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LACK OF APPROPRIATE BEHAVIORAL OR DEVELOPMENTAL RESPONSES BY MAYFLY LARVAE TO TROUT PREDATORS

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Abstract. Many organisms living in heterogeneous environments alter behaviors or morphology when developing in the presence of predators and subsequently incur associated sublethal fitness costs. Larvae of the mayfly *Callibaetis ferrugineus hageni* develop in beaver ponds with or without trout predators. We examined the potential sublethal fitness costs of developing in the presence of trout predators by comparing patterns of timing and size at emergence from ponds over two years, before and after manipulating trout densities. In addition, the behavior, timing, and size at emergence of larvae reared in mesocosms were compared between treatments with and without trout chemical cues. Timing of mayfly emergence and adult size was not affected by the manipulation of trout in the field, or by the presence of trout chemical cues in mesocosms. Observations of mayflies in mesocosms provided no evidence that predator cues induced antipredator behaviors, such as reduced activity or increased crypsis. Surprisingly, late instar larvae swam more frequently in the presence of trout cues during the middle of the day, a behavior that could increase their vulnerability to visually feeding predators. Thus, larvae did not exhibit any traits expected to increase survival in the presence of trout cues. The apparently maladaptive responses to trout may result from phylogenetic inertia or conflicting selection pressures encountered when developing in fishless habitats. The evolution of plasticity to trout in *Callibaetis* may be inhibited by frequent dispersal from fishless source populations.

Key words: Callibaetis; *chemical cues; life history; mayflies; phylogenetic inertia; plasticity; sublethal effects; trout.*

Introduction

Habitat selection in heterogeneous environments can have a strong impact on individual fitness and subsequent population dynamics (Pulliam and Danielson 1991). In spatially structured environments, dispersing organisms may avoid low quality habitats (i.e., those in which population growth rates are low). Habitat site selection should be particularly important when dispersal precedes oviposition, because site selection may strongly influence offspring performance (Price 1997). However, many organisms lack the ability to select optimum habitat (e.g., Morin 1984, Pulliam 1988, Roughgarden et al. 1988, Fonseca and Hart 2001, Murphy 2001), and thus may disperse propagules to low quality habitats.

To increase survival in low quality habitats organisms may alter their behavior, morphology, or life history, often at a cost of potential reproductive effort. For example, many studies have demonstrated such adaptive responses to variation in resources (Emlen 1994, Scrimgeour and Culp 1994, Anholt et al. 2000), competitors (Werner 1991), predators (Skelly and Werner 1990, Skelly 1992, Peckarsky et al. 1993, 2001, Ball and Baker 1996, Hechtel 1997, Peckarsky and McIntosh 1998, Peckarsky et al. 2001), parasites (Feener 1988), or cues signaling the end of the growing season, pond drying, or imminent floods (Roff 1980, Forrest 1987, Rowe and Ludwig 1991, Lytle 2001, 2002). Costs of altered behavior in low quality habitats usually involve reduced feeding (reviews by Sih 1987, Lima and Dill 1990, Lima 1998), which can lead to delayed maturity or smaller size at reproduction (Kohler and McPeek 1989, Peckarsky et al. 1993, Scrimgeour and Culp 1994, Ball and Baker 1996, Schaffner and Anholt 1998). Alternatively, such life history shifts may be adaptive if organisms accelerate development rates to minimize time spent in an unfavorable larval habitat (Werner and Gilliam 1984, Johansson and Rowe 1999, Peckarsky et al. 2001).

In aquatic systems, habitat patches with or without predators frequently occur in the same landscape, and prey populations may develop in both habitat types (e.g., Peckarsky et al. 2001; reviews by Batzer and Wissinger 1996, Wellborn et al. 1996, Wilbur 1997). Antipredator behaviors and associated sublethal fitness costs of developing in dangerous habitats have been observed in several aquatic groups including mayflies (Rahel and Kolar 1990, Flecker 1992, Kolar and Rahel 1993, Peckarsky and McIntosh 1998). Mayflies do not feed as adults and the potential fitness of females is

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clearly linked to larval growth and survival (McPeek and Peckarsky 1998, Caudill 2002).

Mayfly larvae developing in habitats with fish predators may detect and react to predators using visual, hydrodynamic, or water-borne chemical cues (e.g., Kohler and McPeek 1989, Cowan and Peckarsky 1994, Dodson et al. 1994, Scrimgeour and Culp 1994). For example, the larvae of *Baetis tricaudatus* reduced time spent foraging in the presence of chemical cues from the mottled sculpin *Cottus bairdi* (Kohler and McPeek 1989). Similarly, naïve larvae of *B. bicaudatus* (Baetidae) in headwater Rocky Mountain streams altered their behavior within minutes of first exposure to fish cues (McIntosh et al. 1999). Chemical cues also induced life history shifts of this mayfly, resulting in reduced fecundity for females emerging from mesocosms (Peckarsky and McIntosh 1998), or manipulated natural streams (Peckarsky et al. 2002).

In contrast, some prey taxa exhibit ‘‘inappropriate’’ behavioral responses to predators such as high activity rates, which make prey more conspicuous to visually feeding vertebrate predators (e.g., McPeek 1990*a*, *b*, Wissinger et al. 1999*b*, Sih et al. 2000). These inappropriate behaviors are often observed in temporary habitat specialists and may reflect a trade-off between predation risk and the rapid growth and development necessary to avoid death by desiccation (Sih 1987, 1992, Wellborn et al. 1996, Wilbur 1997).

