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# FORAGING TRADE-OFFS ALONG A PREDATOR–PERMANENCE GRADIENT IN SUBALPINE WETLANDS

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*Abstract.* We conducted a series of field and laboratory experiments to determine the direct and indirect effects of a top predator, the tiger salamander (*Ambystoma tigrinum nebulosum*), on larvae of two species of limnephilid caddisflies (*Limnephilus externus* and *Asynarchus nigriculus*) in subalpine wetlands in central Colorado. *Asynarchus* larvae predominate in temporary wetlands and are aggressive intraguild predators on *Limnephilus* larvae, which only predominate in permanent basins with salamanders. We first conducted a field experiment in mesocosms (cattle tanks) to quantify the predatory effects of different life stages of salamanders on the two caddisfly species. Two life stages of the salamanders (larvae and paedomorphs) preferentially preyed on *Asynarchus* relative to *Limnephilus*. Subsequent laboratory experiments revealed that high *Asynarchus* activity rates and relatively ineffective antipredatory behaviors led to higher salamander detection and attack rates compared to *Limnephilus*. In a second field experiment (full factorial for presence and absence of each of the three species), we found that salamander predation on *Asynarchus* had an indirect positive effect on *Limnephilus*: survival was higher in the presence of salamanders + *Asynarchus* than with just *Asynarchus*. In the laboratory we compared the predatory effects of salamanders with and without their mouths sewn shut and found the observed indirect positive effect on *Limnephilus* survival to be mainly the result of reduced numbers of *Asynarchus* rather than salamander-induced changes in *Asynarchus* behavior. We argue that indirect effects of predator–predator interactions on shared prey will be mainly density-mediated and not trait-mediated when one of the predators (in this case, *Asynarchus*) is under strong selection for rapid growth and therefore does not modify foraging behaviors in response to the other predator. The reciprocal dominance of *Limnephilus* and *Asynarchus* in habitats with and without salamanders probably reflects a trade-off between competitive superiority and vulnerability to predation. The high activity levels and aggressiveness that enable *Asynarchus* to complete development in temporary habitats result in strong asymmetric competition (via intraguild predation) with *Limnephilus*. In permanent habitats these same behaviors increase *Asynarchus* vulnerability to salamander predation, which indirectly benefits *Limnephilus*. This and previous work implicate salamanders as keystone predators that exert a major influence on the composition of benthic and planktonic assemblages in subalpine wetlands.

*Key words:* Ambystoma; Asynarchus; *caddisfly; coexistence, predator mediated, Colorado; indirect effects; Keystone predator;* Limnephilus; *pond hydroperiod; predation, intraguild; salamander; wetlands.*

## INTRODUCTION

Top predators in *temporary* wetlands of North America are typically large aquatic insects (e.g., dragonflies, beetles) and amphibians (e.g., salamander larvae) that, through metamorphosis, can escape drying habitats (Batzer and Wissinger 1996, Wellborn et al. 1996). In contrast, the top predators in *permanent* wetlands are typically fish, which often eliminate large predatory invertebrates and salamanders. Wellborn et al. (1996) recently proposed a model for trade-offs among the different types of mortality risks for prey along predator–permanence gradients and noted that the great majority of experimental evidence for the model is based on studies conducted with larval anurans (also see review by Wilbur [1997]). These studies suggest that the behavioral, developmental, and morphological characteristics that promote rapid development and timely metamorphosis in temporary habitats are disadvantageous in permanent habitats where these same traits lead to increased vulnerability to fish predation. Con-

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versely, the low activity rates and risk-sensitive foraging behaviors exhibited by anurans that coexist with fish predators are disadvantageous in temporary habitats, where selection is for rapid growth and metamorphosis (Skelly 1992, Werner and Anholt 1993, Skelly 1995, Wellborn et al. 1996, Wilbur 1997). Experimental studies with larval anurans have also demonstrated the importance of behavioral trade-offs between avoiding fish predators and avoiding invertebrates that are the top predators in fishless habitats (Werner and McPeek 1994).

Many taxa of aquatic invertebrates exhibit similar distributional trends with respect to the presence or absence of vertebrate predators. However, the degree to which differences among habitats are related to trade-offs between antipredatory behaviors vs. the timely completion of development is not well documented for invertebrates (Batzer and Wissinger 1996, Wellborn et al. 1996). McPeek and coworkers have shown that distributional patterns of *Enallagma* damselflies in ponds are based largely on differences in activity rates and foraging behaviors that are alternatively effective in reducing vulnerability to fish and invertebrate predators (McPeek 1990*a*, *b*, 1996, McPeek et al. 1996). However, it is not clear whether differences in the activity rates among *Enallagma* or any other aquatic insects compromise their ability to complete development in temporary habitats.

In this paper we present evidence that distributional patterns of caddisfly (Trichoptera, Limnephilidae) larvae in subalpine wetlands in Colorado are the result of species-specific trade-offs between adaptations for avoidance of vertebrate predation in permanent habitats and rapid development/competitive ability in temporary habitats. Our study was stimulated by the observation that adjacent wetland basins with different hydroperiods contain dramatically different invertebrate assemblages (Wissinger et al. 1999). However, the causal relationships between hydroperiod and invertebrate community composition are confounded by covarying differences in the presence of aquatic stages of the salamander *Ambystoma tigrinum nebulosum* (Hallowell) (Wissinger and Whiteman 1992).

We first present data from field experiments that determined whether differences in caddisfly abundances among wetland basins were related to differential vulnerabilities to salamander predation and how such differences might lead to indirect effects that explain observed patterns of coexistence. Laboratory experiments were designed to quantify caddisfly activity levels, foraging behaviors, and antipredatory responses to the threat of salamander predation. The data presented here and in a previous paper (Wissinger et al. 1996) allowed us to integrate the importance of three factors that taken together could explain patterns of caddisfly distribution and abundance among wetland habitats in this region; (1) physiological and developmental effects of habitat drying, (2) direct and indirect effects of inter-habitat differences in salamander predation, and (3) asymmetric intraguild predation (IGP) between caddisflies (Wissinger and Whiteman 1992, Wissinger et al. 1996). We interpret our results in the context of previous work at this study site (Dodson 1970, 1974, Sprules 1972, Maly 1976) and consider the role of salamanders as keystone predators (sensu Paine [1966], Power et al. [1996]) in maintaining differences in community composition between permanent and temporary subalpine wetlands.

## Background and Natural History

The study was conducted at the Mexican Cut Nature Preserve in central Colorado. The Preserve contains several subalpine (3400–3600 m elevation) fens with numerous open water basins that vary in size (<5 to 4647 $m^2$), water chemistry, and hydroperiod (Wissinger and Whiteman 1992, Wissinger et al. 1999). Basins can be categorized as permanent, temporary autumnal (drying and then refilling in autumn in most years), or temporary vernal (filled only after snowmelt and drying during early summer). There is considerable biological variation among basins, and even those separated by only a few meters can have dramatically different assemblages of planktonic and benthic invertebrates (Dodson 1970, 1974, Sprules 1972, Wissinger et al. 1999).

Larvae of the caddisflies *Asynarchus nigriculus* Banks and *Limnephilus externus* (Hagen) are among the most abundant (in terms of biomass) and conspicuous benthic invertebrates at Mexican Cut. The two species are nearly identical in body size and have similar life histories and similar diets: gut contents by volume for *Limnephilus* and *Asynarchus* are 73 and 80% plant detritus, 20 and 10% benthic algae, and 7 and 10% animal material, respectively (Sparks 1993). *Asynarchus* larvae hatch earlier and develop faster than *Limnephilus* larvae and are therefore about one instar ahead of *Limnephilus* during June and July when our experiments were conducted. The portable cases of *Asynarchus* are a tubular patchwork of spruce bark, needles, and sand grains, whereas those of *Limnephilus* are a rectangular assemblage of cut stems of the macrophyte *Isoetes bolanderi.*

As with many invertebrates in wetlands, the distribution of these caddisflies is correlated with basin hydroperiod (Batzer and Wissinger 1996, Wissinger 1999); *Asynarchus* are most abundant in temporary and *Limnephilus* in permanent basins. A comparative survey of wetlands and shallow alpine lakes in the region revealed that in isolated basins (as opposed to the clusters of basins at Mexican Cut), *Asynarchus* and *Limnephilus* are completely segregated in temporary and permanent ponds, respectively (Wissinger et al. 1999). This distributional pattern can not be explained by fundamental niche constraints (in the Hutchinsonian sense of requirements; see Leibold 1995): both species lay eggs under rocks and logs adjacent to wetland basins

in late summer and early fall and are therefore capable of exploiting both temporary and permanent habitats (see also Wiggins [1973]). Larval growth data in competition experiments show that the two species develop at similar rates in permanent and autumnal basins (Wissinger et al. 1996).

