

THE ROLE OF LARVAL CASES IN REDUCING AGGRESSION AND CANNIBALISM AMONG CADDISFLIES IN TEMPORARY WETLANDS

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Abstract: Larvae of wetland caddisflies supplement their detrital diets with animal material. In some species this supplement is obtained by preying on other caddisflies. In this study, we conducted a series of laboratory experiments to a) compare intraspecific aggression and the propensity for cannibalism among six caddisfly species that occur along a gradient from vernal to autumnal to permanent high-elevation wetlands, and b) determine the importance of cases in preventing or reducing cannibalism and intraguild predation. We predicted that cannibalism and overall levels of aggression should be highest in species that occur in temporary habitats. We found that all of the species that use temporary habitats (*Asynarchus nigriculus*, *Hesperophylax occidentalis*, *Limnephilus externus*, *Limnephilus picturatus*, *Limnephilus secludens*) were extremely aggressive towards and cannibalized conspecifics without cases. Species that typically occur in short-duration temporary wetlands were more aggressive than those in long-duration temporary wetlands. Cases prevented cannibalism in four of these temporary-habitat species, and reduced cannibalism among *Asynarchus* larvae. The latter species occurs in extremely ephemeral habitats where cannibalism provides a dietary supplement that probably facilitates emergence before drying. *Asynarchus* also preys on *Limnephilus* spp., and we found that cases dramatically reduced vulnerability to intraguild predation. Larvae of *Agrypnia deflata*, a species that occurs only in permanent wetlands, were least aggressive and rarely cannibalized conspecifics. Our results are consistent with the hypothesis that intraspecific aggression and the potential for cannibalism are highest in species that live in habitats with developmental time constraints. Many wetland invertebrates face developmental time constraints and selection for aggression in temporary habitats should be especially strong for taxa that rely on animal material to supplement a mainly detrital diet.

Key Words: temporary wetlands, caddisflies, cannibalism, detritus, benthic invertebrates, habitat drying, time constraints, Limnephilidae, Phryganeidae

INTRODUCTION

Aquatic invertebrates that inhabit temporary wetlands exhibit a variety of behavioral, physiological, and morphological adaptations for completing development before larval habitats dry (Wiggins et al. 1980, Williams 1987, 1996, Batzer and Wissinger 1996, Wissinger 1999). Caddisflies, particularly Limnephilidae, are ubiquitous in high latitude and high elevation wetlands (Otto 1976, 1982, 1983, Mackay and Wiggins 1979, Otto and Svensson 1980, Zamora-Muñoz and Svensson 1996, Wiggins 1996), and are often the dominant group of detritus shredders in those habitats (Wissinger 1999). Caddisfly species that inhabit temporary wetlands rely on desiccation tolerance (egg masses, larvae, and/or pupae), adult diapause during the dry season, and/or rapid development to complete

development during the wet phase of the hydroperiod (reviewed by Wiggins 1973, Mackay and Wiggins 1979, Wissinger et al. 2003). In at least some species, rapid growth and development are facilitated by high larval activity rates and aggressive behaviors (including cannibalism) towards conspecifics (Wissinger et al. 1996).

The rapid growth and development exhibited by temporary wetland caddisflies is surprising given the relatively low nutritional value of the vascular plant detritus that dominates their diet (Anderson and Cargill 1987, Jacobsen and Sand-Jensen 1994). Comparison of the protein and energy contents of different aquatic food sources emphasizes that detritus, even after microbial conditioning, is a low quality nutritional resource (1–20 mg/kJ protein; 5–10 kJ/g gross energy)

relative to invertebrate prey and algae (15–28 mg/kJ protein; 20–33 kJ/g gross energy) (Bowen et al. 1995; also see Mihuc 1997). This might explain the many anecdotal reports of animal material in the diets of caddisflies (Winterbourn 1971, Anderson 1976, Iversen 1979, Mackay and Wiggins 1979, Berté and Pritchard 1986, Giller and Sangpradub 1993, Jacobsen and Friberg 1995) and other invertebrates that rely mainly on detritus (e.g., MacNeil et al. 1997). In a previous study, we experimentally manipulated the diet of *Asynarchus nigriculus* Banks, a wetland species that supplements its diet via cannibalism and intraguild predation (Wissinger et al. 2004). Individuals with an animal food supplement developed faster and had higher adult fitness than those fed only on detritus. We concluded that the animal material obtained through cannibalism facilitates the timely emergence of this species from temporary habitats, and hypothesized that this type of dietary supplementation should be common among wetland detritivores that face developmental time constraints (Wissinger et al. 2004).