Aquatic larvae of a metapopulation of the mayfly *Callibaetis ferrugineus hageni* Eaton develop in beaver ponds that are fishless or contain visually feeding brook trout (*Salvelinus fontinalis*; Caudill 2002, 2003*a*). Adult terrestrial females frequently dispersed among ponds and did not selectively oviposit with respect to the presence of trout (Caudill 2003*a*). Additionally, larval survival and local population growth rate were strongly and negatively associated with trout density (Caudill 2002).

Since *Callibaetis* females frequently oviposited in ponds with trout, we tested whether larvae had evolved behavioral and life history responses to these fish predators. Specifically, this study determined (1) whether timing and size at emergence of mayflies differed between ponds with and without trout, (2) whether trout chemical cues caused a reduction in growth rate or accelerated development in larvae, and (3) if larvae emerged at a reduced size or (4) altered their behavior when reared in the presence of trout chemical cues.

METHODS

Callibaetis ferrugineus hageni is a common mayfly that is distributed throughout western North America (McCafferty et al. 1993, 1997). Larvae can be found in a wide variety of habitats (McCafferty et al. 1993), and are locally abundant in montane beaver ponds near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, USA (Wissinger et al. 1999*a*). Males emerge to the prereproductive subimago stage, molt to the imago stage one day later, and then fly in aerial swarms to mate. Females mate precociously as subimagos immediately after emerging. They then molt to the imago stage and return to ponds after two weeks to lay fully developed eggs. (For additional life history details, see Caudill 2002). Females die shortly after ovipositing, and lay all eggs in a single pond.

Field survey

Adult size and timing of emergence in *Callibaetis* were measured at 12 ponds over two years. In the first year, six ponds contained trout while the others were fishless. At the end of the first year, trout densities were estimated by electroshocking using a multiple-pass depletion technique (see Caudill 2002 for further details). Then trout were removed from three ponds (Reduction) and introduced to three fishless ponds (Introduction) at natural densities. Trout density in all Reduction ponds was decreased by the manipulation, but trout were not eliminated (Table 1). Thus in the second year, nine ponds had fish, and three ponds were fishless. Last instar larvae, recognized by the presence of black wing pads (BWP) were used to estimate the timing and size at maturation (as in Peckarsky et al. 2001, 2002). Larvae with black wing pads were sampled from ponds during 8–10 sampling periods each year throughout the emergence season (early June–September; see Caudill 2002 for further details). The analyses presented here were restricted to larvae collected in emergent sedge beds where $>83\%$ of all adults emerged (Caudill 2002).

The timing of emergence among ponds was compared using peak emergence date (the mode of the distribution of BWP larval density over the emergence season). Both sexes were combined to estimate the peak emergence date because of small sample sizes at some ponds; and thus field data could not be used to test for differences between sexes in the timing of emergence (e.g., protandry). All statistical analyses were performed in SAS Version 8 (SAS Institute, Cary, North Carolina, USA). A repeated-measures ANOVA was used to test for differences in the timing of emergence of *Callibaetis* among treatments (fixed effect), between years (fixed), with ponds (random) treated as subjects, and compound symmetry as the covariance structure. The Kenward-Roger method estimated degrees of freedom, resulting in fractional degrees of freedom.

Size at emergence was estimated by measuring the head capsule width of last instar larvae (BWP) to the nearest 0.01 mm with an ocular micrometer. Head capsule width was converted to mass to test for sexual size dimorphism. When available, 10 individuals of each sex were sized from each sampling date (Table 1). The effect of trout on annual mean size at emergence was tested using a repeated-measures ANOVA identical to the model used to test for differences in timing at emergence, with the addition of sex as a fixed factor. In these models, the treatment × year interaction tests for effects of the trout manipulation (Underwood 1993, Bonate 2000).

Larval rearing experiment

We used 12 green Rubbermaid storage boxes (45 cm long × 30 cm wide × 19 cm water depth) as rearing chambers (mesocosms) for *Callibaetis* larvae (design similar to McIntosh and Peckarsky 1996). Water from a fishless stream was gravity fed into two head tanks (121-L Rubbermaid trashcans with 30 cm × 7.5 cm diameter PVC pipe fish shelters), and one tank was randomly chosen to contain two brook trout. Near the top of each head tank water flowed out through a 1-mm screen opening, which prevented *Callibaetis* fed to the trout from entering the mesocosms. Water (with or without trout cues) from the head tanks was gravity fed to the mesocosms through 1.25 cm PVC pipes with valves to control flow rates (mean = 0.31 L/min; range = 0.09–1.0 L/min). Water drained out of the mesocosms through a 500-um Nitex mesh filter (Wildlife Supply Company, Buffalo, New York, USA).

Larvae and benthic substrates used in the mesocosms were collected from a fishless beaver pond (UBBP in Caudill 2003*a*). Each mesocosm contained 1 L of mud and detritus and 75 g wet mass of full length sedge stems (*Carex* sp.) held together with a cable tie and attached to a granite rock (mean intermediate axis = 86.583 mm ± 16.1 mm SD). Mud and sedges were conditioned in the mesocosms for 5 d before larvae were added. One hundred and fifty mid-instar *C. ferrugineus hageni* larvae (85% stage IV and 15% stage V; Caudill 2002) were added to each mesocosm over 2 d beginning 13 July 1999. The experiment began on 15 July when two brook trout (183 mm fork length, 94 g; 218 mm fork length, 130 g) were added to one of the head tanks. The trout were fed 30–50 late instar *Callibaetis* larvae daily. The smaller fish died on 18 August and was replaced with another (211 mm fork length, 125 g) on 23 August. Trout were collected from nearby beaver ponds not included in the field survey.

