

Intraguild Predation and Cannibalism among Larvae of Detritivorous Caddisflies in Subalpine Wetlands

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INTRAGUILD PREDATION AND CANNIBALISM AMONG LARVAE OF DETRITIVOROUS CADDISFLIES IN SUBALPINE WETLANDS[1]

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Abstract. Comparative data from subalpine wetlands in Colorado indicate that larvae of the limnephilid caddisflies, *Asynarchus nigriculus* and *Limnephilus externus,* are reciprocally abundant among habitats—*Limnephilus* larvae dominate in permanent waters, whereas *Asynarchus* larvae dominate in temporary basins. The purpose of this paper is to report on field and laboratory experiments that link this pattern of abundance to biotic interactions among larvae. In the first field experiment, growth and survival were compared in single and mixed species treatments in littoral enclosures. Larvae, which eat mainly vascular plant detritus, grew at similar rates among treatments in both temporary and permanent habitats suggesting that exploitative competition is not important under natural food levels and caddisfly densities. However, the survival of *Limnephilus* larvae was reduced in the presence of *Asynarchus* larvae. Subsequent behavioral studies in laboratory arenas revealed that *Asynarchus* larvae are extremely aggressive predators on *Limnephilus* larvae. In a second field experiment we manipulated the relative sizes of larvae and found that *Limnephilus* larvae were preyed on only when *Asynarchus* larvae had the same size advantage observed in natural populations. Our data suggest that the dominance of *Asynarchus* larvae in temporary habitats is due to asymmetric intraguild predation (IGP) facilitated by a phenological head start in development. These data do not explain the dominance of *Limnephilus* larvae in permanent basins, which we show elsewhere to be an indirect effect of salamander predation.

Behavioral observations also revealed that *Asynarchus* larvae are cannibalistic. In contrast to the IGP on *Limnephilus* larvae, *Asynarchus* cannibalism occurs among same-sized larvae and often involves the mobbing of one victim by several conspecifics. In a third field experiment, we found that *Asynarchus* cannibalism was not density-dependent and occurred even at low larval densities. We hypothesize that *Asynarchus* IGP and cannibalism provide a dietary supplement to detritus that may be necessary for the timely completion of development in these nutrient-poor, high-elevation wetlands.

Key words: Asynarchus nigriculus; *caddisfly larvae; cannibalism; Colorado; hydroperiod; intraguild predation;* Limnephilus externus; *predation; phenologic priority; wetlands.*

INTRODUCTION

Although it has long been documented that potential competitors also prey on each other (e.g., Paine 1963), it is only recently that the taxonomic and ecological ubiquity of intraguild predation (IGP) has been appreciated by ecologists (see reviews by Ebenman and Persson 1988, Polis et al. 1989, Polis and Holt 1992). Cannibalism, which can be considered the special case in which *intra*specific competitors eat each other, is often reported within populations of species that interact as intraguild predators (Fox 1975, Polis 1981, 1988, Elgar and Crespi 1992). Both interactions are common in guilds of omnivorous (sensu Pimm 1978) predators in which larger species (or conspecifics) prey on smaller species or individuals within a species (reviewed by Polis et al. 1989; also see Hurd and Eisenberg 1990, Spiller and Schoener 1990, Wissinger and McGrady 1993). Intraguild predation is also common among similarly sized species that exhibit dramatic size increases during ontogeny (fish, amphibians, long-lived invertebrates such as lobster, scorpions; Werner and Gilliam 1984, Wilbur 1984, 1988, Ebenman and Persson 1988, Polis et al. 1989). Even in short-lived invertebrate predators (e.g., many aquatic and terrestrial insects), phe-

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nological differences between species and/or asynchronous development within generations can lead to temporal overlap of different size classes of conspecifics and heterospecifics, and hence to IGP and cannibalism (Hurd 1988, Wissinger 1989, 1992). Despite increased appreciation for the widespread occurrence of IGP and cannibalism, the community level ramifications of these interactions are understood for only a few well-studied systems (Polis and Holt 1992).

The stimulus for the experiments described in this paper was the observation that two morphologically and ecologically similar limnephilid caddisflies reciprocally dominate in subalpine wetlands that differ mainly in degree of permanence. The two species have nearly identical life cycles and both can exploit temporary waters because adults lay eggs terrestrially at the edge of pond basins (see *Caddisfly Natural History*, in the next section). However, in the wetland complex at our study site, *Asynarchus nigriculus* Banks is always dominant in temporary and *Limnephilus externus* (Hagen) is dominant in permanent basins (S. A. Wissinger and W. S. Brown, *unpublished manuscript*; Fig. 1). This pattern is even more striking in single, isolated ponds near our study site where *L. externus* and *A. nigriculus* are completely segregated in permanent and temporary waters, respectively (S. A. Wissinger and W. S. Brown, *unpublished manuscript*). Previous workers at this site have studied the mechanisms that underlie inter-basin differences in zooplankton species composition (Dodson 1970, 1974, Sprules 1972), but little is known about the factors that are responsible for the dramatic inter-basin differences in the benthic communities (S. A. Wissinger, *unpublished manuscript*).

In this paper we present experimental evidence that intraguild predation and cannibalism occur among larvae of *Limnephilus* and *Asynarchus* and suggest that asymmetric IGP plays a major role in determining patterns of distribution and abundance of these species. We initially assumed that these limnephilid caddisflies were mainly shredders of vascular plant detritus (Wiggins 1973, 1977, Barlocher et al. 1978, Williams and Williams 1980, Berte and Pritchard 1986). Thus, the first experiment was designed to test the hypothesis that habitat-specific differences in the outcome of intra- and/or interspecific competition were responsible for observed patterns of distribution and abundance (as in Park 1954; other examples reviewed by Dunson and Travis 1991, Warner et al. 1993). We report that (1) there is little evidence for resource competition per se between these species; (2) IGP and cannibalism are the main interactions that occur among their larvae; and (3) in the absence of other biotic interactions, the outcome of interactions between these two species should be the same in both permanent and temporary habitats. We also provide evidence that behavioral differences in aggressiveness and phenological differences in the timing of development are mechanisms that underlie the asymmetry in IGP between these species. Finally, we discuss the advantages of IGP and cannibalism for detritivores in the context of the low nutrient quality of detritus in these high elevation, oligotrophic waters.