The purpose of this study was to 1) expand on previous results by comparing levels of aggression and cannibalism in *Asynarchus nigriculus* to that observed among larvae of five other species of caddisflies that occur in high-elevation wetlands in central Colorado, USA, and 2) report on the role of cases in reducing cannibalism and intraguild predation among these species. We predicted that intraspecific aggression and the propensity for cannibalism should be higher in species that typically inhabit temporary vs. permanent habitats. Analysis of stomach contents indicated that all of the species occasionally supplement their diets with animal material (Sparks 1983, Wissinger, unpub. data), but we had previously observed cannibalism only among *Asynarchus* larvae (Wissinger et al. 2003).

Long-term (15 years) comparative data on the distributions of the six species provided the basis for ranking the degree to which development is constrained by drying along a hydroperiod gradient from vernal (always dry in early summer) to autumnal (sometimes dry in late summer) to permanent wetlands (Wissinger et al. 1999b, 2003). Two species, *Asynarchus nigriculus* and *Hesperophylax occidentalis* Banks occur mainly in short-duration temporary habitats that typically dry in early summer. In drought years, entire cohorts of larvae and/or pupae die as a result of desiccation. *Asynarchus nigriculus* occurs mainly in isolated depressional wetlands and vernal pools, whereas *H. occidentalis* inhabits intermittent headwater streams and associated riparian habitats. Three other species, *Limnephilus externus* Hagen, *Limnephilus picturatus* McLachlan, and *Limnephilus secludens* Banks occur in both autumnal and permanent depressional wetlands (Wissinger et al. 2003). Time constraints on develop-

ment in these species occur mainly in drought years when autumnal habitats dry in mid-summer (July–August). A sixth species, *Agrynia deflata* Milne only occurs in shallow permanent habitats. Although the precise position of species replacements along this permanence gradient (c.f. Wellborn et al. 1996) shifts slightly at different elevations, their relative positions remain the same (Wissinger et al. 2003).

METHODS

The experiments were conducted in microcosms (100 cm² aquaria; 7 cm depth; mesh substrate) that we used previously to study mob cannibalism among *Asynarchus* larvae (Wissinger et al. 1996). The microcosms were housed in a portable field adjacent to the wetlands at our main study site in the Mexican Cut Nature Reserve in the White River National Forest, Colorado (see Wissinger et al. 1999b for additional information). Rates of cannibalism and mobbing behaviors in these microcosms were nearly identical to those observed in natural populations of *Asynarchus*. Because all of the species are univoltine, and development is relatively synchronous, most encounters in natural populations occur between same-instar larvae (Wissinger et al. 2003). We initiated each experiment following the protocol previously used for *Asynarchus* by introducing one “focal” animal into an arena with 10 “resident” final instars [final instar size data (head width and mass) for each species given in Wissinger et al. 2003]. These densities are similar to those observed in feeding and mobbing aggregations in the field (Wissinger et al. 1996). All animals were held individually for 24 hr before the trials to standardize hunger levels and then were assigned randomly to the treatments (resident, cased focal animal, caseless focal animal). Residents were added to the behavioral arenas 1 hr before the trials. Focal animals were forced out of their cases by probing the posterior end of the animal with a blunt applicator stick. Focal animals were either allowed to re-enter their case before being added to the arenas (“cased” focal animal) or added without a case (“caseless” focal animal). Cased focal animals were marked with a small dot of non-toxic paint to distinguish them from residents. We conducted 15 trials of control (focal animal with a case) and caseless treatments for each species except *Asynarchus*, for which we conducted 30 trials as part of additional studies on cannibalism behaviors (Wissinger, unpub. data). In preliminary studies, we found that all instances of cannibalism on caseless larvae occurred within the first 15 minutes of observation, and we therefore conducted 20-minute trials. During each of the 210 trials, we recorded 1) number of encounters between residents and focal animals, 2) number of encounters