White bridal veil emergence nets were placed over all mesocosms when emergence began on 2 August and remained in place until 28 August. Mayflies emerged from the mesocosms between 1000 and 1645 hours, as observed in natural ponds (Caudill 2002). During the emergence period, subimagos were collected daily from the emergence nets and preserved in 80% ethanol. At the end of the experiment, all larvae remaining in the mesocosms were preserved to compare sizes of BWP larvae and larval survival among treatments.

Larval development time was estimated for each sex using the date of emergence for the first 10 subimagos of each sex emerging from each mesocosm. This protocol minimized potential effects of declining densities in the mesocosms as individuals emerged. A nested mixed model two-way ANOVA was used to test for fixed effects of trout cues and sex on emergence date; sex was nested within mesocosm.

Mean size at emergence for each sex was estimated from the first 10 subimagos and the size of BWP larvae remaining in the tank at the end of the experiment. Differences in size at emergence in subimagos and BWP larvae between treatments and sexes were tested using a nested mixed model MANOVA, followed by univariate ANOVAs. Trout cues and sex were fixed effects, mesocosm was a random effect, and sex was nested within mesocosm.

Comparison of mass–length relationships revealed head capsule width as the best predictor of mass in larvae and mesonotum length as the best measure in subimagos (Caudill 2002). Linear measures of size were converted to mass using the following mass–length relationships: male larvae ln (mg dry mass) = 2.807 × head capsule width −2.832 ($P < 0.001$, adj. $r^2 = 0.922$, $n = 10$); female larvae ln (mg dry mass) = 3.063 head capsule width −3.121 ($P < 0.001$, adj. $r^2 = 0.962$, $n = 15$); male subimagos dry mass = 1.779 mesonotum length −1.896 ($P < 0.001$, adj. $r^2 = 0.421$, $n = 40$); female subimagos dry mass = 4.235 mesonotum length −6.296 ($P < 0.001$, adj. $r^2 = 0.879$, $n = 30$). Potential differences in size between the first 10 and all emerging subimagos from each mesocosm were tested using two-sample Kolmogorov-Smirnov tests for each sex. A single factor ANOVA was used to test for differences in larval survival between treatments.

Size at emergence determines potential fecundity in female mayflies because adults do not feed and females produce a single egg mass (Needham et al. 1935, Berner and Pescador 1988). Hence the magnitudes of treatment effects were estimated in terms of fecundity using size–fecundity relationships for female larvae and subimagos (Caudill 2002): larval fecundity = 1580 × head capsule width (mm) −1668 ($P < 0.001$, $r^2 = 0.965$, $n = 7$); subimago fecundity = 2333–2409 mesonotum length (mm) +745 mesonotum length^2 ($n = 20$, $P < 0.0001$, $r^2 = 0.94$).

Behavioral observations in mesocosms

Behavioral observations of larvae were conducted on stages IV and V larvae starting three days after the experiment began, and on stages VI and VII (BWP) larvae one day after emergence began. Observations were made four times daily (early morning, noon, dusk, and midnight) for four days every other day (18, 20, 22, and 24 July and 3, 5, 7, and 9 August). An observer sat motionless beside each mesocosm for a 1-min acclimation period and then counted the number of mayfly swim events for 1 min. Multiple swims by the same larva could not be distinguished due to the large number of larvae in the mesocosms. The number of larvae visible (= number exposed) on the sides of the mesocosm, the sedge, and the rock were tallied at the end of each observation. Midnight observations were conducted using a flashlight with a red filter (Allan et al. 1986). Water temperature in a randomly selected mesocosm was recorded at 15-min intervals for the du-

TABLE 1. Mean mass of *Callibaetis* larvae measured from the field survey, number of larvae, and number of weeks that last instar larvae were present in samples (in parentheses).

		1998			
		Females		Males	
Pond	Treatment	Mass (mg) [mean ± 1 SD]	No. larvae (no. wk)	Mass (mg) [mean ± 1 SD]	No. larvae (no. wk)
Avery	NFC	7.82 ± 1.54	74 (8)	5.17 ± 0.93	75 (9)
Rustler’s	NFC	5.04 ± 1.05	10 (2)	4.13 ± 0.83	5 (4)
UBBP	NFC	4.74 ± 0.85	65 (6)	3.53 ± 0.46	55 (7)
Marmot	TC	7.00 ± 1.42	15 (4)	4.77 ± 0.49	16 (4)
TxFsBr	TC	5.46 ± 1.56	3 (3)	5.07 ± 0.79	7 (4)
Gothic	TC		0		0
Avalanche	T(+)	5.48 ± 1.24	29 (4)	3.79 ± 0.60	23 (7)
Bellview	T(+)	6.20 ± 1.19	31 (4)	4.47 ± 0.53	30 (4)
Fouroone	T(+)	7.48 ± 1.62	51 (7)	4.63 ± 1.05	28 (6)
Quigley	T(−)	3.01 ± 0.43	12 (3)	2.79 ± 0.25	13 (4)
Levy	T(−)	6.05 ± 1.61	3 (1)	4.20	1 (1)
Friends cut	T(−)	6.83 ± 0.92	21 (3)	4.42 ± 0.61	15 (3)

Notes: Ponds are arranged in increasing order of trout density prior to manipulation. All ponds were sampled on eight dates with equal effort. Trout densities were manipulated between 1998 and 1999, and three ponds were allocated to each of four treatments: no fish controls (NFC), trout pond controls (TC), ponds where trout were introduced (T+), and ponds where trout densities were reduced (T−).

ration of the experiment using a digital temperature logger (Tidbit model, Onset Corporation, Bourne, Massachusetts, USA). The diel temperature cycle was similar to the source pond (range source pond = 4.7–19.4°C; mesocosms = 3.6–18.7°C). Water temperature in mesocosms differed among times of day (three-way ANOVA, $P < 0.001$), but did not differ between treatments ($P = 0.576$), nor between 4-day observation periods ($P = 0.546$).