Study Site and Caddisfly Natural History

The study was conducted in the Elk Mountains of central Colorado at the Mexican Cut Nature Preserve, a pristine, subalpine (3640 m elevation) wilderness area owned by The Nature Conservancy and managed by the Rocky Mountain Biological Laboratory. The preserve contains several wetland complexes with >50 shallow basins that vary in area (5–4650 m^2), water chemistry, hydroperiod, and community composition (Dodson 1970, 1974, 1982, Maly 1970, 1973, Sprules 1972, Wissinger and Whiteman 1992). Basins are either permanent, temporary autumnal (sometimes dry in autumn), or temporary vernal (always dry in early summer; after Ward 1992) depending on their size, morphometry, and exposure (see additional details in Wissinger and Whiteman 1992). Hydroperiod is the most predictive abiotic correlate of distributional patterns among the 15 planktonic and >70 benthic invertebrates that occur in the wetland complex (S. A. Wissinger, *unpublished manuscript*). The only aquatic vertebrate in the system is the tiger salamander, *Ambystoma tigrinum nebulosum* (Hallowell), which breeds in the permanent and some autumnal basins on the preserve (Whiteman et al. 1994). Only permanent habitats contain the life stages (>1-yr-old larvae and paedomorphs) that prey on benthic invertebrates (Whiteman et al. 1994, 1996).

Asynarchus nigriculus and *Limnephilus externus* are among the most abundant and conspicuous macroinvertebrates at Mexican Cut. Dietary analyses revealed that the two species have nearly identical diets, with vascular plant detritus and benthic algae comprising ≈95% of gut contents by volume (Sparks 1993). *Limnephilus* larvae build haphazardly constructed cases from fragments of aquatic plants (mainly *Isoetes bolanderi*), whereas *Asynarchus* build exquisite patchwork tubes from fragments of spruce bark, spruce needles, and bits of stone. Despite differences in case structure, the two species are nearly identical in body size at each of the five larval instars, and have generally similar life histories that differ slightly in phenology. Adults of both species lay eggs under rocks and logs along the shoreline of basins. Eggs overwinter under 10–15 m of snow and hatch in spring when all basins are full. *Asynarchus* hatch earlier and develop faster than *Limnephilus* so that at a given time within basins, *Asynarchus* are typically one to two larval instars ahead of *Limnephilus* (S. A. Wissinger and W. S. Brown, *unpublished manuscript*). This developmental head start allows *Asynarchus,* but not *Limnephilus,* to exploit rock pools and other vernal basins that dry early in summer (Fig. 1). However, both species complete larval development, pupate, and emerge before autumnal basins

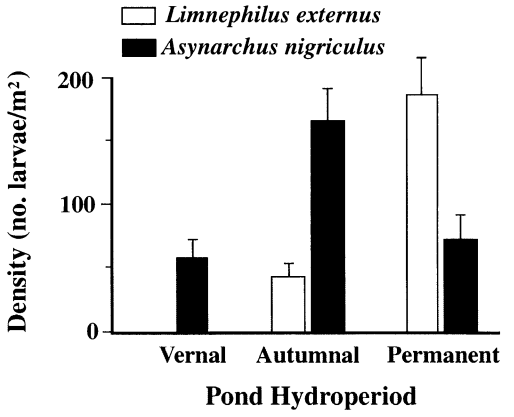


FIG. 1. Average peak larval densities of *Limnephilus externus* and *Asynarchus nigriculus* in four vernal, four autumnal, and five permanent basins at the Mexican Cut Nature Reserve (see Wissinger and Whiteman 1992) during 1990. Four 0.25-m^2 drop box samples (after Wissinger 1988) were taken weekly during June, July, and August. Data represent mean and 1 SE.

dry (S. A. Wissinger and W. S. Brown, *unpublished manuscript*). Thus, the pattern of reciprocal dominance between autumnal and permanent habitats is not the result of life cycle/history constraints (Fig. 1).

METHODS

Competition field experiment

The first experiment was conducted in July 1992 and was designed to (1) quantify the relative strengths of intra- and interspecific competition among larvae of the two caddisflies and (2) determine if the outcome of competition varied between permanent and autumnal habitats. Six screened (1-mm mesh) wood frame cages (0.5 m cubes; 0.25 m^2 bottom area) were placed in the littoral zone of four permanent and four autumnal basins. Both species were abundant in these eight habitats, and natural densities in open areas near the cages were similar to those in the cages during the experiment. After the cage bottoms were sealed with clay, salamanders, caddisflies, and large invertebrate predators (e.g., *Dytsiscus* beetle larvae) were removed. We re-checked the cages several times for caddisfly immigration before the experimental organisms were introduced.

The following treatments were randomly assigned to the cages in each pond: (1) *Asynarchus* at low density, (2) *Asynarchus* at high density, (3) *Limnephilus* at low density, (4) *Limnephilus* at high density, (5) both species at high density, and (6) cage control for immigration (no caddisflies). The cage controls revealed that the cages were effective in excluding immigrants during the duration of this and subsequent experiments. Low and high (single and mixed) density treatments of 200 and 400 larvae/m^2, respectively, bracket combined densities of shoreline populations of the two species in these habitats. The larval instars used for each species were representative of those present in the natural populations at the time of experimental set-up (9:1—fifth (final): fourth instar *Asynarchus,* and 3:2 second: third instar *Limnephilus*). Twenty larvae of each species at these instar ratios were sampled from the pool of larvae used for the experiment to estimate the initial masses of each instar. These larvae were killed in 90% ethanol and immediately dried at 50°C for 24 h and the mass determined to the nearest microgram on a Cahn C31 electrobalance (Cahn, Incorporated, Cerritos, California). All values for mass reported in this paper were determined in this way.