The correlation between caddisfly abundance and habitat permanence is confounded by the distribution of tiger salamanders, *Ambystoma tigrinum nebulosum* (Hallowell). Unlike at lower elevations, salamanders are absent from temporary habitats except for some of the largest autumnal ponds where metamorphic adults breed and then remain during the summer to forage almost exclusively (90% of diet) on fairy shrimp (Whiteman et al. 1994, 1996). First-year larvae, which typically die when these habitats dry in late summer (Wissinger and Whiteman 1992), prey exclusively on zooplankton. Thus, salamander predation on caddisflies should be minimal in temporary basins. In contrast, permanent basins contain paedomorphs and several year classes of larvae (time to metamorphosis at this elevation is 2–5+ yr) that are known to prey on benthic invertebrates including caddisflies (Collins and Holomuzki 1984, Holomuzki and Collins 1987, Zerba and Collins 1992, Whiteman et al. 1996). The effects of salamander predation on the composition of zooplankton communities have been well documented (Dodson 1970, 1974, Sprules 1972), but little is known about the impact on the benthic community.

## Methods

### *Field mesocosms and laboratory arenas*

The two field experiments were conducted in polyethylene cattle watering tanks (1.75 $m^2$ bottom area) located near the wetland basins at Mexican Cut. Water temperature and chemistry did not differ among tanks and was comparable to those in the adjacent natural habitats as determined by monthly water samples during 1990–1992 (Wissinger and Whiteman 1992). Benthic substrates were established by adding equal volumes of detritus (5-cm depth) and two patches (15 × 15 cm) of emergent vegetation (*Carex aquatilis* and *C. nebraskensis* [Buck 1960]) taken from one of the wetlands. Several invertebrate taxa that were added with the substrate established sustained populations in the tanks, including oligochaetes, water mites, chydorid and daphniid cladocerans, and several chironomid dipterans (mainly *Chironomus riparius*). Several other invertebrate taxa (corixid and gerrid hemipterans, dytiscid beetles) immigrate to the artificial ponds each spring, complete one or several generations, and then return to the natural basins to overwinter (Wissinger 1997). Prior to the experiments in 1992 and 1993, we supplemented this resident invertebrate fauna by adding zooplankton from one permanent and one autumnal basin (mainly *Branchinecta coloradensis, Leptodiaptomus shoshone, Hesperodiaptomus coloradensis,* and *Daphnia middendorfiana.* Our goal was to create experimental arenas with alternative prey and sufficient habitat complexity that salamander hunger levels and salamander–caddisfly encounter rates were ecologically relevant (Connell 1983, Wilbur 1997).

Laboratory experiments were conducted under natural photoperiod and diel temperature conditions in a portable field laboratory located near the ponds: metal frame, translucent canvas, length 6 m × width 4 m × height 3 m (Weatherport, Gunnison, Colorado). The behavioral experiments were conducted in plastic storage containers designed to replicate small patches of littoral habitat (0.25 $m^2$ bottom area, 57 cm × 42 cm × 15 cm depth); they contained 2.5 cm of detrital substrate, three rocks, three fragments of wood, a small clump of emergent vegetation, and 10 cm depth of pond water.

### *Salamander predation field experiment*

In the first field experiment we compared the predatory impact of different life stages of salamanders on *Asynarchus* and *Limnephilus* larvae. Four salamander treatments (1) no salamanders, (2) metamorphic adults (snout–vent length [SVL] = 93.5 ± 3.0 mm [mean ± 1 SD]), (3) third year larvae (73.2 ± 2.4 mm), and 4) paedomorphic adults (83 ± 5.1 mm) were replicated four times. Salamander density (two per tank) was based on that of the three stages in natural populations (H. H. Whiteman, *unpublished data*). In July 1992, the sixteen tanks were stocked with 100 larvae of each caddisfly species (total density 133 individuals/$m^2$) using the same instar ratios for each species (60 fifth and 40 fourth instars). In this experiment, we used the same instars of the two species to eliminate confounding effects of caddisfly size on salamander prey choice and to minimize the effects of intraguild predation (IGP) by *Asynarchus* on *Limnephilus. Asynarchus* rarely prey on same sized *Limnephilus* (Wissinger et al. 1996).

During the experiment we compared microhabitat use by two caddisfly species by counting the number of larvae of each species on four different microhabitats in the tanks (vegetation, tank sides, floating debris, benthic material (detritus + rocks). Habitat-use surveys were conducted during the first four days of the experiment when the densities of the two species should have been most similar. We compared effects of species and treatment on the proportion of individuals (arcsine transformed) of each species in each microhabitat using a two-way MANOVA.

The experiment was terminated after 20 d when *Asynarchus* began to pupate. Salamanders were returned to source ponds and remaining caddisfly larvae were counted and preserved. Because survival of the two species was potentially correlated, we first used one-way MANOVA to analyze the effects of the different salamander treatments on caddisfly survival. We used Bartlett's test of sphericity to determine whether the dependent variables were correlated with each other.

When appropriate, subsequent protected univariate $F$ tests and Scheffé's unplanned a posteriori contrasts were used to isolate the effects of the independent variable on each dependent variable and to compare treatment means, respectively (Day and Quinn 1989, Scheiner 1993*b*). For all MANOVA/ANOVA statistics used in this paper, departures from homoscedasticity and normality were tested using Bartlett-Box and Liliefors tests, respectively (Norusis 1990).

### *Caddisfly behaviors and salamander foraging*

We conducted two types of experiments in the laboratory behavioral arenas. First, in July 1992 we conducted 10-min focal animal samples (after Altmann [1974]) on individual caddisfly larvae in the presence and absence of salamanders (third year larvae, SVL range 70–78 mm) and recorded activity levels (time spent crawling, distance crawled, and time spent foraging; see Wissinger et al. [1996] for additional details). Four replicates of each of the four treatments ([1] fifth instar *Asynarchus,* [2] fifth instar *Asynarchus* with salamander, [3] fourth instar *Limnephilus,* and [4] fourth instar *Limnephilus,* with salamanders) were randomly assigned to sixteen arenas. Densities for both caddisfly species were maintained at 200 individuals/$m^2$. The instars and densities used in this experiment reflected those that occurred in the ponds at the time of the experiment. Four observers conducted trials simultaneously on one of each of the four treatments; thus, time of day and between-day effects should not bias species and treatment comparisons. Observations were made during midday, between 0900 and 1600. Because of the multiple dependent variables, we analyzed the data using a two-way MANOVA (caddisfly species and salamander treatment).