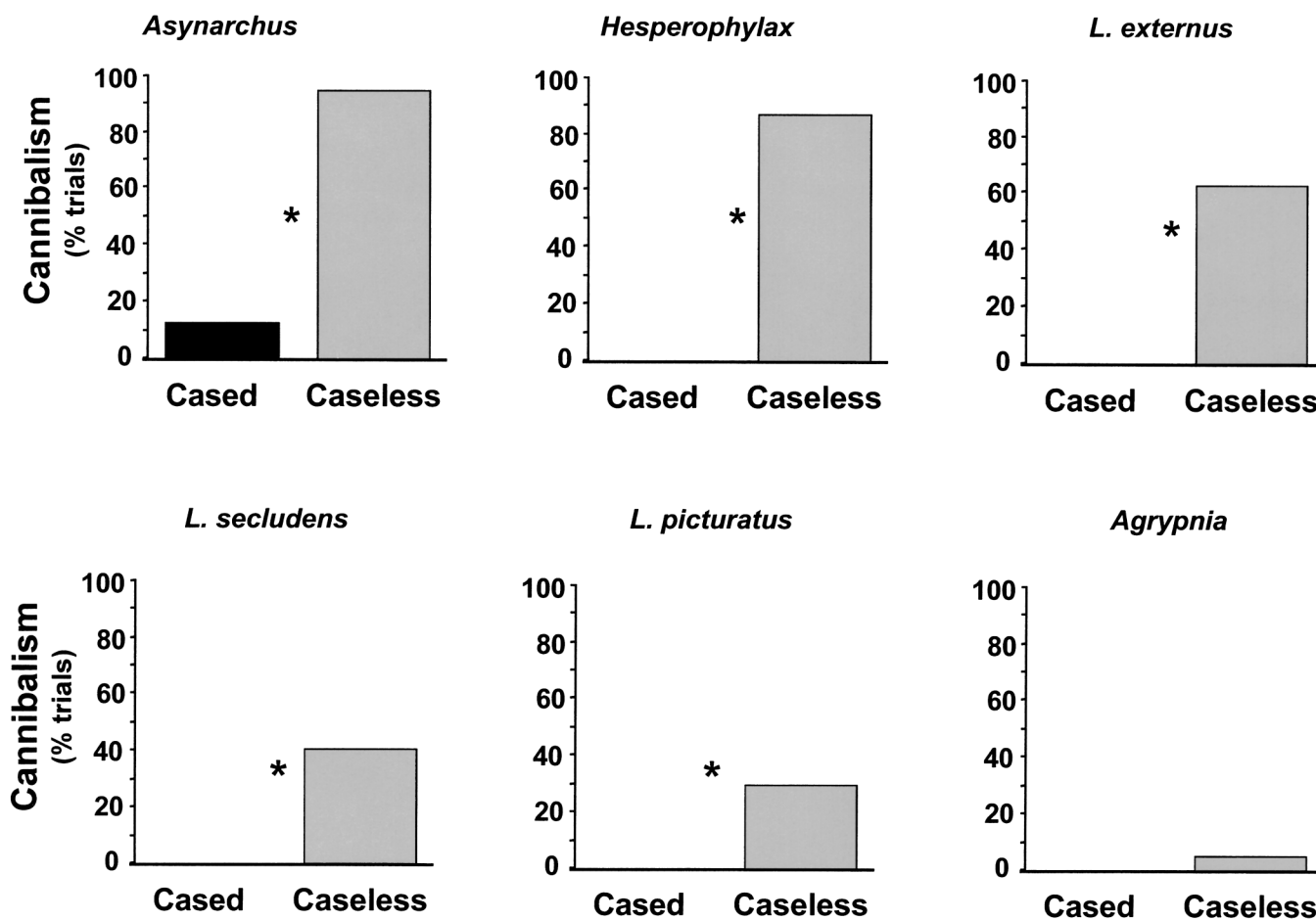


Figure 1. Cannibalism on cased and caseless larvae of six species of wetland caddisflies. Values indicate the percentage of trials ($n = 15$ for all species except $n = 30$ for *Asynarchus*) in which larvae were cannibalized. Asterisks indicate $\chi^2 < 0.05$ for the null hypothesis that the occurrence of cannibalism is not contingent on the presence of cases.

that escalated into fights (biting, foreleg wrestling, case or body shaking; after Wissinger et al. 1996), and 3) occurrence of cannibalism.