Larval development proceeded rapidly during the experiment, which was terminated after 10 d when *Asynarchus* began to pupate. All surviving animals were removed, sorted into instar classes, and counted. Pupae and larvae from each experimental unit were killed in 90% ethanol, and all pupae and 20 larvae were dried and the mass determined to the nearest microgram.

The experiment was analyzed as a split-plot design with four ponds nested in each hydroperiod type (i.e., $n = 4$), and treatments replicated over all basins (i.e., $n = 8$). We initially analyzed the growth and survival of larvae simultaneously using MANOVA and found that the dependent variables were not correlated (Bartlett's tests of sphericity all $\gg 0.05$; see Norusis 1990). Thus, the analyses presented here are based on split-plot ANOVA for the effects of hydroperiod and treatment on the growth and survival of each species. In this and subsequent ANOVA models, significant differences among means were based on Scheffe's method for unplanned a posteriori contrasts (see Day and Quinn 1989). Proportional survivorship data were arcsine-transformed to approximate assumptions of normality. Bartlett-Box and Lilliefors statistics in this and subsequent analyses were used to test for assumptions of homoscedasticity and normality, respectively (Norusis 1990).

Laboratory behavioral studies

The results of the competition field experiment prompted several behavioral studies that were conducted in July through August 1992 in a portable field laboratory at the site. We observed caddisfly behaviors in plastic storage containers (0.25 m^2 bottom area) that contained $\approx$2.5 cm of detritus, a clump of emergent vegetation, three small rocks, and several pieces of woody debris. Twelve arenas were filled with pond water to a depth of $\approx$10 cm and then assigned one of the following treatments: (1) fifth-instar *Asynarchus* alone, (2) fourth-instar *Limnephilus* alone, and (3) both species. Densities in all arenas were maintained at 200 larvae/m^2, which corresponded to the low density treatments in the competition field experiment. Two observational protocols were used in the arenas. First, we conducted 10 min focal animal samples and recorded activity levels (time spent crawling, distance crawled, and time spent foraging), and behaviors associated with

aggression (proleg wrestling, case shaking, and biting). Secondly, we recorded all encounters observed during 10 min of scanning an arena and noted whether the encounter was aggressive and which species was the aggressor. Three observers worked simultaneously with one of the three treatments; thus, time of day and between-day effects should not bias comparisons among treatments. Observations were made between 0900 and 1600.

Because of the multiple dependent variables (time spent foraging, time spent crawling, and distance crawled), we analyzed the data from focal animal observations using a two-way MANOVA (species × treatment). The proportion of encounters that resulted in aggression was analyzed using a two-way ANOVA (species × treatment) on arcsine-transformed data.

Size-dependent intraguild predation

The results of the competition field experiment and the laboratory experiments prompted a second field experiment designed to determine whether *Asynarchus* predation on *Limnephilus* was facilitated by a size advantage that results from a phenologic head start. In July 1993, we placed 16 enclosures (same as in the competition experiment) in the littoral zone of one of the permanent basins (Wissinger and Whiteman 1992: pond L1). The following treatments were randomly assigned to the enclosures: (1) same-sized *Limnephilus* and *Asynarchus* (all fifth instars), (2) large *Asynarchus* (fifth instars) with small *Limnephilus* (third instars), (3) small *Asynarchus* (third instars) with large *Limnephilus* (fifth instars), and (4) a no-caddisfly cage control to monitor cage permeability. Densities were the same as those used in the mixed species treatments in the first field experiment (200 + 200 = 400 larvae/m^2). Large *Asynarchus* and small *Limnephilus* were obtained from the Mexican Cut ponds where they naturally coexist. We exploited intraspecific differences in phenology across elevations to obtain the other size combinations. Small *Asynarchus* were taken from several ponds near Mexican Cut that occur at a higher elevation (3700 m) than the experimental ponds, and large *Limnephilus* were obtained from ponds at lower elevations (3100 m) near the Rocky Mountain Biological Laboratory.

The experiment was terminated after 10 d, when all surviving larvae and pupae were removed from the cages and counted. We initially analyzed the number of each species surviving with a one-way MANOVA and found no correlation between *Limnephilus* and *Asynarchus* survival. We subsequently conducted a one-way ANOVA on each species.

Density-dependent Asynarchus *cannibalism*

Results of the competition experiment, laboratory studies, and field observations all suggested that cannibalism is a commonplace interaction among *Asynarchus* larvae. To determine if cannibalism is density-dependent, we conducted a third field experiment in one of the autumnal basins that supports especially high densities of *Asynarchus* (Wissinger and Whiteman 1992: pond L8). Peak densities for final instar *Asynarchus* in that pond were 300–400 larvae/m^2 (S. Wissinger and J. Jannot, *unpublished data*). Because we were interested in determining whether cannibalism would occur at lower than ambient densities, we stocked the field enclosures with 100, 200, and 400 *Asynarchus* larvae/m^2. Each of the density treatments and an empty cage control were replicated three times with the treatments randomly assigned to the 12 enclosures. We initiated the experiment in early July using 1:2:1 ratios of second : third : fourth instars of *Asynarchus,* which reflected the natural ratios in that pond at the time of experimental set-up. Ten individuals of each of these instars were collected at the start of the experiment and weighed to the nearest microgram. The experiment was conducted for 14 d, after which all larvae and pupae were removed and counted. Twenty animals from each experimental unit were kept to determine final mass. We analyzed the effect of density on larval mass and survival with one-way MANOVA and on the proportion that pupated with one-way ANOVA on arcsine-transformed data.

Results

Competition field experiment

Growth.—Both species grew rapidly in permanent and autumnal habitats (Fig. 2). By the end of the experiment, all *Asynarchus* were in the final instar or had begun to pupate. Final average masses of *Limnephilus* and *Asynarchus* larvae were consistently greater in permanent than in autumnal habitats, although this hydroperiod effect was not statistically significant (Table 1, Fig 2). Neither an increase in intra- nor interspecific densities resulted in a change in growth rates for either species (Table 1, Fig. 2). However, there was a treatment effect on the final mass of *Asynarchus* pupae (split-plot ANOVA; treatment effect $F_{2,12} = 15.2$, $P = 0.001$). *Asynarchus* pupae in the mixed species treatments had significantly more mass than those in either the low or high single-species treatment (Scheffe's a posteriori contrast, $P = 0.001$ and $P < 0.001$, respectively). Hydroperiod did not affect pupal mass (split-plot ANOVA; hydroperiod effect $F_{1,6} = 1.4$, $P = 0.28$).