In a second laboratory experiment we observed the foraging of salamanders on *Asynarchus* and *Limnephilus.* One third-year larval salamander (SVL range 68–75 mm) was added to laboratory arenas (total of 16 individuals per day) that contained equal numbers of the two caddisfly species using the same instars and total densities as described in the paragraph above. Salamanders were isolated and starved for 24 h and then added to the arena each morning at 0800. During the 30-min trials we recorded the number of each of the following salamander behaviors directed at each caddisfly species: (1) prey detection—a stereotypic head turn oriented towards moving caddisflies; (2) pursuit—directed walking or swimming towards a potential prey that often resulted in the salamander contacting the caddisfly case with their snout; (3) attack—caddisfly and case were drawn into the salamander's mouth with a suction created by buccal pumping (see Lauder and Shaffer [1986]); and (4) capture—the caddisfly was extracted from the case and case discarded, or less commonly, both the case and caddisfly were swallowed. We conducted 54 trials, each of which was 30 min in duration and conducted during the morning, between 0900 and 1200, on four consecutive days in July 1993. We did not use salamanders more than once on a given day. We found no systematic differences among time periods and days; thus, analyses presented here are for data pooled across all trials. Because of dramatic departures from normality and homoscedasticity, we used Mann-Whitney $U$ tests to compare each of the salamander behaviors directed towards *Asynarchus* and *Limnephilus.* We also compared the proportion of times that (1) a detection led to a contact (contacts/detection), (2) a contact led to an attack (attacks/contact), and (3) an attack led to a capture, for each species. Because of the large number of pairwise tests, we use Bonferroni's correction for establishing significance criteria.

### *Indirect effects field experiment*

We conducted a second field experiment to test the hypothesis that salamander predation on *Asynarchus* had an indirect positive effect on *Limnephilus.* We used a complete factorial design ($2 \times 2 \times 2$) for all combinations of the presence and absence of paedomorphic salamanders, *Limnephilus,* and *Asynarchus,* to test the (1) direct effects of salamander predation on each caddisfly species, (2) direct effects of *Asynarchus* intraguild predation on *Limnephilus* in large arenas, and (3) indirect effects of salamander predation on caddisfly–caddisfly interactions (Table 1). Salamander treatments contained three paedomorphic salamanders (79–86 mm SVL) that had been isolated and starved for 48 h before the experiment. Single and mixed caddisfly treatments contained the same total densities (133 individuals/$m^2$) of caddisfly larvae with instar ratios that reflected those in natural populations at the time of collection (Table 1).

On day six of the experiment we sampled the gut contents of one salamander from each treatment using a nondestructive stomach flushing technique (see Whiteman et al. 1994). Because of differential predation rates, *Asynarchus* densities were probably lower than those of *Limnephilus* at the time we flushed salamander stomachs: thus conclusions about the preferential predation on *Asynarchus* are conservative. Because many of the guts were empty, sample distributions were distinctly nonnormal; thus, we compared the number of each caddisfly species in the salamander guts using a Mann-Whitney $U$ test.

The experiment ended after 2 wk when *Asynarchus* began to pupate. Remaining larvae and pupae were counted and preserved in 90% ethanol. We used MANOVA, and subsequently ANOVA, to test for the direct and indirect effects of species treatment on *Limnephilus* and *Asynarchus* survival. We analyzed the data using per capita survival ({ln[initial number/final number]}/time), to account for changes in density during the course of the experiment (after Billick and Case [1994]).

TABLE 1. (A) Experimental design used to quantify the direct and indirect effects of salamander predation and *Asynarchus* intraguild predation (IGP) on the survival of *Limnephilus* in artificial ponds in central Colorado. (B) Initial sizes of caddisfly larvae.

| A) Experiment Design | Density (inds./1.5-m$^2$ experimental ponds) | | |
|---|---|---|---|
| Treatment | *Asynarchus* | *Limnephilus* | Salamanders† |
| *Asynarchus* control | 200 | 0 | 0 |
| *Limnephilus* control | 0 | 200 | 0 |
| Salamander control | 0 | 0 | 3 |
| Salamander predation on *Asynarchus* | 200 | 0 | 3 |
| Salamander predation on *Limnephilus* | 0 | 200 | 3 |
| *Asynarchus* IGP on *Limnephilus* | 100 | 100 | 0 |
| Indirect effects of salamander predation on *Asynarchus* IGP | 100 | 100 | 3 |
| Tank control | 0 | 0 | 0 |

B) Initial Sizes of Caddisfly Larvae

| Caddisfly genus | Instar | Head width (mm) | Percentage of total |
|---|---|---|---|
| *Asynarchus* | 4th | 1.35 | 20 |
| | 5th | 0.95 | 80 |
| *Limnephilus* | 3rd | 0.55 | 80 |
| | 2nd | 0.35 | 20 |

*Note*: Caddisfly instar ratios approximate those in natural populations at the time of experimentation.
† Salamander snout–vent length: 82 ± 6.3 mm (mean ± 1 SD).

### *Mechanism(s) of indirect effects*

We conducted a third laboratory experiment to test alternative hypotheses about mechanism(s) that underlie the indirect effects observed in the field experiments. In particular we were interested in determining the degree to which the indirect positive effect of salamanders on *Limnephilus* was caused by a reduction in the number of *Asynarchus* vs. a salamander-induced change in *Asynarchus* behavior. The experiment was conducted in the laboratory arenas and entailed comparing the survival of 20 fourth instar *Limnephilus* in the presence of: (1) no predators, (2) 20 fifth instar *Asynarchus,* (3) 20 fifth instar *Asynarchus* larvae and one salamander (SVL 70–75 mm), and (4) *Asynarchus* and one salamander with a sutured mouth that prevented the capture of caddisflies. Each treatment was replicated four times. Salamanders were anesthetized with tricaine methylchloride and their mouths were sutured with a single stitch of black thread immediately posterior to the mandible 24 h before the experiments were initiated. Each salamander was monitored closely throughout the 10-d duration of the experiment. Sutured salamanders stalked and attempted to attack caddisfly larvae in a manner comparable to that observed in unsutured salamanders, but were unable to capture prey. We conducted 10-min focal animal trials in a manner identical to that described below in *Results: Caddisfly activity and salamander foraging behavior* to compare *Asynarchus* activity levels in the different treatments.

At the end of the experiment, sutures were removed and salamanders returned to the ponds. Although sutured salamanders lost body mass during the experiment, no other negative consequences were observed. We pumped the stomachs of sutured and unsutured salamanders before releasing them at the end of the experiment to provide corroborative data to complement caddisfly densities and to verify that sutured salamanders were not eating. *Limnephilus* survival was analyzed using one-way ANOVA and Scheffé a posteriori contrasts to distinguish among means.

## RESULTS

### *Salamander predation field experiment*

The goal of this experiment was to compare the predatory effects of different salamander life stages on *Asynarchus* and *Limnephilus* survival and microhabitat use. Across all experimental units (artificial ponds), numbers of surviving *Asynarchus* and *Limnephilus* were not correlated (Bartlett's test of sphericity, $\chi^2_3 = 1.89$, $P = 0.17$). Thus, we tested the effects of salamander predation on the two species separately using MANOVA univariate $F$ tests and subsequent one-way ANOVA. These univariate tests revealed that salamander predation did not significantly affect the survival of *Limnephilus* larvae (Fig. 1; $F_{3,12} = 0.43$, $P = 0.73$), but did affect the survival of *Asynarchus* larvae ($F_{3,12} = 3.84$, $P = 0.039$). *Asynarchus* survival was lower in the presence of salamander larvae and paedomorphs than in the presence of metamorphs and in control treatments, which did not differ (one-way ANOVA, Scheffé a posteriori contrast $P < 0.05$).