Differences in the swimming frequency of larvae (swims/min) and the number exposed were examined with a three-way MANOVA followed by univariate ANOVAs. Trout chemical cue treatment (present, absent) was a fixed factor and observation period and time of day were repeated measures. Observations were averaged within mesocosms and 4-day observation periods and only the midnight and noon observations were included in the analysis due to limited degrees of freedom. Both response variables were square root transformed to meet the assumptions of normality and homogenous variance.

Power analyses

For tests that were not statistically significant, the power of the test ($1 - \beta$) was calculated, where β is the probability of type II error (Cohen 1988) using G*power (Faul and Erdfelder 1992, A. Buchner, E. Erdfelder, and F. Faul, *unpublished manuscript*, available online).[2] The power analyses calculated the ‘‘minimum detectable effect size ($\text{mean}_{\text{control}} - \text{mean}_{\text{treatment}}$/SD; Cohen 1988)’’ for a one-tailed test at $\beta = 0.8$ and $\alpha = 0.05$. Power values were interpreted descriptively rather than inferentially (Hoenig and Heisey 2001), by comparing the minimum detectable effect size in *Callibaetis* to the effect sizes observed in *Baetis bicaudatus*, calculated using data from Peckarsky and McIntosh (1998) and Peckarsky et al. (2001, 2002). We expected sample size to be adequate because replication ($n = 12$ mesocosms) was the same as that used in an experiment that detected significant trout odor effects in *B. bicaudatus* (Peckarsky and McIntosh 1998).

RESULTS

Field patterns of date and size at emergence

There were no differences in the peak date of emergence of *Callibaetis* among treatments ($F_{1,7.14} = 0.02$, $P = 0.995$), or evidence of a significant trout manipulation effect (treatment × year: $F_{1,6.83} = 0.15$, $P = 0.926$). Similarly, there were no significant effects of treatment or the trout density manipulation on *Callibaetis* size at emergence (treatment: $F_{3,8.2} = 0.56$, $P = 0.659$; treatment × year: $F_{3,8.2} = 0.13$, $P = 0.943$). Notably, among ponds the mean size at emergence differed by more than a factor of two (Table 1), and individual female fecundity in the field, estimated from size, varied from 441 to 1733 eggs. However, that variance could not be attributed to trout. Females were significantly larger than males (sex: $F_{1,28.3} = 70.1$, $P < 0.0001$).

Larval rearing experiment

Survival of larvae in the mesocosm experiment was high, averaging 96% and did not differ between treatments (one-way ANOVA, $P = 0.331$). Fourteen to 41 individuals of each sex emerged from each mesocosm over the 26-d trial. Within mesocosms of both treatments, the first 10 males emerged significantly earlier than the first 10 females (sex: $F_{1,10} = 111.20$, $P < 0.0001$; sex × treatment: $F_{1,10} = 0.27$, $P = 0.601$; Fig. 1) as in other insects (Thornhill and Alcock 1983, Price

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[2] URL: ⟨http://www.psycho.uni-duesseldorf.de/aap/projects/gpower/how_to_use_gpower.html⟩

TABLE 1. Extended.

1999				Trout density (no./100 m^2)	
Females		Males			
Mass (mg) [mean ± 1 SD]	No. larvae (no. wk)	Mass (mg) [mean ± 1 SD]	No. larvae (no. wk)	1998	1999
8.41 ± 1.72	47 (5)	5.66 ± 1.06	44 (7)	0	0
5.70 ± 1.09	43 (4)	4.15 ± 0.48	41 (3)	0	0
4.44 ± 0.84	56 (5)	3.30 ± 0.41	52 (5)	0	0
7.11 ± 1.35	32 (5)	4.72 ± 0.57	33 (5)	0.17	0.09
5.51 ± 1.11	8 (3)	4.57 ± 0.73	10 (4)	7.12	4.24
5.25 ± 1.52	3 (2)	5.11 ± 1.24	2 (2)	15.2	2.2
6.66 ± 2.13	5 (2)	3.86 ± 0.53	4 (2)	0	4.099
6.27 ± 1.00	20 (2)	4.44 ± 0.44	17 (2)	0	4.53
6.78 ± 1.65	13 (3)	4.36 ± 0.66	13 (3)	0	5.75
3.60 ± 0.46	4 (1)	3.82 ± 0.80	3 (3)	3.72	1.03
4.93	1 (1)		0	9.06	1.58
6.32 ± 1.11	19 (2)	4.38 ± 0.52	18 (4)	17.84	0.73

1997). However, trout chemical cues did not alter development time of either sex ($F_{1,10} = 0.02$, $P = 0.8845$; Fig. 1).

Despite the large variance in individual size at emergence within each sex from the mesocosms, as in the field data, trout cues did not affect size at emergence of subimagos or BWP larvae remaining in the tanks (Fig. 2A, B; Table 2). Also, consistent with field patterns, males were smaller than females in both subimagos and BWP larvae (Fig. 2, Table 2). Mesonotum size in subimagos ranged from 1.74 mm to 2.22 mm in males and from 1.82 mm to 2.50 mm in females (Fig. 2A), representing approximately a two-fold difference in mass from the smallest to the largest individuals within both sexes, and fecundities ranged from 416 to 967 eggs in females.