Asynarchus larvae prey on *L. externus* and *L. picturatus* in autumnal, subalpine wetlands (Wissinger et al. 1996). We therefore conducted two additional experiments (15 trials of each treatment) to determine the role of cases in protecting larvae from intraguild predators. In these experiments, we used 10 final (5th) instar *Asynarchus* as potential predators and then introduced cased or caseless 3rd instar *L. externus* or *L. picturatus*. These instar combinations reflect ecologically relevant differences in phenology in natural populations (Wissinger et al. 2003).

For all experiments, we analyzed the proportion of cased and caseless focal animals that were cannibalized using a χ^2 test for deviations from the two-way contingency null hypothesis that case status had no effect on the distribution of cannibalism events between treatments (i.e., expected values were based on the total number of cannibalism events observed for a

species). In one species (*Agrypnia*), the rarity of cannibalism precluded statistical analysis. We compared the percentage of the total encounters with focal animals that escalated into aggression (biting, foreleg grappling, case shaking) using two-way ANOVA, after testing for significant departures from normality and homoscedasticity. Analysis of arcsine-transformed data produced results nearly identical to untransformed data; thus, the untransformed data are presented for ease of interpretation. We conducted a protected one-way ANOVA and Scheffe' aposterior contrasts on levels of aggression to distinguish differences among species (after Day and Quinn 1989).

RESULTS

Caseless larvae were frequently attacked and often cannibalized in all five species that use temporary habitats. For each species, caseless larvae were much more likely to be cannibalized than those with cases (all $\chi^2 < 0.05$; Figure 1). In four of the taxa (*Hesperophylax*

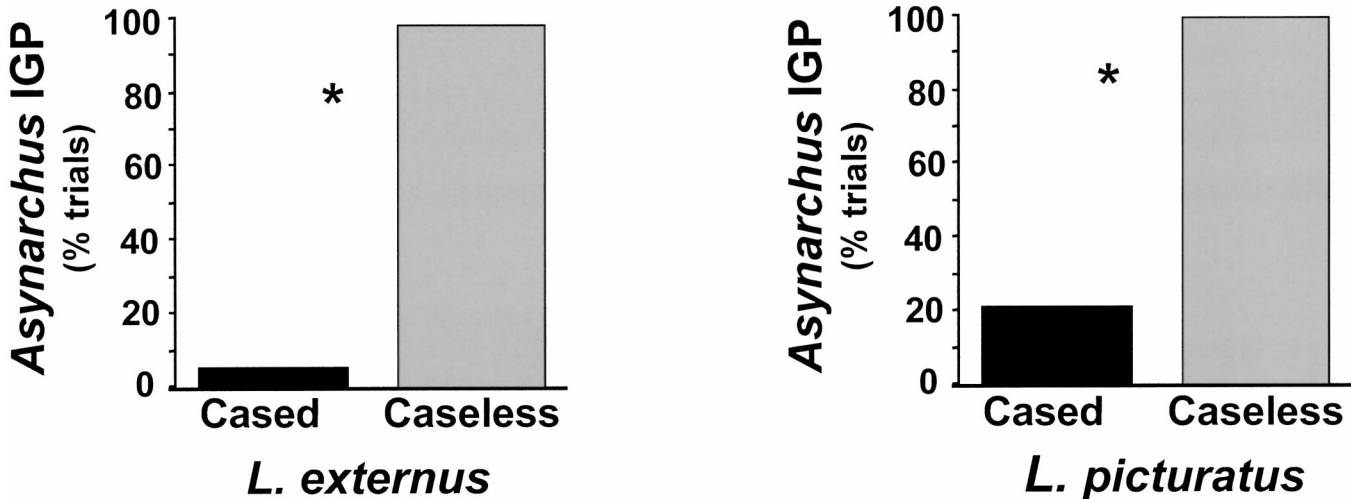


Figure 2. Intraguild predation on 3rd instars of two species of *Limnephilus* caddisfly by 5th instar *Asynarchus*. Asterisks indicate $\chi^2 < 0.05$ for the null hypothesis that the occurrence of cannibalism is not contingent on the presence of cases.