Survival.—Neither *Asynarchus* nor *Limnephilus* survival was affected by hydroperiod, and *Asynarchus* survival did not differ among treatments (Table 1, Fig. 3). However, *Limnephilus* survival was much lower in the presence of *Asynarchus* than in either of the single-species treatments (Table 1, Fig. 3). Over 80% of the *Limnephilus* survived in the high and low single-species treatments, but only ≈20% survived in the presence of *Asynarchus.* Across all ponds, *Limnephilus* survival in single-species treatments (low density, 0.84 ± 0.11; high density 0.87 ± 0.15; mean ±1 SE) was higher

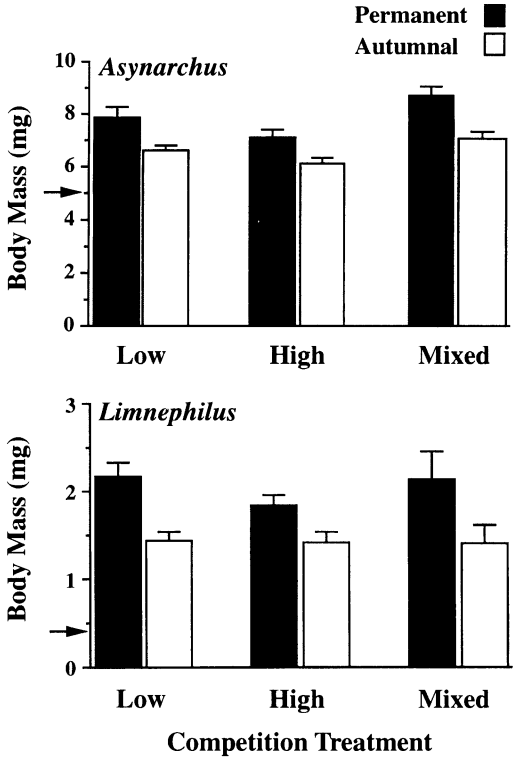


FIG. 2. Average final mass of *Asynarchus* and *Limnephilus* larvae in the competition field experiment conducted in permanent and autumnal ponds. Low, high, and mixed treatments correspond to 200, 400, and 400 (200 + 200) larvae/m^2, respectively. Arrows on the ordinate indicate initial masses. See Table 1 for statistical analysis. Data represent mean and 1 SE.

than that of *Asynarchus* (low density, 0.75 ± 0.07; high density, 0.67 ± 0.05; ANOVA, $F_{3,26} = 3.55$, $P = 0.03$).

Laboratory behavioral studies

Asynarchus was more active than *Limnephilus* in the observation arenas, and was clearly the more aggressive of the two species. Head-to-head *Asynarchus* encounters with *Limnephilus* and conspecifics often involved proleg wrestling and biting, and occasionally escalated into intraguild predation or cannibalism. *Asynarchus* larvae also "attacked" and vigorously shook the posterior end of the cases of other larvae. *Limnephilus* often responded to aggressive encounters by retreating into their cases. The presence of heterospecific larvae did not affect the level of aggressiveness for either species (two-way ANOVA main effects of treatment: *Asynarchus* $F_{1,18} = 0.635$, $P = 0.55$; *Limnephilus* $F_{1,14} = 0.335$, $P = 0.60$). Across all treatments, >30% of the encounters initiated by *Asynarchus* resulted in aggressive behavior, compared to only 7% for *Limnephilus* ($F_{1,20} = 6.87$, $P = 0.01$; Fig. 4). The predation events we observed during focal animal samples, during encounter samples, between samples, and in holding containers always involved *Asynarchus* as the predator, either on *Limnephilus* or on a conspecific. *Asynarchus* predation on *Limnephilus* usually occurred between one predator and one prey, whereas *Asynarchus* cannibalism typically involved several predators mobbing a single conspecific. After conspecific victims were consumed, the aggressors dismantled the case and added the fragments to their own cases before dispersing. *Limnephilus* cases were not dismantled after *Asynarchus* IGP.

Size-dependent intraguild predation

In this field experiment, we manipulated the relative size of the two caddisfly species and found that *Asynarchus* survival did not differ among treatments (univariate $F_{2,9} = 2.34$, $P = 0.16$). However, *Limnephilus* survival did differ among treatments ($F_{2,9} = 67.2$, $P < 0.001$; Fig. 5). Fewer *Limnephilus* survived in the presence of large *Asynarchus* than in treatments in which the two species were similar in size, and in treatments in which large *Limnephilus* were with small *Asynarchus* (Scheffe's a posteriori contrast, $P < 0.001$). There was no evidence that large *Limnephilus* prey on small *Asynarchus,* and *Limnephilus* and *Asynarchus* survival rates varied independently across treatments (Bartlett Test of Sphericity = 1.37, $P = 0.24$).

Density-dependent Asynarchus *cannibalism*

In the cannibalism field experiment, *Asynarchus* survival was relatively low (≈40%) in all treatments as compared to in the competition field experiment. The average mass of survivors was not correlated with the proportion of larvae that survived (MANOVA Bartlett Test of Sphericity = 1.04, $P = 0.35$). *Asynarchus* survival did not differ across the different treatment densities (Fig. 6; MANOVA univariate F test for survival $F_{2,9} = 0.265$, $P = 0.77$), but density did affect the final mass of larvae (MANOVA univariate $F_{2,9} = 7.53$, $P = 0.012$; Fig. 7). At the end of the experiment, average final mass of larvae at the highest density (400 larvae/m^2) was lower than at the other two densities (Scheffe's a posteriori contrast, $P < 0.05$).