The size of the first 10 subimagos emerging was significantly smaller than the size of all emerging subimagos ($P < 0.001$ for both sexes, two-sample Kolmogorov-Smirnov tests; Fig. 2B), possibly because larvae grew larger as densities declined. The variability in size at emergence from the mesocosms was similar to that observed for BWP larvae in the source population collected during the 1999 field survey (source population: $\mathrm{CV}_{\mathrm{males}} = 0.033$, $\mathrm{CV}_{\mathrm{females}} = 0.044$; first 10 reared subimagos: $\mathrm{CV}_{\mathrm{males}} = 0.045$, $\mathrm{CV}_{\mathrm{females}} = 0.056$). Thus, this systematic bias did not affect the ability of the experiment to test for differences between trout cue treatments.

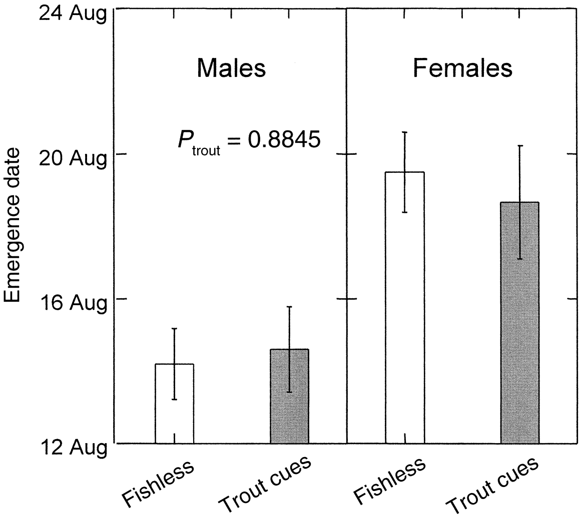

FIG. 1. Mean date (±1 SE) when the 10th subimago emerged from each mesocosm in the presence or absence of brook trout chemical cues.

Behavioral responses

Callibaetis larvae were more exposed (visible on the rock, sedge and sides of mesocosms) at night, particularly during the observation period after the onset of emergence (Fig. 3, Table 3, period × time interaction). However, there was no significant effect of trout cues on the number of larvae exposed (Fig. 3, Table 3). Similarly, larvae swam more frequently at night than during the day and, counter intuitively, increased swimming activity in mid-day during the late observation period (Fig. 3, Table 3). However, fish cues did not affect swimming frequency (Fig. 3, Table 3).

Power analyses

Power analyses suggested that field and mesocosm experiments had statistical power to detect much smaller effect sizes than those observed in *Baetis bicaudatus*. The *Callibaetis* field experiment had power ($1 - \beta$) to detect effect sizes of 1.07 and 0.772 for the timing of emergence in the field and mesocosms, respectively. In comparison, development time for summer generation *B. bicaudatus* was reduced three weeks in trout streams, with estimated effect sizes of 1.99–2.19 (Peckarsky et al. 2001). The tests to detect changes in body size in *Callibaetis* had power to detect effect sizes of 0.787 and 0.916 in the field and mesocosms, respectively. Body mass in the presence of trout cues in summer generation *B. bicaudatus* was reduced 32–47%, with