occidentalis *Limnephilus externus*, *L. secludens*, and *L. picturatus*), cannibalism was not observed on cased larvae, although interactions among *Hesperophylax* larvae were extremely aggressive. *Asynarchus* cannibalism was much less likely on cased (4/30 trials) than on caseless larvae (28/30 trials; $\chi^2 < 0.05$; Figure 1). In one *Asynarchus* cannibalism trial, a resident larva was attacked and consumed by a mob of conspecifics that included a cased focal animal. *Asynarchus* intraguild predation on *L. externus* and *L. picturatus* was also much less likely on cased than caseless focal animals (Figure 2). Final instar *Asynarchus* larvae were extremely aggressive towards cased and caseless *Limnephilus* larvae, and mobbing was often preceded by one-on-one attacks that resulted in injury.

Agrypnia deflata was the least cannibalistic of the taxa studied (Figure 1). The addition of a caseless *Agrypnia* to the experimental arenas typically resulted in the focal animal displacing one of the residents, leading to a cascade of successive case takeovers. These displacements often continued throughout the 20-minute trials. In two trials, a caseless *Agrypnia* larva (one focal animal and one resident larva that had been displaced from its case) was injured and then subsequently cannibalized by multiple conspecifics.

The proportion of encounters between residents and focal animals that escalated into aggression (biting, leg grappling, case shaking) differed among species (main effect of species $F_{5, 168} = 75.8$, $p < 0.001$; Figure 3). In all species, a greater percentage of encounters escalated into aggression in caseless than in cased trials (protected one-way ANOVA within all species $P < 0.001$). Aggressive encounters with focal animals were most frequent among *Asynarchus nigriculus* and *Hesperophylax occidentalis* larvae. In these two taxa, case-

less focal animals were typically attacked immediately after entering the arena by one or more conspecifics, and then most or all other larvae joined in the mobbing of the victim. Thus, nearly all encounters between residents and caseless larvae of these taxa were aggressive (Figure 3). Aggressive encounters were intermediate in frequency for the three *Limnephilus* spp. and varied markedly between trials, depending on whether a cannibalism event did or did not occur. Aggression among *Agrypnia* larvae was lowest and differed qualitatively from that observed among the limnephilids. In cased trials, there was little aggression among *Agrypnia* larvae (Figure 3). In caseless trials, aggression occurred mainly between case defenders and potential case displacers.

DISCUSSION

Cannibalism and Time Constraints In Temporary Wetlands

Our results suggest that aggression and the propensity for cannibalism is greatest in species that live in habitats with developmental time constraints (c.f. Ludwig and Rowe 1990). The two taxa (*Asynarchus nigriculus* and *Hesperophylax occidentalis*) that live in the shortest duration habitats were the most aggressive towards conspecifics with or without cases and most likely to engage in mob cannibalism (Figures 1 and 2). Although they live in different types of habitats (*Asynarchus* in isolate vernal wetlands and *Hesperophylax* in intermittent headwater streams and associated riparian wetlands), both are vulnerable to desiccation and suffer mass mortality in drought years (Wissinger et al. 2003). Larvae of these taxa have ex-