DISCUSSION

Asymmetric Asynarchus *IGP on* Limnephilus

Our results suggest that *Asynarchus* and *Limnephilus* interact mainly as intraguild predator and prey, respectively. Although the two species have nearly identical diets and exploit similar microhabitats, it does not appear that exploitative intra- or interspecific competition is an important interaction, at least at the densities at which larvae naturally occur at and near our study site. By manipulating the relative sizes of these two species, we found that *Asynarchus* IGP on *Limnephilus* is facilitated by a developmental size advantage that *Asynarchus* enjoys as a result of earlier hatching in spring. Phenological priority appears to be extremely important in creating the potential for asymmetric IGP

TABLE 1. Split-plot ANOVAs on the effects of hydroperiod and treatment on the final mass and survival of *Asynarchus* and *Limnephilus* larvae in the competition field experiment.

Effect	df	Denominator MS for *F* ratio†	Mass		
			Asynarchus		
			MS	*F*	*P*
1) Hydroperiod	1	(2)	9.45	0.73	0.43
2) Ponds {Hydroperiod}	6		12.99		
3) Treatment	2	(5)	1.23	2.92	0.09
4) Treatment × {Hydroperiod}	2	(5)	1.00	2.38	0.13
5) Treatment × Pond{Hydroperiod}	12		0.42		

† Entries in this column refer to the numbered effects in the leftmost column.

interactions among aquatic predators (Benke 1978, Morin 1984, Wilbur and Alford 1985, Wissinger 1989). As has been noted for amphibians (e.g., Wilbur and Alford 1985), early and rapid development in caddisflies both facilitates the exploitation of ephemeral habitats and confers a competitive and/or predatory advantage over other species.

Asymmetry in IGP between these two species is also related to differences in aggressiveness. In the second field experiment, we observed that *Limnephilus* did not prey on *Asynarchus* even when they had a size advantage. This result is not surprising given the differences in aggressive behavior that we observed in the laboratory experiments. In the laboratory arenas, we observed that *Asynarchus* frequently disrupt *Limnephilus* foraging by forcing them to retreat into their cases upon attack. Thus, in addition to the mortality effect, *Asynarchus* should have sublethal effects on *Limnephilus* fitness (as in Skelly and Wemer 1990; Peckarsky and Cowan 1991; Peckarsky et al. 1993 and references therein). Such sublethal effects would have been difficult to detect in the field experiment because *Asynarchus* IGP greatly reduced the densities of *Limnephilus* and was probably selective on the smallest *Limnephilus*.

Our results suggest that the dominance of *Asynarchus* in autumnal habitats at Mexican Cut is a result of asymmetric IGP, but they do not explain the dominance of *Limnephilus* in permanent ponds. Both species grew slightly faster in permanent than in temporary habitats, and survival did not differ among habitats for either species. Thus, in the absence of other biotic interactions, *Asynarchus* should dominate in all habitats. Elsewhere, we show that the dominance of *Limnephilus* in permanent habitats is in part an indirect positive effect of salamander predation on *Asynarchus* (S. A. Wissin-

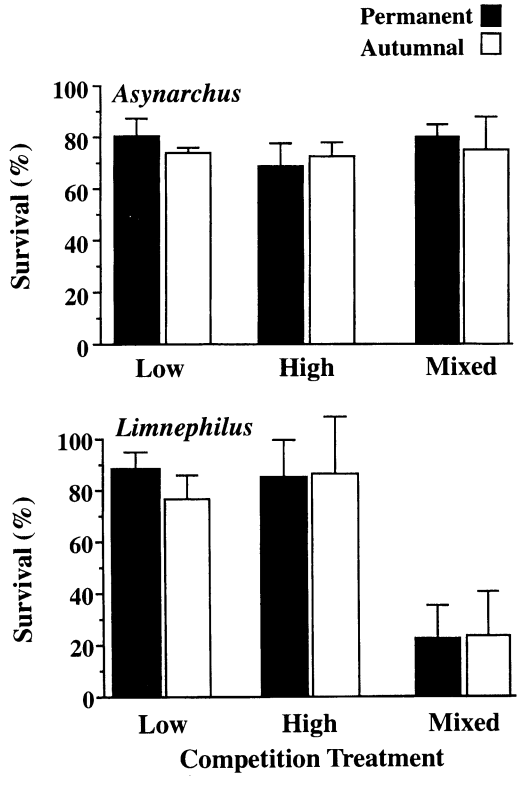


FIG. 3. Percentage of *Asynarchus* and *Limnephilus* larvae that survived to the end of the competition field experiment. Densities are as in Fig. 2. *Limnephilus* survival was significantly lower in the mixed treatment than in either single-species treatment (Scheffe's a posteriori contrast; see Table 1). Data represent mean and 1 SE.

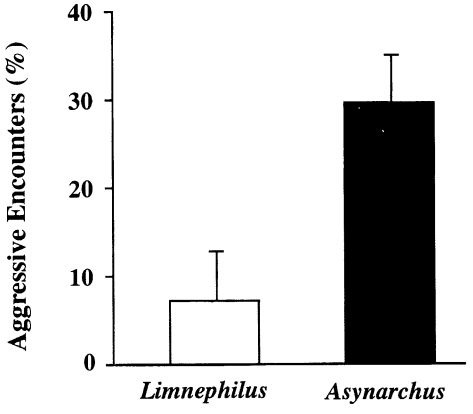


FIG. 4. Percentage of encounters initiated by each species of caddisfly that resulted in aggression during behavioral observations. Data represent mean and 1 SE.

TABLE 1. Continued.

Mass			Survival					
Limnephilus			*Asynarchus*			*Limnephilus*		
MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
1.79	2.76	0.15	0.010	0.769	0.425	0.001	0.038	0.961
0.65			0.013			0.026		
0.05	0.38	0.70	0.014	1.718	0.226	1.184	74.130	<0.001
0.07	0.54	0.60	0.007	0.875	0.443	0.008	0.499	0.622
0.13			0.008			0.016		

ger, G. L. Rouse, G. B. Sparks, W. S. Brown, and H. H. Whiteman, *unpublished manuscript*).