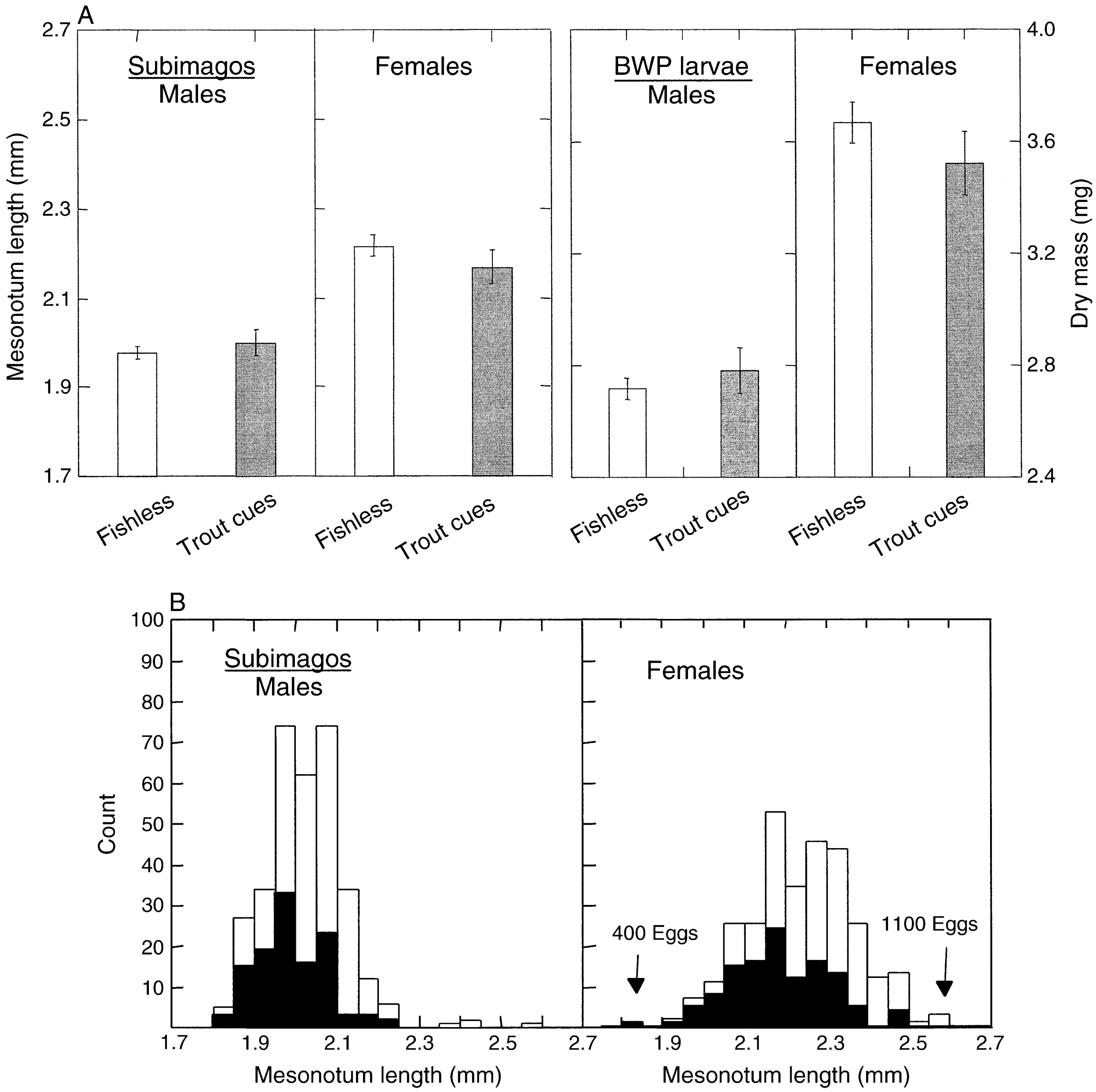

FIG. 2. (A) Mean size (±1 SE) at emergence of the first 10 male and female subimagos from each mesocosm in the presence and absence of trout cues (left panels), and mean size of last instar larvae (identified by black wing pads) remaining in the mesocosms at the end of the experiment (right panels). (B) Observed variation in size at emergence for the first 10 subimagos emerging from the mesocosms (solid bars) and the size of all individuals emerging during the experiment (open bars).

corresponding effect sizes of 1.70–1.92 in field surveys (Peckarsky et al. 2001). Similarly, *B. bicaudatus* body mass in mesocosms was reduced 20–25% (effect size 4.46–5.15) in the presence of trout cues (Peckarsky and McIntosh 1998).

DISCUSSION

Despite a large amount of individual variation in size at emergence of *Callibaetis* in the field and the mesocosms, this variation could not be attributed to the presence of trout or to trout chemical cues. Similarly, *Callibaetis* larvae showed no detectable differences in phenology or behavior in the presence or absence of trout cues. The field and mesocosm experiments had adequate statistical power to detect moderate or large effects; and hence, the power analyses support the conclusion that the response of *Callibaetis* to trout predators was lacking or very weak compared to that observed in the cofamilial *Baetis bicaudatus*.

One or more of the following mechanisms may explain the observed lack of behavioral or developmental responses to trout predators. (1) The mayflies may not recognize the chemical cues of brook trout because brook trout are nonnative predators. (2) Larvae may use nonchemical cues to detect fish predators. (3) *Callibaetis ferrugineus hageni* may not face a trade-off

TABLE 2. Results of nested MANOVA and univariate ANOVA tests for the effects of trout cues and sex on *Callibaetis* size at emergence.

Test	Response variable	df	Wilks' lambda	*F*	*P*
MANOVA					
Trout cues		2, 9	0.894	0.53	0.605
Sex		2, 9	0.176	21.13	0.0004
ANOVA					
Sex	subimago	1, 11		125.01	<0.0001
	last instar larvae	1, 11		31.32	0.0002

Notes: Mesonotum length was measured in subimagos, and mass was estimated from head capsule width in last instar larvae (identified by black wing pads) remaining in the mesocosms at the end of the experiment. There was no effect of trout cues on size of subimagos or size of last instar larvae. Sex was nested within mesocosm, and males were significantly smaller than females.

between foraging and predation risk or the trade-off may be weak. (4) The evolutionary history of *Callibaetis* may have been largely in fish-free habitats, where selection pressures are in conflict with those experienced in habitats with trout.

Detection of predator chemical cues

Callibaetis ferrugineus hageni larvae may not perceive the presence of brook trout chemical cues because these trout are nonnative predators. For instance, a New Zealand mayfly, *Nesameletus ornatus*, did not alter its behavior in the presence of introduced brown trout (*Salmo trutta*) in laboratory trials, but displayed antipredator behavior when exposed to native galaxias (*Galaxaias vulgaris*; McIntosh and Townsend 1994). Brook trout were introduced from eastern North America in the mid- to late 1800s and have become naturalized throughout much of Colorado (Behnke 1992). *Callibeatis ferrugineus hageni* is restricted to the Rocky Mountain West (McCafferty et al. 1993, 1997; = *C. americanus* in McCafferty et al. 1993). Brook trout have largely displaced the native cutthroat trout (*Oncorhynchus clarki*) in streams surrounding the study sites (McIntosh et al. 1999); and cutthroats are completely absent from beaver ponds (Caudill 2002, 2003*a*). Thus, the period of interaction between brook trout and *C. f. hageni* has been approximately one century.