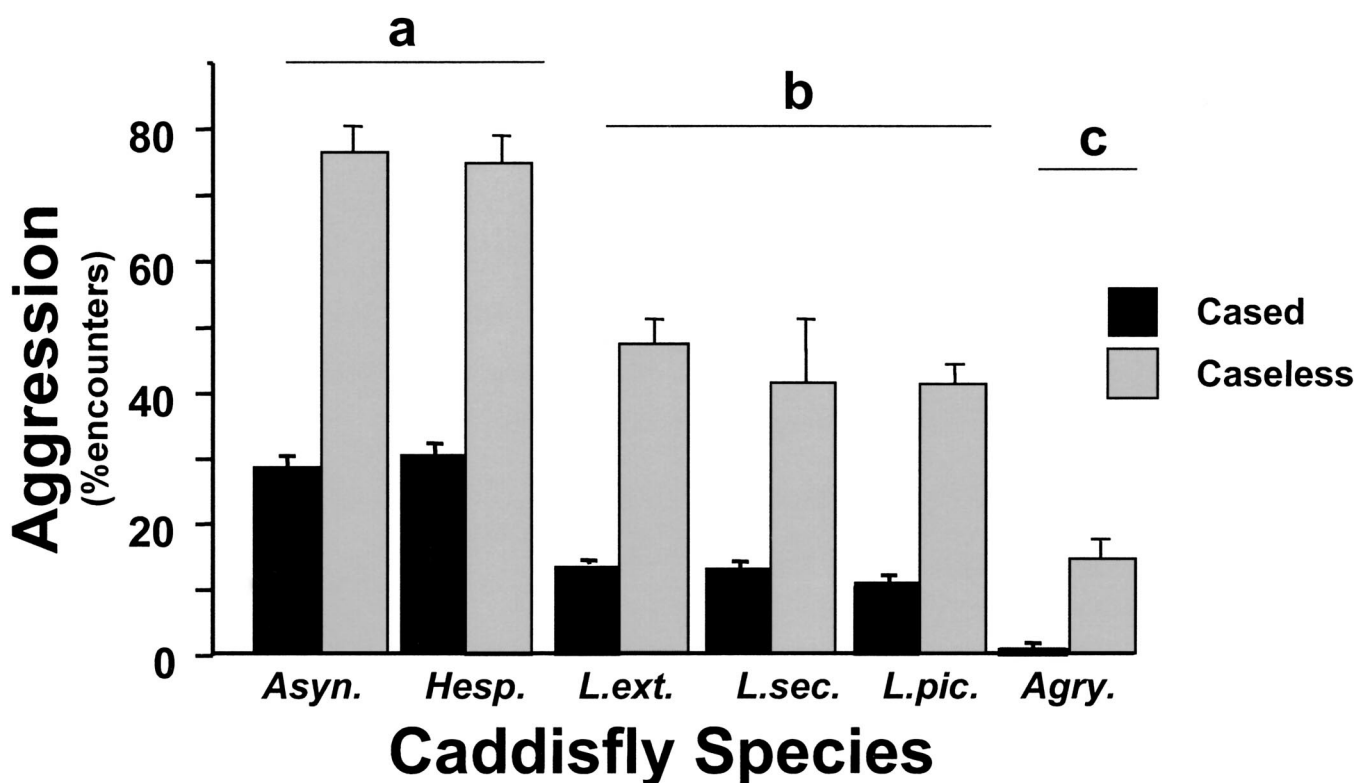


Figure 3. Larval aggression (percent of encounters that escalate into agonistic interactions) towards cased and caseless conspecifics for six species of wetland caddisflies. Values are the mean percent ($n = 15$ trials) \pm S.E. Bars with lower case letters group species that do not differ, based on Scheffe' aposterior contrasts of a protected one-way ANOVA.

tremely high activity rates and become especially aggressive during the latter stages of habitat drying. In contrast, the species that occurs in the most permanent habitats (*Agrypnia deflata*) was least cannibalistic and least aggressive towards conspecifics. The three species that occur in temporary wetlands with a relatively long hydroperiod (*Limnephilus externus*, *L. picturatus*, *L. secludens*) showed intermediate levels of aggression and cannibalism. Although we cannot eliminate other variables that might explain observed differences in aggression and cannibalism among species (e.g., food levels), there is clearly a correlation with habitat permanence.

Previous experimental data demonstrate that a dietary supplement of animal material facilitates early emergence in *Asynarchus* (Wissinger et al. 2004), and data presented here are consistent with the prediction that opportunistic cannibalism plays an important role for this species in obtaining that supplement in temporary habitats. Curiously, cannibalism, and not predation on other invertebrates appears to be the main source of animal material in the diet of *Asynarchus* (Wissinger et al. 2004). In contrast, interspecific predation appears to be the dominant source of that supplement in other detritivorous caddisflies (Winterbourn 1971, Anderson 1976, Pritchard and Berté 1987, Giller

and Sangpradub 1993). Dietary supplementation should be common in many detritivorous invertebrates, especially in high elevation and high latitude temporary wetlands where cold temperatures, short open-water growing seasons, habitat drying, and low nutrient levels all constrain growth and development (Wissinger et al. 1999b).