Asynarchus *cannibalism*

Asynarchus predation on *Limnephilus* is usually a one-on-one phenomenon, whereas *Asynarchus* cannibalism usually involves a mob of attacking conspecifics. The phenomenon is easily observed in the field at our study site because of the clear, shallow waters; the number (3–10) of animals that coalesce to devour the victim; and the frenetic behavior of the attackers. We do not as yet understand the cues by which these mobs form or the characteristics of victims that make them vulnerable. Preliminary experiments suggest that animals that have recently molted might be especially vulnerable (S. A. Wissinger, *personal observation*). To our knowledge, group cannibalism has not been previously described in limnephilid caddisflies or in any aquatic insect.

Asynarchus cannibalism also differs from predation on *Limnephilus* in that it frequently occurs among larvae that are of similar size. Non-filial cannibalism in many, if not most species for which it has been described, usually involves larger animals preying on smaller conspecifics (see reviews by Fox 1975, Polis 1981, 1988). In contrast, *Asynarchus* development is univoltine and relatively synchronous so that most animals are the same size at the same time, and a priori, the opportunity for cannibalism might be predicted to be relatively low (Wissinger 1992). That attackers and victims are the same size may explain why we rarely observed one-on-one cannibalism events between *Asynarchus*.

Asynarchus cannibalism is apparently not an extraordinary event related to crowded conditions or starvation. We observed similar rates of cannibalism at lower than ambient densities in the cannibalism experiment, and cannibalism probably explains why *Asynarchus*

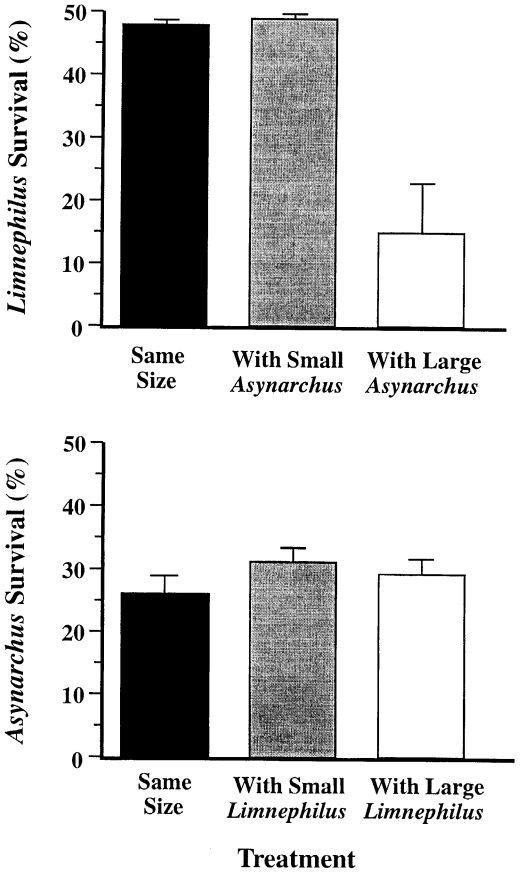


FIG. 5. Percentage survival of caddisfly larvae at the end of the size-specific IGP field experiment. *Limnephilus* survival in the presence of large *Asynarchus* was significantly lower than in the other two treatments (Scheffe's a posteriori contrast). Data represent mean and 1 SE.

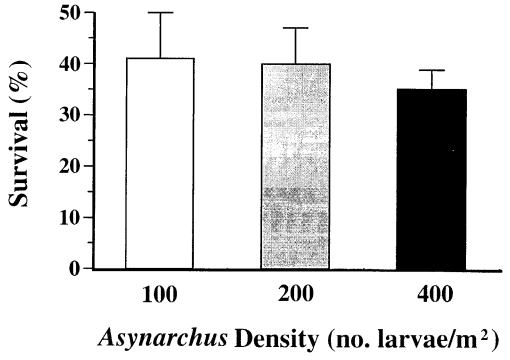


FIG. 6. Percentage of *Asynarchus* larvae surviving to the end of the cannibalism field experiment at low, ambient, and high larval densities. Treatments did not differ based on ANOVA. Data represent mean and 1 SE.

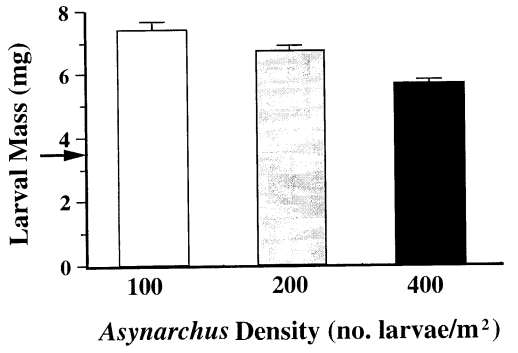


FIG. 7. Average mass of *Asynarchus* larvae at the end of the cannibalism field experiment in low ambient and high larval densities. Larvae in the highest density treatment were significantly smaller than those in either of the other treatments (Scheffe's a posteriori contrast). Arrow on the ordinate axis indicates average initial mass of larvae. Data represent mean and 1 SE.

survival was lower than that of *Limnephilus* survival in the competition experiment. The density independent occurrence in *Asynarchus* populations suggests that cannibalism in this case might be more related to nutritional supplementation than to population regulation.

IGP, cannibalism, and detritivory

IGP and cannibalism are best documented among aquatic insects with predaceous nymphs (e.g., Odonata: Van Buskirk 1989, Wissinger 1989, Johnson 1991, Johansson 1993, Wissinger and McGrady 1993) and/or predaceous aquatic adults (e.g., aquatic hemiptera: Fox 1975, Sih 1978, Orr et al. 1990 and references therein). In these taxa IGP and cannibalism are often considered to be consequences of relatively indiscriminate foraging behavior (Orr et al. 1990, Johnson 1991). In contrast, limnephilid caddisflies are typically considered detritivores on plant material (Wiggens 1974, 1977, Barlocher et al. 1978, Williams and Williams 1980, Berte and Pritchard 1986), although we found several anecdotal and dietary references that indicate there is an increasing propensity for carnivory during development (Slack 1936, Mecom and Cummins 1964, Winterbourn 1971*a*, Mecom 1972, Anderson 1976). This tendency has been observed in several other taxa of aquatic detritivores (Winterbourn 1971*b*, Fahy 1972, Fuller and Stewart 1977, Shapas and Hilsenhoff 1978, Benke and Wallace 1980), and may be more a more general phenomenon than has been previously recognized (Giller and Sangpradub 1993). Our study provides experimental evidence that this shift towards carnivory can include intraguild predation and cannibalism.