The two species differed in their use of microhabitats. *Asynarchus* larvae occurred mainly (80–90%) on benthic substrates, whereas *Limnephilus* were more generally distributed across the different microhabitats (Fig. 1). Across all treatments, *Limnephilus* larvae were significantly more abundant on rooted vegetation and on floating plant debris, and less abundant in benthic habitats than were *Asynarchus* larvae (vegetation: $F_{1,62}$

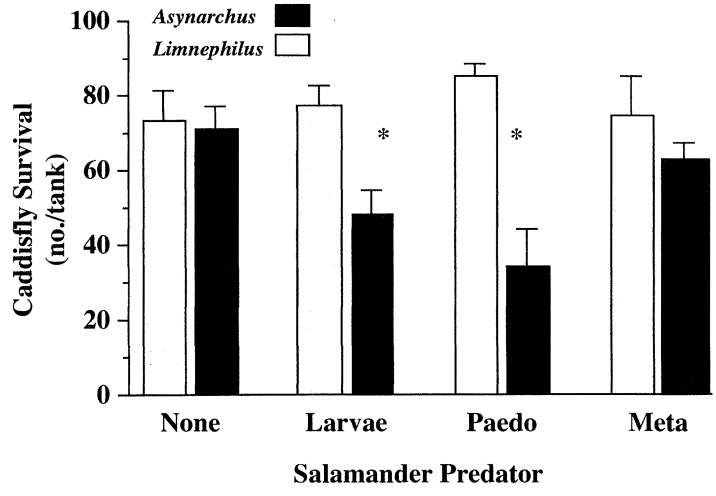



FIG. 1. Survival (mean and 1 SE) of *Asynarchus* and *Limnephilus* caddisfly larvae in artificial ponds with different life stages of the salamander *Ambystoma tigrinum nebulosum*. Asterisks (*) indicate a significant difference ($P < 0.05$) in survival between species within a salamander treatment. (Paedo = paedomorphic adults; Meta = metamorphic adults.)

= 158.9, $P < 0.001$; floating: $F_{1,62} = 121.0$, $P < 0.001$; benthos: $F_{1,62} = 158.9$, $P < 0.001$). Salamander treatment did not affect microhabitat use by either caddisfly species (Fig. 2, Table 2, univariate $F$ tests; tank sides: $F_{3,56} = 0.81$, $P = 0.49$; vegetation: $F_{3,56} = 2.65$, $P = 0.08$; floating debris: $F_{3,56} = 1.62$, $P = 0.19$; benthos: $F_{3,56} = 1.65$, $P = 0.419$). *Limnephilus* and *Asynarchus* abundances in the different microhabitats were negatively correlated across all treatments (Bartlett's sphericity test, $\chi^2_6 = 189.3$, $P < 0.001$).

*Caddisfly activity and salamander foraging behavior*

During 10-min focal animal trials conducted in the laboratory arenas, we observed that *Asynarchus* larvae were more active and frenetic in their movements than *Limnephilus* larvae. *Asynarchus* foraging activities were frequently punctuated by movements between foraging sites. They spent more time crawling and crawled farther during the trials than *Limnephilus* larvae which spent much more of their time foraging at one location (Table 3; Fig. 3). The multiple response variables were correlated across all individuals observed (Bartlett's test of sphericity, $\chi^2_3 = 50.4$, $P < 0.001$); i.e., time spent foraging was negatively associated with time spent crawling and distance crawled. The presence of salamanders did not significantly affect the activity patterns of either caddisfly species (Table 3).

During the 30-min salamander foraging trials, we observed that the movements of larval caddisflies stimulated a stereotypic foraging response by the salamanders that involved (1) approach to the general vicinity of a moving caddisfly larva (detection), (2) fine-scale position adjustments that brought the salamander's snout into contact with the larva or larval case (pursuit), (3) buccal suctioning of the caddisfly and case into the mouth (attack), and (4) manipulation of the case to extract and swallow the larva (capture). Salamanders detected larval *Asynarchus* movements more than twice as often as *Limnephilus* movements (Fig. 4; Mann-Whitney $U = 139.2$, $P = 0.003$). Aggressive interactions initiated by *Asynarchus* on conspecifics and on *Limnephilus* preceded 43% of all *Asynarchus* detections and 74% of *Limnephilus* detections. Once a larva or group of larvae were detected, salamanders pursued *Limnephilus* and *Asynarchus* similarly (Fig 4; for pursuits/detections, Mann-Whitney $U = 77.5$, $P = 0.179$). When salamanders approached fighting caddisfly larvae, both combatants quickly withdrew into their cases. *Limnephilus* larvae always remained in their cases longer than *Asynarchus* larvae, which always emerged earlier in the presence of the salamanders and hence were selectively attacked. Overall, the emergence of *Asynarchus* larvae from their cases while under the scrutiny of pursuing salamander led to more frequent attacks (for attacks, Mann-Whitney $U = 95$, $P < 0.001$) and for attacks per pursuit on *Asynarchus* than *Limnephilus* larvae (Fig. 4; attacks/pursuit, Mann-Whitney $U = 151$, $P = 0.005$). Interestingly, once attacked, *Limnephilus* larvae were as likely to be captured (i.e., swallowed) as *Asynarchus* (Fig. 4; Mann-Whitney $U = 75.2$, $P = 0.17$). The total number of *Asynarchus* larvae captured by salamanders was more than twice that of *Limnephilus* larvae. In summary, the significantly higher overall capture rate of *Asynarchus* as compared to *Limnephilus* (Fig 4; Mann-Whitney $U = 199.3$, $P = 0.003$) was due to an initial bias in detection and then a higher attack rate once pursued. Preferential predation on *Asynarchus* was not the result of a higher pursuit rate per detection nor to a higher capture rate per attack.

*Indirect effects field experiment*

The goal of this experiment was to determine the interactive effects of salamander predation and caddisfly intra- and interspecific interactions on caddisfly survival. MANOVA indicated that *Limnephilus* and *Asynarchus* survival was not correlated in those treatments that contained both species (MANOVA Bartlett's

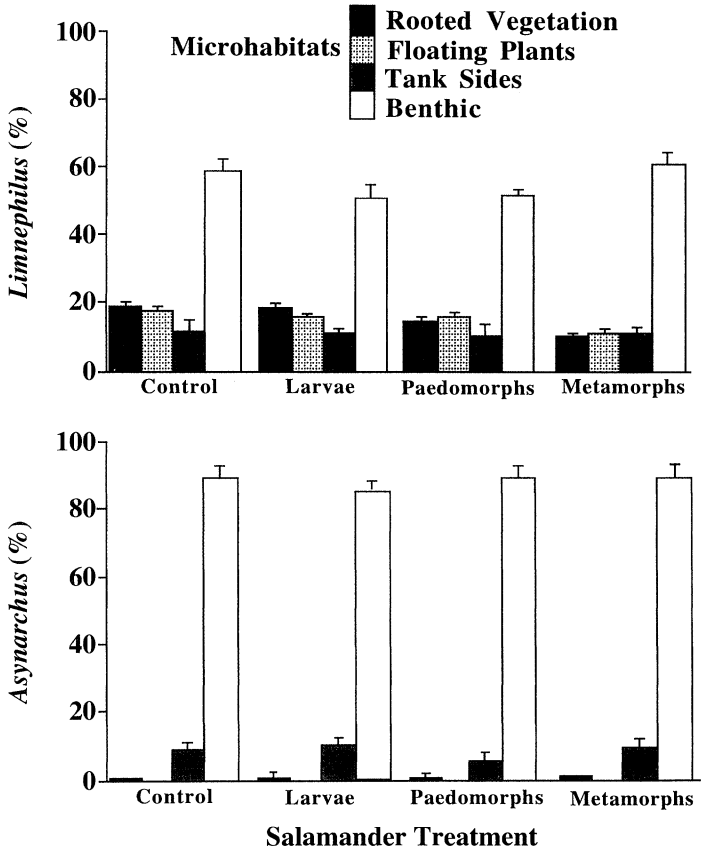



FIG. 2. Number (mean and 1 SE) of *Asynarchus* and *Limnephilus* larvae observed in different microhabitats in the artificial ponds during the salamander predator experiment (see statistics in Table 2).

test of sphericity, $\chi^2_1 = 0.289$, $P = 0.59$); thus, we analyzed the survival of each species separately using two-way ANOVA (salamander effects × caddisfly competitor effect). We found that, as in other experiments, the survival of *Limnephilus* larvae in this experiment was reduced by *Asynarchus.* However, the presence of salamanders significantly reduced the impact of *Asynarchus* on *Limnephilus* survival, hence, the significant two-way interaction between the presence of *Asynarchus* and the presence of salamanders on *Limnephilus* survival (Table 4, Fig. 5). This two-way interaction complicates the interpretation of the main effect of salamanders on *Limnephilus* survival. In the absence of *Asynarchus,* salamanders have a small, but statistically significant negative effect on *Limnephilus* survival (one-way ANOVA $F_{1,6} = 15.4$, $P = 0.008$), whereas in the presence of *Asynarchus,* salamanders have a significant net positive effect on *Limnephilus* survival ($F_{1,6} = 7.4$, $P = 0.03$). The effects of salamanders on *Asynarchus* did not depend on the presence or absence of *Limnephilus.* Salamanders significantly reduced *Asynarchus* numbers both in treatments with and without *Limnephilus* (Fig. 6, Table 4). Overall, only 30% of the initial *Asynarchus* survived to the end of the experiment in salamander treatments. *Asynarchus* survival was not affected by *Limnephilus* (Table 4, Fig. 6). Finally, in single species treatments with no salamanders, *Limnephilus* survival was significantly higher than that of *Asynarchus* (one-way ANOVA, $F_{1,6} = 20.54$, $P = 0.004$).