Several types of corroborative evidence suggest that the levels of aggression and cannibalism reported here are not simply microcosm artifacts. First, the levels of overall aggression (~ 30 – 40% of all encounters are agonistic) and frequency of cannibalism among cased *Asynarchus* larvae (10% of trials) observed in the microcosms here were nearly identical to those previously reported from experiments in littoral cages and in large mesocosms (cattle tanks) with semi-natural levels of habitat heterogeneity and alternative prey (Wissinger et al. 1996, Wissinger et al. 1999a, Wissinger et al. 2004). Second, larval behaviors are easy to observe in the extremely clear, shallow water in these alpine wetlands, and behavioral observations in natural habitats closely mirror those in the microcosms (i.e., activity rates and levels of aggression are greatest in *Asynarchus* and *Hesperophylax* > *Limnephilus* spp. > *Agrypnia*). Third, the introduction of caseless *Asynarchus*, *Hesperophylax*, and *Limnephilus externus* into

feeding aggregations in natural habitats incites mob cannibalism (Wissinger, unpub. data). We cannot, of course, directly extrapolate to absolute rates of cannibalism in nature from microcosm experiments (Polis 1981, Dong and Polis 1982), but field observations strongly suggest that the *relative levels of aggression* and the *relative potential for cannibalism* observed in microcosms are ecologically relevant and correspond to the degree to which larval development is constrained by drying.

Agrypnia deflata (Family Phryganeidae) was the only species that occurs only in permanent habitats, and including this species in our analyses potentially adds an element of phylogenetic bias to our interpretations—many phryganeids are both less aggressive and more likely to be restricted to permanent waters than limnephilids (Wissinger et al. 2003). In both *A. deflata*, and a European congener, *A. pagatena* (Curtis), the typical fate of caseless larvae is to displace case owners rather than be cannibalized (Otto 1987a,b, Englund and Otto 1991). However, there are some phryganeid species that complete development in temporary habitats [e.g., *Trichostegia minor* (Curtis), *Ptilostomus ocellifera* (Walker), *Fabria inornata* (Banks); Wiggins 1996, 1998, Wissinger and Gallagher 1999], and cannibalism occurs among cased larvae of one of these species (*P. ocellifera*) in temporary woodland pools (Wissinger, unpub. data). Clearly, additional replication (N = species) would improve our ability to test the hypothesis that developmental time constraints select for larval aggression and cannibalism in temporary-habitat species. There is abundant potential for a metadata approach for testing this hypothesis for other wetland invertebrates given that nearly all taxa exhibit species replacements along permanence gradients (Wellborn et al. 1996), and such permanence gradients are available for study in many types of wetlands (e.g., prairie potholes, playas, peatlands, etc.; see Batzer et al. 1999).

Cannibalism and Caddisfly Cases

A variety of hypotheses have been proposed for the evolution of case building in caddisflies. For lentic caddisfly species with tubular cases (e.g., Limnephilidae, Phryganeidae, Leptoceridae), these hypotheses include 1) reduced vulnerability to invertebrate predators, fish, and wading birds (Otto and Svensson 1980, Otto 1982, Johansson 1991, Johansson and Johansson 1992, Nislow and Molles 1993, Johansson and Englund 1995), 2) reduced mortality associated with freezing and drying in temporary habitats (Otto 1983, Zamora-Munoz and Svensson 1996), and 3) enhanced gas exchange (Williams et al. 1987, Williams and Feltmate 1992, Wiggins 1996; but see Otto 1976). Our

results suggest that larval cases also play an important role in reducing intra- and interspecific aggression and in deterring cannibalism and intraguild predation, especially in species with time constraints on larval development. It is perhaps not surprising that we have only observed larvae of the least aggressive species (*Agrypnia*) out of their cases in natural populations (S. Wissinger and W. Brown, personal observation). As in previous studies, the experimental removal of cases provides considerable insight into the importance of cases in reducing vulnerability to predation (Power et al. 1992). If, indeed, ancestral tube-making caddisflies were carnivorous (Mackay and Wiggins 1979), then reduced aggression and protection from cannibalism might be as parsimonious of an explanation for the evolution and maintenance of case building as is protection from heterospecific predators.

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