However, the rapid evolution of behavioral responses of prey to nonnative predators has occurred in some species within the family Baetidae. Larvae of *Baetis bicaudatus*, which also has a western North American

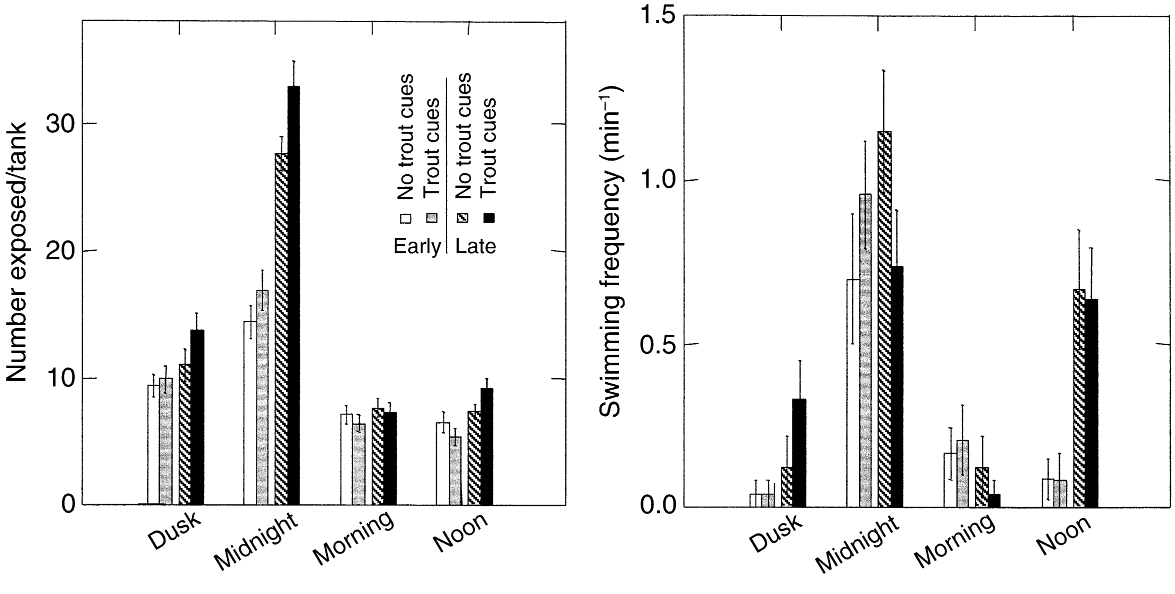

FIG. 3. Mean number of exposed larvae (number visible per mesocosm) and swimming frequency of larvae in mesocosms with and without trout cues. The early observation period was near the beginning of the experiment, and the late period began during the emergence period. Four days of observations were pooled during each period. Error bars denote ±1 SE of the mean within each observation period.

TABLE 3. Results of (a) MANOVA and (b, c) ANOVA, using repeated measures on the number of mayfly larvae exposed (visible) and larval swimming frequency in relation to trout cues (present, absent), time of day (noon, midnight), and observation period (beginning of experiment, during adult emergence).

a) MANOVA	df	Wilks' lambda	*F*	*P*
Between mesocosms				
Trout cues	1, 10	0.175	0.321	0.584
Within mesocosms				
Period	1, 10	11.428	45.082	<0.001
Period × Trout cues	1, 10	0.193	0.761	0.403
Time	1, 10	42.180	554.002	<0.001
Time × Trout cues	1, 10	0.111	1.461	0.255
Period × Time × Trout cues	1, 10	0.316	4.790	0.053

b, c) ANOVA	df	MS	*F*	*P*
b) Number exposed				
Between mesocosms				
Trout cues	1	0.439	0.793	0.394
Error	10	0.554		
Within mesocosms				
Period	1	13.356	71.988	<0.001
Period × Trout cues	1	0.397	2.142	0.174
Error	10	0.186		
Time	1	52.949	240.530	<0.001
Time × Trout cues	1	0.416	1.891	0.199
Error	10	0.220		
Period × Time	1	3.470	52.775	<0.001
Period × Time × Trout cues	1	0.122	1.859	0.203
Error	10	0.066		
c) Swimming frequency				
Between mesocosms				
Trout cues	1	0.005	0.031	0.864
Error	10	0.166		
Within mesocosms				
Period	1	1.268	8.404	0.016
Period × Trout cues	1	<0.001	0.001	0.981
Error	10	0.151		
Time	1	3.641	137.110	<0.001
Time × Trout cues	1	0.030	1.133	0.312
Error	10	0.027		
Period × Time	1	0.329	3.563	0.088
Period × Time × Trout cues	1	0.198	2.146	0.174
Error	10	0.092		

Note: Four days within each observation period were averaged for the analysis.

distribution, reacted strongly to brook trout chemical cues in behavioral assays (Peckarsky and McIntosh 1998, McIntosh et al. 1999). Similarly, a neotropical *Baetis* sp. has apparently evolved nocturnal drift periodicity in response to introduced brook and rainbow trout (*Oncorhynchus mykiss*) over a period of ~50 yr in piedmont streams of Venezuela (Flecker 1992).

It is possible that the ancestral *C. ferrugineus* had a western distribution, and then spread east, encountering brook trout. Regardless, it is doubtful that the lack of response to trout chemical cues results from the recent introduction of a nonnative predator. This hypothesis needs to be tested explicitly by comparing mayfly behavior and life histories when reared in fishless water, or with brook trout cues or cutthroat cues.

Detection of nonchemical predator cues

Alternatively, larvae may rely on nonchemical cues to detect trout. For instance, hydrodynamic and visual cues from a model fish caused lowered growth and fecundity in *B. tricaudatus* (Scrimgeour and Culp 1994). However, no such effects were observed for *Callibaetis* in the field experiment, where all cues were available. In contrast, Rahel and Kolar (1990) and Kolar and Rahel (1993) found that *Callibaetis montanus* (= *C. fluctuans*; McCafferty et al. 1997) reduced its activity in the presence of brook and brown trout (*Salmo trutta*), both nonnative predators. Larvae approached by cutthroat trout attempted evasion by rapidly swimming away (Luecke 1986). Although the specific cues causing these responses were not determined, the ability of other *Callibaetis* species to detect trout casts doubt that the lack of response by *C. f. hageni* is explained by a sensory constraint.