Intraguild predators and cannibals face the potential cost of attacking prey that can attack back, and cannibals face the additional risks of disease and parasite transmission, and the potential loss of inclusive fitness from eating kin (Elgar and Crespi 1992). Given these costs, the regular occurrence of these interactions among these caddisflies suggests there must be benefits (Dong and Polis 1992). One hypothesis is that, because IGP and cannibalism result in both an energy gain and the elimination of a potential competitor, these interactions have evolved as an extreme form of interference competition (Johnson et al. 1985, Polis 1988). However, our results suggest that competition for food resources (detritus) is relatively benign at our study site and that IGP and cannibalism occur across a wide range of larval densities.

An alternative hypothesis is that IGP and cannibalism provide these caddisflies with a qualitative dietary supplement. The detritus (spruce needles, wood fragments, aquatic macrophytes) that volumetrically dominates the diet of both species is mainly lignin, cellulose, and hemicellulose (Sparks 1993), has a high carbon to nitrogen ratio, and is probably nutritionally incomplete (Suberkropp et al. 1976, Cummins and Klug 1979, Sinsabaugh et al. 1985, Anderson and Cargill 1987). Carnivory, and specifically IGP and cannibalism, would provide a high-protein and/or lipid supplement that could be necessary for metamorphosis, or at the least, a timely escape from drying habitats (see also Anderson 1976, Iverson 1979, Cargill et al. 1985). The need for such a dietary supplement should be independent of density and especially important under the extremely low nutrient (N, P) conditions and short growing season (see Wissinger and Whiteman 1992) in subalpine and boreal wetlands. Consistent with this hypothesis is the observation that, despite the relatively short-term nature of the first field experiment, *Asynarchus* pupae were significantly larger in treatments with *Limnephilus* prey than in those without. Future research on the population consequences of IGP and cannibalism in aquatic insects should focus on quantifying the effects of these interactions on fitness correlates such as time to pupation and emergence, adult size, and adult fecundity.

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LITERATURE CITED

Anderson, N. H. 1976. Carnivory by an aquatic detritovore, *Clistorina magnifica* (Trichoptera Limnephilidae). Ecology **57**:1081–1085.

Anderson, N. H., and A. S. Cargill. 1987. Nutritional ecology of aquatic detritivorous insects. Pages 903–925 *in* F. Slansky and J. G. Rodriquez, editors. Nutritional ecology of insects, mites, spiders, and related invertebrates. John Wiley, New York, New York, USA.

Barlocher, F., R. J. Mackay, and G. B. Wiggens. 1978. Detrital processing in a temporary vernal pool in southern Ontario. Archiv fur Hydrobiologie **81**:269–295.

Benke, A. C. 1978. Interactions among coexisting predators: a field experiment with dragonfly larvae. Journal of Animal Ecology **47**:335–350.

Benke, A. C., and B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology **65**:1–13.

Berte, S. B., and G. Pritchard. 1986. The life histories of *Limnephilus externus, Anabolia bimaculata,* and *Nemotaulius hostilis* (Trichoptera: Limnephilidae) in a pond in southern Alberta, Canada. Canadian Journal of Zoology **64**: 2348–2356.

Cargill, A. S., K. W. Cummins, B. J. Hanson, and R. R. Lowry. 1985. The role of lipids as feeding stimulants for shredding aquatic insects. Freshwater Biology **15**:455–464.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics **10**:147–172.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs **59**:433–463.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnology and Oceanography **15**:121–127.

———. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology **55**:605–613.

———. 1982. Chemical and biological limnology of six west-central Colorado mountain ponds and their susceptibility to acid rain. American Midland Naturalist **107**:1733–1739.

Dong, Q., and G. A. Polis. 1992. The dynamics of cannibalistic populations: a foraging perspective. Pages 12–37 *in* M. A. Elgar and B. J. Crespi, editors. Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York, New York, USA.

Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist **138**:1067–1091.

Ebenman, B., and L. Persson, editors. 1988. Size-structured populations. Springer-Verlag, New York, New York, USA.

Elgar, M. A., and B. J. Crespi. 1992. Ecology and evolution of cannibalism. Pages 1–12 *in* M. A. Elgar and B. J. Crespi, editors. Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York, New York, USA.

Fahy, E. 1972. The feeding behavior of some common lotic insect species in two streams of different detrital content. Journal of Zoology **76**:337–350.

Fox, L. 1975. Cannibalism in natural populations. Annual Review of Ecology and Systematics **6**:87–106.

Fuller, R. C., and K. W. Stewart. 1977. The food habits of stoneflies in the upper Gunnison River, Colorado. Environmental Entomology **6**:293–302.

Giller, P. S., and N. Sangradub. 1993. Predatory foraging behavior and activity patterns of larvae of two species of limnephilid cased caddis. Oikos **67**:351–357.

Hurd, L. E. 1988. Consequences of divergent egg morphology to predation and coexistence in two sympatric, congeneric mantids (Orthoptera: Mantidae). Oecologia **76**: 547–550.

Hurd, L. E., and R. M. Eisenberg. 1990. Arthropod community responses to manipulation of a bitrophic predator. Ecology **71**:2107–2114.

Iverson, T. M. 1979. Laboratory energetics of larvae of *Sericostoma personatum* (Trichoptera). Holarctic Ecology **2**: 1–5.

Johansson, F. 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behavior and zooplankton availability. Oikos **66**:80–87.

