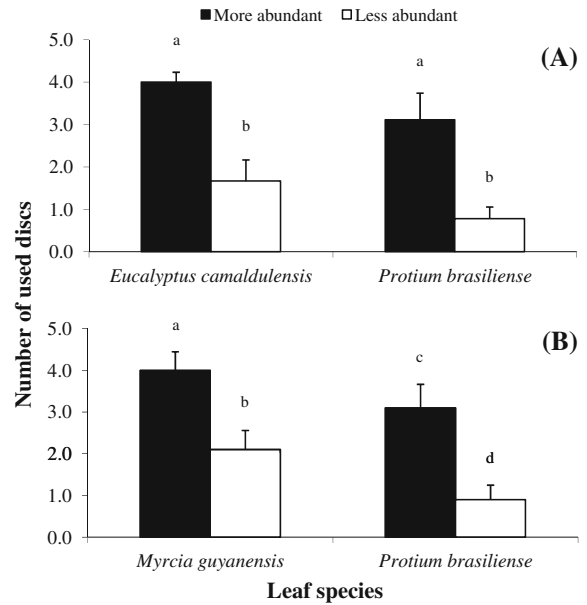


Fig. 3 Number of discs used by *Phylloicus* larvae when *Eucalyptus camaldulensis* (A) and *Myrcia guyanensis* (B) were offered combined with *Protium brasiliense* in different leaf disc abundances. Values sharing superscript letters are not statistically different ($P > 0.05$)

case-building may be a strategy to make their cases less attractive to other invertebrate shredders (Bastian et al., 2007) and to microbial degradation since phenolics are known to retard microbial colonization (Campbell & Fuchshuber, 1995; Salusso, 2000).

Phylloicus preference was independent of leaf toughness. This may indicate that among all leaf characteristics that set the preferences for case-building, toughness might be one of lower importance. Bastian et al. (2007) observed that two species of caddisfly differed in their choice of leaves for case-building, with *Anisocentropus kirramus* using relatively tough leaves and *Lectrides varians* using much softer leaves. The effect of toughness should be more systematically tested in future studies using a larger number of plant species.

In the multiple-choice experiment, *Phylloicus* larvae used more discs of species with faster decomposition (*E. camaldulensis* and *M. guyanensis*). However, even having differences in their breakdown rates, we must remark that breakdown rates of Cerrado plant species are among the slowest observed in tropical environments (see Moretti et al., 2007) and *E. camaldulensis* decomposes approximately 2.5

Table 3 Leaf toughness (g), phenolic concentration (% g⁻¹ dry mass) and biomass:area ratio (mg cm⁻²) of the four plant species tested (mean ± SE; *n* = 4), Kruskal–Wallis *H* and probability *P*

	Toughness	Phenolics	Biomass:area
<i>Myrcia guyanensis</i>	276.95 ± 16.25 ^a	10.70 ± 0.25 ^{a,b}	39.32 ± 0.83 ^a
<i>Miconia chartacea</i>	100.35 ± 23.83 ^b	9.38 ± 0.10 ^{a,b}	47.83 ± 1.28 ^a
<i>Protium brasiliense</i>	210.85 ± 28.45 ^a	7.55 ± 0.11 ^a	30.01 ± 0.61 ^{a,b}
<i>Eucalyptus camaldulensis</i>	83.62 ± 10.26 ^b	10.94 ± 0.06 ^b	24.48 ± 0.61 ^b
<i>H</i>	27.83	10.46	27.44
<i>P</i>	<0.001	0.015	<0.001

Values sharing superscript letters are not statistically different (*P* > 0.05)

times faster than *M. guyanensis* (J. F. Gonçalves, unpublished data), the native species with the highest breakdown rate. Based on this, we believe that *Phylloicus* cases built with *E. camaldulensis* are not as durable as the ones made with native species. Then, in environments in which *Eucalyptus* leaves are available alone or in larger quantities, larvae would tend to build and/or add more leaf pieces to their cases, spending more energy than in natural conditions. This fact could have significant consequences to adult maturation of insects, such as caddisflies, which present minimal adult feeding (Stevens et al., 1999).

Despite preference for some plant species, *Phylloicus* case-building behaviour is sufficiently flexible to adapt to the abundance of leaves available in their habitats, and this pattern was observed independently of the presence of *E. camaldulensis*, the non-native species. According to some authors, the type of organic material used by caddisflies for case-building may vary depending on its abundance (Hanna, 1961; Otto & Svensson, 1980). Moreover, Moretti & Loyola (2005) demonstrated that larvae of *Barypen-thus concolor*, a tube-case-building trichopteran, use particle sizes in the same proportions as they are available in the habitat to build their cases. All these findings imply great selective pressure operating on this behaviour.

Our results corroborate in part those of Rincón & Martínez (2006), who observed *Phylloicus* preference for leaves of low palatability and higher lignin contents for case-building. This fact is probably related to the intrinsic traits of plant species used in these two studies, which belong to different vegetation types. For example, the lignin contents of the

species used here are on average 1.6 times higher than the ones from the species used by Rincón & Martínez (2006) in Venezuela (M. S. Moretti, unpublished data). Due to harsh conditions (e.g. high solar radiation, water stress and herbivory), Brazilian Cerrado plant species have leaves with thick cuticles and high contents of structural and inhibitory compounds (Marques et al., 2000; Oliveira & Marquis, 2002; Wantzen & Wagner, 2006). On the other hand, plant species used by Rincón & Martínez (2006) are native from a dry tropical semideciduous forest located in Northwestern Venezuela (Rincón et al., 2005), a region where annual precipitation is higher and plant species are subject to fewer environmental stresses than in Cerrado. However, the results of both studies suggest that *Phylloicus* larvae build cases with less palatable leaves when exposed to a group of tough leaves (present study) or with the toughest leaves among the ones that were available in the system (Rincón & Martínez, 2006).

Since *E. camaldulensis* is not present in the site where larvae were collected, preferences observed here were measured in a non-natural environment where animals responded to leaf traits they have not faced before, suggesting that our results could be different if we had used only native species. In spite of this, we decided to include *E. camaldulensis* in our experiments because this is one of the biggest threats to the Cerrado biome in southeastern Brazil (Klink & Machado, 2005) and leaves of this species will probably reach several streams in the near future.

According to our results, *Phylloicus* larvae select, for case-building, those leaves that are chemically protected against microbial degradation and shredder consumption, even if they are from a non-native

species such as *E. camaldulensis*. Moreover, we found that this preference is also influenced by leaf abundance, indicating that larvae are dependent on species composition in the riparian zone. Therefore, changes in riparian vegetation providing leaf substrates (i.e. change of species and/or substrate homogenization caused by reforestation with a single species) can be important to *Phylloicus* larvae due to the impact on growth and reproduction. In this way, our findings also reinforce the importance of riparian resources and their diversity to the maintenance of aquatic consumers in tropical shaded streams.

To summarize, our results indicate that *Phylloicus* larvae present a high plasticity on case-building behaviour. Furthermore, it seems that their selection depends on each situation, i.e. which plant species are present and their relative abundance. A combination of variables such as leaf chemistry, availability and toughness will determine larvae preferences. Other factors, such as the breakdown rates of different leaf types and the presence of predators, may influence case construction also and should be evaluated.

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