Dietary data provided corroborative evidence for the species-specific nature of salamander predation on caddisfly larvae in the field experiment. On average, the gut contents of the eight salamanders used in the ex-

TABLE 2. Summary of two-way MANOVA for the effects of salamander treatment and caddisfly species on microhabitat use (benthos, vegetation, surface, pond sides) during a salamander predation experiment in artificial ponds in central Colorado.

| Source of variation | Numerator df | Denominator df | Wilks' lambda | *F* | *P* |
|---|---|---|---|---|---|
| Species | 4 | 53 | 0.171 | 63.92 | <0.001 |
| Treatment | 12 | 140 | 0.697 | 1.70 | 0.083 |
| Species × treatment | 12 | 140 | 0.751 | 1.79 | 0.202 |

TABLE 3. Summary of two-way MANOVA for *Limnephilus* and *Asynarchus* activity patterns (time spent foraging, time spent crawling, distance crawled) during 10-min focal-animal trials. Salamander treatments involved presence vs. absence of larval salamanders.

A) Multivariate Test

| Source of variation | Numerator df | Denominator df | Wilks' lambda | $F$ | $P$ |
|---|---|---|---|---|---|
| Caddis species | 3 | 26 | 0.447 | 10.71 | <0.001 |
| Salamander | 3 | 26 | 0.967 | 0.29 | 0.828 |
| Species × salamander | 3 | 26 | 0.828 | 1.79 | 0.173 |

B) Univariate Tests for Caddisfly Species Effect

| Variable | Variable MS | Error MS | $F_{1,30}$ | $P$ |
|---|---|---|---|---|
| Time foraging | 2666.32 | 271.7 | 9.83 | 0.004 |
| Time crawling | 3069.2 | 123.1 | 24.94 | <0.001 |
| Distance crawled | 336.7 | 10.6 | 31.82 | <0.001 |

periment contained 3.25 ± 1.25 *Asynarchus* [mean ± 1 SE] as compared to only 0.125 ± 0.14 *Limnephilus*. Overall, we found a total of 23 *Asynarchus* in salamander guts as compared to one *Limnephilus*. Other prey items in the stomach contents included Diptera (chironomid and ceratopogonid) larvae and pupae, several small zooplankters (*Daphnia middendorfiana, Simocephalus vetulus*), and fairy shrimp (*Branchinecta coloradensis*).

### *Mechanism(s) underlying indirect effects*

In this experiment we determined the degree to which the indirect positive effect of salamanders on *Limnephilus* survival in the field experiment was the result of (a) reduced *Asynarchus* abundance and/or (b) a salamander-induced change in the foraging behavior of *Asynarchus*. *Limnephilus* survival varied significantly among treatments (ANOVA $F_{3,12} = 28.6$, $P < 0.01$), and in particular was lower with *Asynarchus* alone and *Asynarchus* + sutured salamanders than with *Asynarchus* + unsutured salamanders and no predators (Fig. 7). Thus, the presence of salamanders did not modify *Asynarchus* foraging behavior to the extent that it changed *Limnephilus* survival. *Limnephilus* survival in the presence of *Asynarchus* + unsutured salamanders did not differ from that in the no-predator control.

Data on *Asynarchus* survival, salamander gut contents, and *Asynarchus* behaviors corroborate the absence of a salamander-induced change in *Asynarchus* foraging behavior. Only 9 *Asynarchus* survived the experiment in the presence of unsutured salamanders, whereas 18 survived with sutured salamanders and 19 in the *Asynarchus* + *Limnephilus* treatment, respectively. The stomachs of all sutured salamanders were empty whereas those of unsutured salamanders contained an average of 3.1 ± 0.88 *Asynarchus* and 0.55 ± 0.46 *Limnephilus* larvae [means ± 1 SE]. Focal animal observations conducted during the experiments revealed that *Asynarchus* were similarly active (time spent crawling) in treatments with and without salamanders ($F_{1,14} = 0.06$, $P = 0.81$). In summary, these laboratory data suggest that the indirect positive effects of salamanders on *Limnephilus* survival were due mainly to a decrease in *Asynarchus* numbers rather than to salamander-induced changes in *Asynarchus* behavior.

## DISCUSSION

### *Caddisfly behaviors and vulnerability to salamander predation*

*Asynarchus* larvae are more vulnerable than *Limnephilus* larvae to predation by aquatic stages of *Ambystoma tigrinum* salamanders. This vulnerability is in part related to differences in overall activity rates and in part to differences in the antipredatory response of the two species to salamander pursuit. Differences in case construction and larval morphology do not appear to contribute to the differential vulnerability of these caddisfly larvae to salamander predators. Neither caddisfly species modified foraging activities or habitat use in response to changes in the risk of salamander predation. We first discuss the role of these underlying mechanisms in explaining differences in *Asynarchus* and *Limnephilus* survival in the presence of salamanders. We then interpret the lack of behavioral plasticity in these species in the context of ecological constraints that should favor fixed vs. risk-sensitive foraging behaviors.

*Caddisfly foraging activities and detection by predators.*—The differential vulnerability of *Asynarchus* to salamander predation is in part a consequence of *Asynarchus*' high activity rates and conspicuous foraging activities. *Asynarchus* larvae are extremely active and spend more time moving and move greater distances between foraging sites than *Limnephilus,* and are therefore detected more frequently by salamanders. This is consistent with previous studies in which prey species with the highest activity rates are most vulnerable to predation (Sih and Moore 1989, McPeek 1990*a*, *b*, Werner and Anholt 1993, Peckarsky 1996, Wellborn et al. 1996). Particular foraging activities exhibited by *Asynarchus* also contributed to high detection rates. For