Johnson, D. M. 1991. Behavioral ecology of dragonflies and damselflies. Trends in Ecology and Evolution **6**:8–13.

Johnson, D. M., P. H. Crowley, R. E. Bohanan, C. N. Watson, and T. H. Martin. 1985. Competition among larval dragonflies: a field enclosure experiment. Ecology **66**:119–128.

Maly, E. J. 1970. The influence of predation on the adult sex ratios of two copepod species. Limnology and Oceanography **15**:131–137.

———. 1973. Density, size, and clutch of two high-altitude diaptomid copepods. Limnology and Oceanography **18**: 840–848.

Mecom, J. O. 1972. The feeding habits of Trichoptera in a mountain stream. Oikos **23**:401–407.

Mecom, J. O., and K. W. Cummins. 1964. A preliminary study of the trophic relationship of the larvae of *Brachycentrus americanus* (Trichoptera: Brachycentridae). Transactions of the American Microscopical Society **83**:233–243.

Morin, P. J. 1984. Odonate guild composition: experiments with colonization history and fish predation. Ecology **65**: 1866–1873.

Norusis, M. J. 1990. SPSS/PC=4.0. SPSS, Incorporated. Chicago, Illinois, USA.

Orr, B. K., W. W. Murdoch, and J. R. Bence. 1990. Population regulation, convergence, and cannibalism in *Notonecta* (Hemiptera). Ecology **71**:83–98.

Paine, R. T. 1963. Trophic relationships of eight sympatric gastropods. Ecology **44**:63–72.

Park, T. 1954. Experimental studies of interspecific competition II. Temperature, humidity, and competition in two species of *Tribolium.* Physiological Zoology **27**:177–238.

Peckarsky, B. L., and C. A. Cowen. 1991. Consequence of larval intraspecific interference to stonefly growth and fecundity. Oecologia **88**:277–288.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology **74**:1836–1846.

Pimm, S. L. 1978. On feeding on more than one trophic level. Nature **275**:542–544.

Polis, G. A. 1981. The evolution and dynamics of interspecific predation. Annual Review of Ecology and Systematics **12**:240–255.

———. 1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size structured populations. Pages 183–202 *in* B. Ebenmen and L. Persson, editors. Size-structured populations. Springer-Verlag, New York, New York, USA.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution **7**:151–155.

Polis, G. A., C. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation, potential competitors that eat each other. Annual Review Ecology and Systematics **20**:297–330.

Shapas, T. J., and W. L. Hilsenhoff. 1978. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. Great Lakes Entomologist **9**:269–311.

Sih, A. 1978. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmani.* Ecology **63**:786–796.

Sinsabaugh, R. L., A. E. Linkings, and E. F. Benfield. 1985. Cellulose digestion and assimilation by three leaf-shredding aquatic insects. Ecology **66**:1464–1471.

Skelly, D. A., and E. E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. Ecology **71**:1213–2322.

Slack, H. D. 1936. The food of caddisfly (Trichoptera) larvae. Journal of Animal Ecology **5**:105–115.

Sparks, G. B. 1993. Competition and intraguild predation between two species of caddisfly (Trichoptera) larvae in permanent and semi-permanent high elevation ponds. B.S. Thesis. Allegheny College, Meadville, Pennsylvania, USA.

Spiller, D. A., and T. W. Schoener. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. Oecologia **83**:150–161.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology **53**:375–386.

Suberkropp, K. F., G. L. Godshalk, and M. J. Klug. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology **57**:720–727.

Van Buskirk, J. 1989. Density-dependent cannibalism in larval dragonflies. Ecology **70**:1442–1449.

Ward, J. V. 1992. Aquatic insect ecology: 1. Biology and habitat. John Wiley and Sons, New York, New York, USA.

Warner, S. C., J. Travis, and W. A. Dunson. 1993. Effect of pH variation on interspecific competition between two species of hylid tadpoles. Ecology **74**:183–194.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393–425.

Whiteman, H. H., S. A. Wissinger, and A. Bohonak. 1994. Seasonal movement patterns and diet in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. Canadian Journal of Zoology **72**:1780–1787.

Whiteman, H. H., S. A. Wissinger, and W. S. Brown. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. Evolutionary Ecology **10**:429–422.

Wiggins, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Life Science Contributions of the Royal Ontario Museum **88**:1–28.

———. 1977. Larvae of North American caddisflies (Trichoptera). University of Toronto Press, Toronto, Ontario, Canada.

Wilbur, H. M. 1984. Complex life cycles and community organization in amphibians. Pages 195–224 *in* P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, editors. A new ecology: novel approaches to interactive systems. John Wiley and Sons, New York, New York, USA.

———. 1988. Interactions in size-structured populations: from individual behavior to ecosystem dynamics. Pages 157–170 *in* B. Ebenman, and L. Persson, editors. Size-structured populations. Springer-Verlag, New York, New York, USA.

Wilbur, H. M., and R. A. Alford. 1985. Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. Ecology **66**:1106–1114.

Williams, N. E., and D. D. Williams. 1980. Distribution and feeding records of the caddisflies of the Matamek River region. Canadian Journal of Zoology **57**:2402–2412.

Winterbourn, M. J. 1971*a*. The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. Canadian Journal of Zoology **49**:623–635.

———. 1971*b*. An ecological study of *Banksiola crotchi* Banks (Trichoptera: Phyrganeidae) in Marion Lake, British Columbia. Canadian Journal of Zoology **49**:636–645.

Wissinger, S. A. 1988. Spatial distribution, life history, and larval survivorship in a 14-species assemblage of larval dragonflies (Odonata:Anisoptera). Freshwater Biology **20**: 329–340.

———. 1989. Seasonal variation in the intensity of competition and intraguild predation among dragonfly larvae. Ecology **70**:1017–1027.

———. 1992. Niche overlap and the potential for competition and intraguild predation in size-structured populations. Ecology **73**:1421–1444.

Wissinger, S. A., and J. McGrady. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. Ecology **74**:207–218.

Wissinger, S. A., and H. H. Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: anthropogenic acidification or natural variation? Journal of Herpetology **26**:377–391.