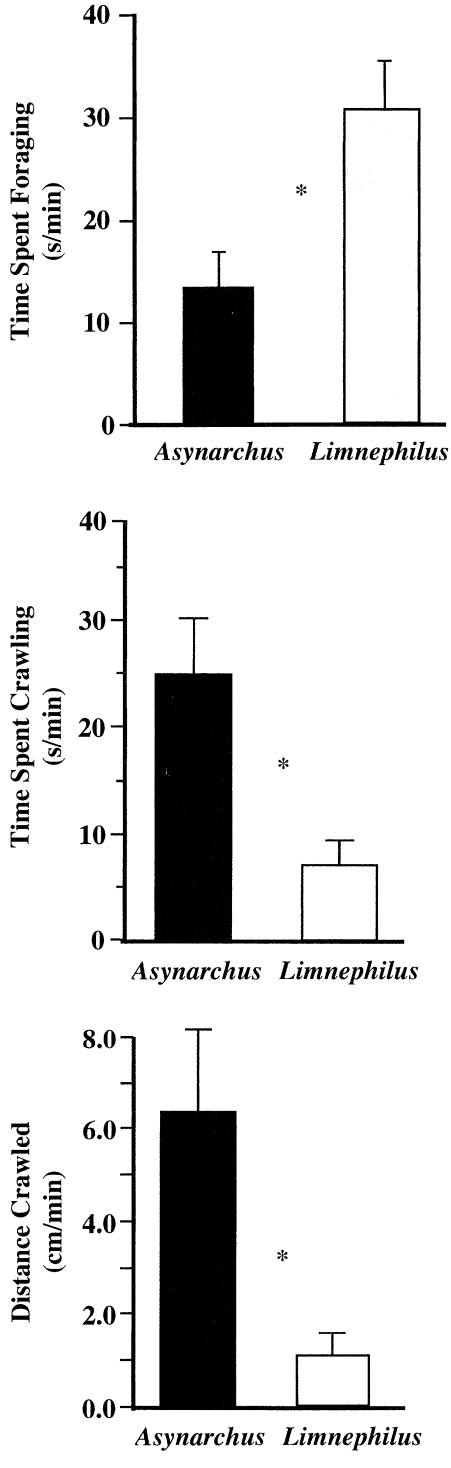



FIG. 3. Activity of larval caddisflies during 10-min focal animal samples in laboratory arenas. Data for each activity represent mean and 1 SE. Asterisks (*) indicate significant differences ($P < 0.05$) between the two species based on Scheffé a posteriori contrasts (see Table 3 for statistics).

example, the frenetic movements associated with *Asynarchus*' attacks on *Limnephilus* and on conspecifics (case tugging and shaking, biting, proleg grappling), were especially conspicuous to foraging salamanders.

Despite the importance of movement to risk of detection, neither species modified activity levels or types of activity as a function of predation risk. We also did not observe any microhabitat shifts in response to predation risk. This apparent inflexibility is in contrast to the numerous studies that demonstrate that prey adjust foraging activities and locations in response to the presence of predators (see reviews by Lima and Dill 1990, Sih 1992, Werner and Anholt 1993). The fixed nature of foraging behavior in *Limnephilus* is especially surprising given that this species typically coexists with salamander larvae and might be expected to exhibit traits that reflect some history of coevolution (McPeek et al. 1996). Previous studies have shown that more active individuals encounter resources faster, grow faster, and are better competitors than less active individuals (Werner and Anholt 1993). The apparently canalized (Stearns 1992, Scheiner 1993*a*) activity rates exhibited by *Limnephilus* suggest that either the *benefits* of a flexible strategy are low, as when there is a constant threat of predation or when competition is weak (Glasser 1979, McIntosh and Townsend 1994), and/or the *costs* of adjusting activity levels are high, as when prey are unable to accurately assess short term changes in predation risk (see review by Sih [1992]).

*Limnephilus* should benefit from a flexible strategy for two reasons. First, *Limnephilus*' vulnerability to *Asynarchus* intraguild predation (IGP) is size dependent and facilitated by early phenology and high growth rates. *Asynarchus* IGP on *Limnephilus* is benign when larvae are similar in size (Wissinger et al. 1996). Thus, any behavior that increases *Limnephilus* growth rates would reduce *Asynarchus* IGP. Second, risk-sensitive adjustments in foraging behavior should benefit *Limnephilus* because of short-term variability in the risk of predation associated with spatial and temporal shifts in salamander foraging activities. It is precisely in the context of short-term changes in the threat of predation that species should exhibit risk-sensitive foraging behaviors (Sih 1992, Werner and Anholt 1993). An assumption that underlies this prediction is that prey are able to perceive changes in risk in time to adjust (Sih 1992). Our data suggest that *Limnephilus* larvae are not able to assess changes in the risk of salamander predation before they are detected and pursued by salamanders. In the absence of precise information about the spatial location of foraging salamanders, *Limnephilus* appear to use a risk-averaging strategy based on the mean probability that predators are present (after Sih 1987, 1992, also see Soluk and Collins [1988], McPeek [1990*b*]). For *Limnephilus,* this risk-averaging strategy is expressed as a fixed, slow life style. Slower development is a cost and the evolution of such a strategy might only be possible in permanent habitats where

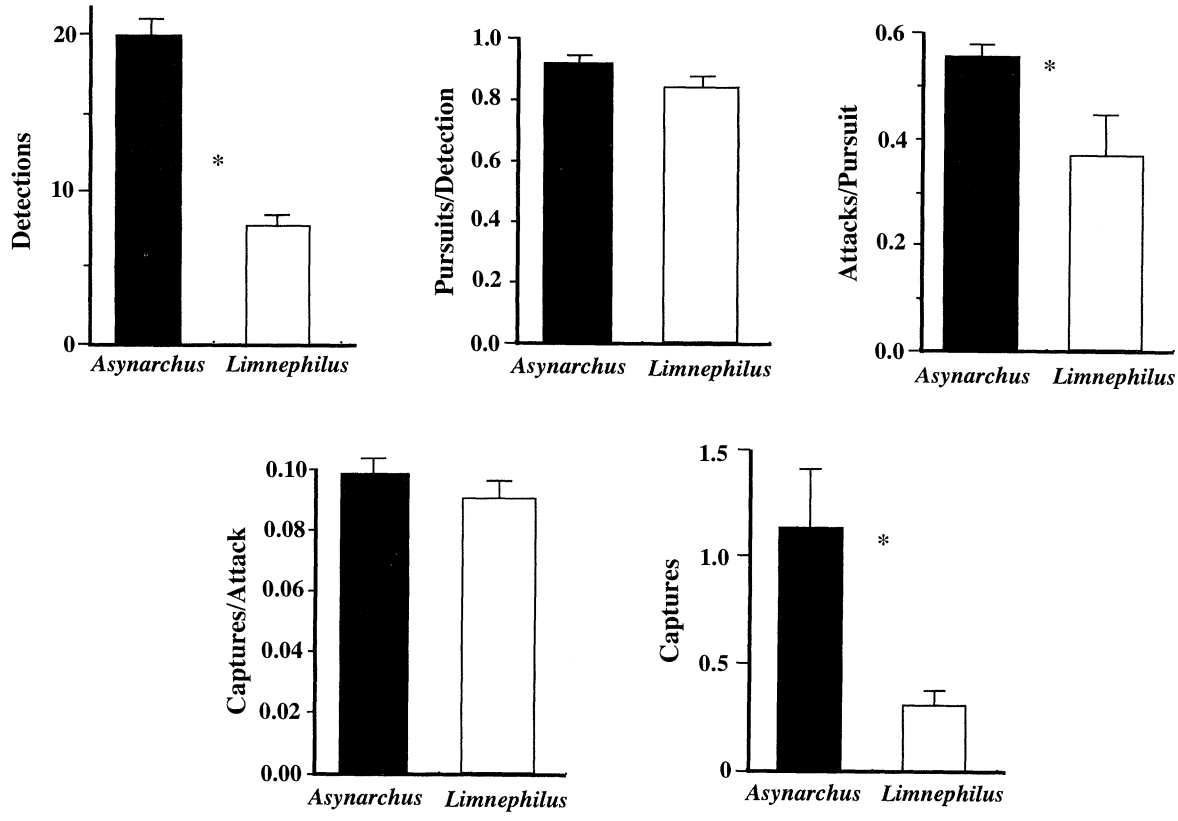



FIG. 4. Salamander foraging on caddisfly larvae in laboratory arenas. All data are means and 1 SE during 30-min trials. Asterisks (*) denote significant differences ($P < 0.05$) between caddisfly species based on Mann-Whitney $U$ test (see *Results: Caddisfly activity . . .*).

time constraints on development are relatively benign (Stein 1977, Ludwig and Rowe 1990, Werner 1986).

*Asynarchus* larvae also exhibit fixed activity levels and foraging behaviors, but their behaviors increase vulnerability to salamander predators. One explanation is that this species is typically under strong selection for rapid growth in predator-free, temporary habitats. *Asynarchus* larvae and pupae are not desiccation tolerant, yet they are often among the most conspicuous invertebrates in temporary high elevation wetlands in the central Rockies. Selection for traits that maximize growth is undoubtedly strong in these temporary habitats (Ludwig and Rowe 1990, Wellborn et al. 1996). In *Asynarchus* these traits are (1) constant and high-rate foraging activities (2) the use of all microhabitats including benthic habitats where salamander encounter rates are highest, and (3) predation on other conspecifics and heterospecifics (Wissinger et al. 1996). The fixed, fast life style of *Asynarchus* differs from that described for species that can afford high activity levels because they are good at assessing short-term changes in predation risk (Sih 1987, 1992). In contrast, the fast-

TABLE 4. Summary of two-way ANOVA for the effects of presence of salamanders and a second species of caddisfly on the survival of *Limnephilus* and *Asynarchus*.

| Source of variation | df | MS | $F$ | $P$ |
|---|---|---|---|---|
| A) *Limnephilus* survival | | | | |
| Salamander | 1 | 0.017 | 1.86 | 0.201 |
| *Asynarchus* | 1 | 0.790 | 87.30 | <0.001 |
| Salamander × *Asynarchus* | 1 | 0.082 | 9.03 | 0.011 |
| Error | 12 | 0.009 | | |
| B) *Asynarchus* survival | | | | |
| Salamander | 1 | 0.380 | 35.80 | <0.001 |
| *Limnephilus* | 1 | 0.001 | 0.03 | 0.850 |
| *Salamander × Limnephilus* | 1 | 0.007 | 0.66 | 0.432 |
| Error | 12 | 0.011 | | |

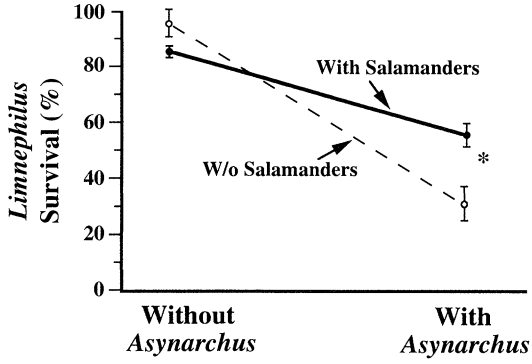



FIG. 5. Survival of *Limnephilus* larvae (mean ± 1 SE) in artificial ponds with different combinations of interacting predators (*Asynarchus* and salamanders). The asterisk (*) indicates a significant ($P < 0.05$) interaction between the effect of salamanders and *Asynarchus* larvae on *Limnephilus* survival (see *Results: Indirect effects . . .*).

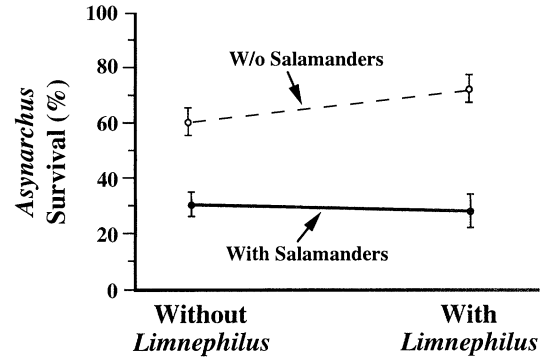



FIG. 6. Survival of *Asynarchus* larvae (mean ± 1 SE) in artificial ponds with and without salamander predators and *Limnephilus* caddisfly larvae. Salamanders significantly ($P < 0.05$) reduced *Asynarchus* survival regardless of the presence of *Limnephilus* (see *Results: Indirect effects . . .*).

paced life style of *Asynarchus* probably manifests selection for rapid development in temporary wetlands that lack top vertebrate predators.

*Risk-sensitive vs. fixed foraging behaviors and types of indirect effects.*—Predation by salamanders on *Asynarchus* has a positive effect on the survival of *Limnephilus*. This type of indirect effect can result from two basic underlying mechanisms. The first is when predator–predator interactions benefit shared prey because of reduced predator densities (*trophic linkage interaction* [Miller and Kerfoot 1987], *cascade in abundances* [Strauss 1991], *interaction chain* [Wooten 1994*a*, *b*], *indirect effect* [Billick and Case 1994], *density-mediated indirect interactions* [Abrams 1995]). A second is when predators exhibit risk-sensitive foraging in response to each other's presence (=behavioral indirect effect (Miller and Kerfoot 1987 and Strauss 1991), *interaction modification* (Wooten 1994*a*, *b*, Billick and Case 1994), or *trait-mediated indirect interactions* (Abrams 1995). The presence of trait-mediated indirect effects implies that the strength of interaction coefficients between two species will change when a third species is added to a web; thus, the successful prediction of the dynamics of that web will require experiments that include all possible combinations of the species of interest (also see Wilbur and Fauth [1990]). Clearly, understanding the ecological contexts that favor each of these mechanisms is important for generating appropriate models that predict the community-level interplay of competition and predation.

Our experiment with sutured salamanders indicated that the positive indirect effect of salamanders on *Limnephilus* appeared to be due mainly to density-mediated (i.e., reduced numbers of *Asynarchus*) and not to trait-mediated indirect effects. This outcome is perhaps not surprising given that in all of our experiments *Asynarchus* larvae did not modify their behavior or foraging location in response to the risk of salamander predation. We predict that conditions such as habitat drying that favor the evolution of fixed, high activity rates in prey will lead to indirect interactions that are due mainly to changes in predator densities. Alternatively, in permanent habitats where growth rates are less constrained, the evolution of risk-sensitive foraging behaviors by prey should lead to trait mediated indirect interactions among populations (as in Turner and Mittelbach [1990], Huang and Sih [1990], Werner [1991, 1992], Wissinger and McGrady [1993]).

*Caddisfly defenses against salamander attack.*—Once detected, the two caddisfly species also respond differently to salamander pursuit and attack. *Limnephilus* retreat into their cases when approached by salamanders and remain motionless until after salamanders have moved to a different foraging location. This extended hiding behavior is predicted when prey are

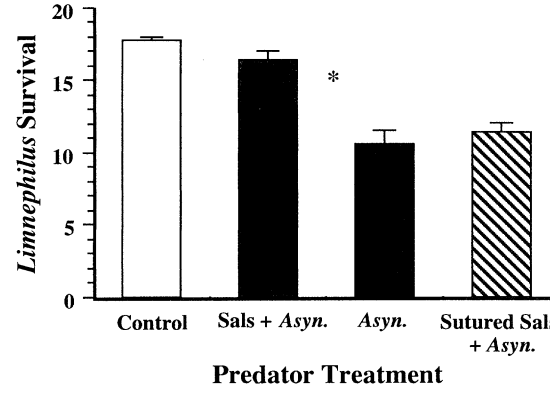



FIG. 7. Survival of *Limnephilus* larvae (mean and 1 SE) in laboratory arenas with four different predator treatments. The asterisk (*) indicates that control and salamanders + *Asynarchus* treatments differed significantly ($P < 0.05$) from *Asynarchus* alone and *Asynarchus* + salamanders with their mouths sutured shut (see statistics in Table 4).

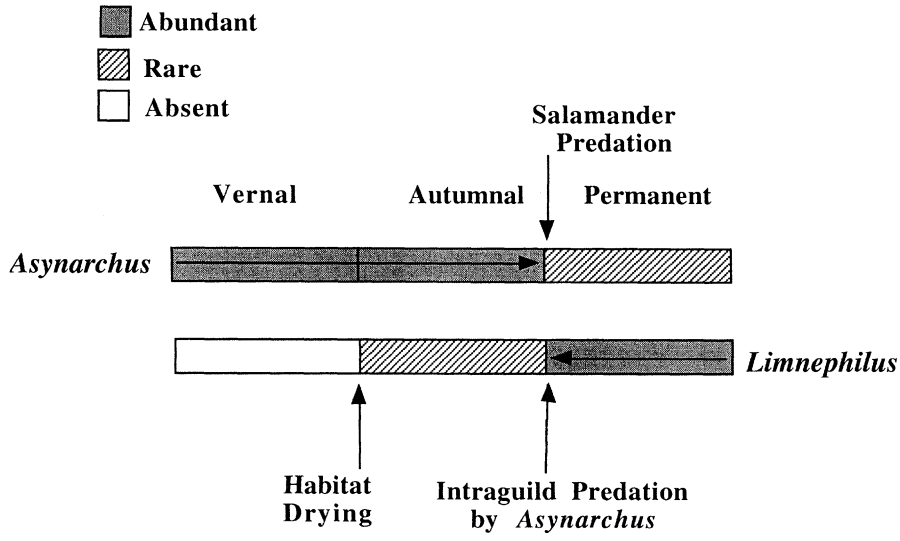



FIG. 8. Summary of the interacting effects of habitat permanence, salamander predation, and interspecific interactions between caddisfly larvae on the distribution and abundance of *Limnephilus externus* and *Asynarchus nigriculus* in subalpine wetlands in central Colorado. *Asynarchus* can complete their life cycle in all habitats, whereas *Limnephilus* are limited to autumnal and permanent ponds (Wissinger et al. 1999). Salamander life stages (>1 yr old larvae and paedomorphic adults) of the salamander *Ambystoma tigrinum nebulosum* that prey on *benthic* invertebrates occur only in permanent habitats. In the absence of salamander predation, asymmetric intraguild predation by *Asynarchus* larvae should reduce or eliminate *Limnephilus* from all habitats (Wissinger et al. 1996). However, salamander predation on *Asynarchus* indirectly benefits *Limnephilus,* which dominate in permanent habitats.

uncertain about the continued presence of a predator (Sih 1992). In contrast, *Asynarchus* larvae often emerge in the presence of salamanders and are attacked more than twice as often as *Limnephilus.* Coexistence of *Limnephilus* and salamanders in permanent habitats probably depends in part on the effective use of cases as short-term refugia (McNair 1986, Walls 1995).

Because *Asynarchus* and *Limnephilus* cases differ in size and construction design, we hypothesized that case morphology might underlie differences in their vulnerability (Otto and Svensson 1980, Otto 1982, Williams et al. 1987, Johansson 1991, Johansson and Johansson 1992, Johansson and Nilsson 1992, Nislow and Molles 1993). However, we found no evidence that cases provided different levels of mechanical protection from attacking salamander larvae. For both species only ~10% of attacked larvae with cases were successfully captured (Fig 4, captures/attacks), whereas 100% of caseless larvae were captured by salamanders (S. Wissinger, *unpublished data*). Thus, although differences in case construction did not contribute to the differential vulnerability of the two species, their cases are effective in reducing salamander predation (see also Otto and Svensson [1980], Williams et al. [1987], Wiggins [1996]).

### *Salamanders, habitat drying, and caddisfly distribution and abundance*

The distribution of *Asynarchus* and *Limnephilus* at and near our study site appears to be the result of the combined effects of habitat drying, *Asynarchus* intraguild predation on *Limnephilus,* and the mediating effects of salamander predation (Fig. 8) (Wissinger and Whiteman 1992, Whiteman et al. 1994, Wissinger et al. 1996). The rapid growth of *Asynarchus* larvae, which is in part facilitated by an ontogenetic shift from detritivory to carnivory (including other caddisflies as prey) enables this species to complete larval development, pupate, and emerge before vernal and autumnal habitats dry (S. Wissinger and W. S. Brown, *unpublished data*). In the absence of salamander predation, *Asynarchus* should dominate in permanent habitats (Wissinger et al. 1996). The results of this study suggest their absence or scarcity in permanent habitats is largely due to their vulnerability to salamander predation. In contrast, *Limnephilus* cannot complete development in time to exploit vernal habitats but they can exploit autumnal habitats that dry in late summer. Their scarcity or absence in autumnal wetlands appears to be largely a result of intraguild predation by *Asynarchus* (Wissinger et al. 1996), and their dominance in permanent habitats is largely an indirect positive effect of salamander predation on *Asynarchus* (see *Results: Indirect effects . . .*).

This scenario for subalpine wetlands is similar to that observed for the effects of fish predation on amphibians along a gradient from permanent lakes to temporary ponds (Werner and Anholt 1993, Skelly 1995, Wellborn et al. 1996). As in previous work with amphibians, the high activity rates and aggressiveness that allow *Asynarchus* to exploit ephemeral and nutrient-poor subalpine wetlands exact a high cost in permanent

basins where these behaviors increase vulnerability to salamander predators. Conversely, the low activity rates and passive behaviors that enable *Limnephilus* to coexist with salamanders reduce their ability to compete with *Asynarchus* in autumnal wetlands and precludes the timely completion of development in vernal pools (Fig. 8).

Survey data from relatively isolated wetlands near our study site indicate that *Limnephilus* and *Asynarchus* are completely segregated into habitats with and without salamanders, respectively (Wissinger et al. 1999). That the two species are not as completely segregated at Mexican Cut is probably related to adult migration between adjacent habitats. Temporary wetlands without salamanders are likely sources, and permanent wetlands with salamanders likely sinks for *Asynarchus* and vice versa for *Limnephilus* (as in Cooper et al. [1990] and Schlosser [1995]; see also Pulliam 1988, Pulliam and Danielson 1988, Danielson 1991, 1992). Reciprocal source–sink dynamics of this type are probably of general importance for maintaining the overall diversity of wetland complexes that contain numerous basins with different hydroperiods and different top predators (Jeffries 1994, Wissinger and Gallagher 1999).

### *Salamanders as keystone predators in subalpine wetlands*

Previous research has shown that salamander predation plays a primary role in maintaining interbasin differences in the composition of zooplankton assemblages at our study site (Dodson 1970, 1974, Sprules 1972). Large taxa (e.g., *Branchinecta coloradensis, Hesperodiaptomus shoshone,* and *Daphnia middendorfiana*), which dominate assemblages in temporary basins, are rare or absent from permanent basins as a result of size-selective predation by salamanders. Small zooplankton in permanent basins indirectly benefit from salamanders, which eliminate the large and competitively dominant species (Sprules 1972, Dodson 1974, Maly 1976). In our study, caddisflies preferentially preyed on the dominant salamander competitor, but in this case differences in behavior rather than body size underlie the trade-off between competitive superiority and vulnerability to salamanders. For both zooplankton and caddisflies, salamanders act as keystone predators (sensu Paine [1966]) in that they preferentially consume prey species that would otherwise eliminate inferior competitors. The impact of salamanders on community composition is disproportionately large compared to their abundance in terms of total numbers ($<1\%$) and total animal biomass (8%) at Mexican Cut; thus salamanders can be considered keystone species in the broadest sense (see Mills et al. [1993], Menge et al. [1994], Leibold [1996], Power et al. [1996]).

Comparative data from other montane and subalpine wetlands in this region suggest that the correlation between salamanders and alternative invertebrate communities is not unique to our study site and includes invertebrate taxa other than those that we have studied experimentally (Wissinger et al. 1999). Understanding the causal relationships between salamander predation and invertebrate community composition in these wetlands will require long term manipulations that focus on whole-community responses (e.g., as in Mittelbach et al. [1995]). Interpreting the whole-community effects of top vertebrate predators in littoral freshwater habitats has been notoriously difficult because of indirect and potentially compensatory interactions among invertebrate predators in the underlying food web (Gilinsky 1984, Yodzis 1988, Richardson and Threlkeld 1993). This may be further complicated in wetlands by strong interactions between benthos and plankton (Wissinger 1999). Thus, it will be important to conduct such manipulations in the context of a priori hypotheses about alternative pathways of community response to top predator manipulation (e.g., Wooten [1994*a*]). Our findings and those of previous workers (Dodson 1970, 1974, Sprules 1972) provide the basis for an hypothesis testing, path analytical, approach to understanding the effects of salamander predation on the invertebrate communities of subalpine wetlands.

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