Trade-offs between foraging and predation risk

A third possibility is that the appropriate predator avoidance behavior in ponds with trout may be indistinguishable from the optimal foraging strategy for *Callibaetis*. *Callibaetis* larvae are most abundant in *Carex* spp. sedge beds in fish and fishless ponds (Caudill 2003*a*). Structural complexity of sedges provides protection from predation (Huffaker 1958, Crowder and Cooper 1982) as well as a rich source of detritus for developing larvae (Edmunds et al. 1976, Berner and Pescador 1988, Da Silva 1997). Therefore, within trout ponds, the best refuge from predators may also be the best place to forage, as has been shown for other wetland invertebrates (Batzer and Wissinger 1996, Batzer 1998). To test this hypothesis, both food resources and trout predation rates need to be measured in different microhabitats. If resource levels are highest in predation refuges, then perhaps growth rates and size at emergence should be similar in fish and fishless ponds.

However, even without a foraging–predation risk trade-off, ponds with trout may be a high risk environment overall, suggesting a mortality cost to developing in ponds with trout. Larval survival rates and population growth from sedges decreased in high trout density ponds (Caudill 2002). Several other studies suggest that *Callibaetis* larvae are highly vulnerable to trout predation. Many larvae were consumed by trout in the Kolar and Rahel studies, despite the presence of a refuge. Native cutthroat trout selectively consumed *Callibaetis* sp. larvae from emergent vegetation beds in Utah lakes (Carlisle and Hawkins 1998), even in the presence of a potential spatially complex refuge. Similarly, *Callibaetis* abundance was significantly reduced in alpine Sierra Nevada ponds where trout were introduced (Knapp et al. 2001).

Optimality theory suggests that in environments that are more dangerous, larvae should accelerate development, emerge early, and behave to reduce the probability of mortality (Werner and Gilliam 1984, Werner 1986, Rowe and Ludwig 1991). Emergence at a smaller size may further reduce the probability of mortality since trout prefer larger prey (Allan 1978, 1981) including larger *Callibaetis* (Luecke 1990). It is puzzling that *Callibaetis* shows no such responses to this apparently risky environment. In fact, not only did *Callibaetis* larvae fail to respond adaptively to fish cues, but they swam more frequently late in development and during the day, which probably increased their vulnerability to trout (e.g., McPeek 1990*b*). In laboratory feeding trials with cutthroat trout, moving *Callibaetis* larvae were quickly detected and readily consumed, while stationary prey were rarely detected or attacked (Luecke 1986). Interestingly, a sensitivity analysis suggested that direct mortality effects have a greater influence on rates of population growth in this species than do nonlethal effects of trout on fecundity (Caudill 2002).

In summary, risk of predation may not reduce foraging efficiency or growth rates in *Callibaetis* larvae, but this does not explain the lack of an adaptive life history shift or appropriate antipredator behaviors.

Phylogenetic inertia and dispersal in heterogeneous landscapes

The fixed behavior and development irrespective of trout in *Callibaetis* may be explained by phylogenetic inertia, where traits that are adaptive in one habitat are maladaptive in a new habitat type (Sih et al. 2000). Selection in historically fishless habitats may favor traits that increase vulnerability to fish predators. *Callibaetis* spp. are common in temporary fishless habitats (Wiggins et al. 1980, Berner and Pescador 1988) where there is a high risk of mortality during habitat drying (Wellborn et al. 1996). Temporary habitat specialists often have high activity rates, high growth rates, and are conspicuous compared to related taxa that co-occur with fish (Sih 1992, Wellborn et al. 1996, Wissinger et al. 1999*b*, Sih et al. 2000). For instance, *Ambystoma barbouri* salamander larvae invaded temporary (fishless) headwater stream habitats from temporary ponds within the last few thousand years (Sih et al. 2000). When larvae drift to downstream habitats with sunfish, they suffer high mortality (Sih et al. 1992). Sih et al. (2000) suggest that the lack of an evolved response to fish in *A. barbouri* may stem from continued selection for high activity in temporary habitats. Furthermore, frequent and asymmetrical dispersal from sources (without predators) to sinks (with predators), could inhibit the evolution of effective antipredator traits (Holt and Gaines 1992), a hypothesis that was supported by estimates of gene flow and relative antipredator behaviors among streams in *A. barbouri* (Storfer and Sih 1998).

The lack of response by *Callibaetis* to trout may result from a similar evolutionary history and contemporary ecological processes. Several traits including ovovivipary, short generation times, and high activity rates suggest an evolutionary association with temporary habitats. Notably, the same traits that increase vulnerability to trout might be effective antipredator behaviors in fishless habitats, which often have high densities of sit-and-wait predators such as odonates (McPeek 1990*a*) that readily consume *Callibaetis* larvae (Johnson 1995). Rapid swimming responses reduce predation of damselfly larvae by dragonfly larvae, but increase the risk of predation by fish (McPeek 1990*b*, McPeek et al. 1996). Similarly, the fixed *Callibaetis* behaviors may deter sit-and-wait predators, such as adult dytiscid beetles and *Ambystoma trigrinum nebulosum* salamanders. The fishless beaver ponds had higher densities of these predators (Caudill 2002), possibly similar to the ancestral habitat of *Callibaetis*.

Dispersal between habitat types may also inhibit the evolution of plasticity to trout predators. Adult female *C. f. hageni* frequently disperse from fishless sources to sinks with high trout density, and females do not avoid oviposition in ponds with trout (Caudill 2003*a*, *b*). Recent theoretical work suggests that adaptation to the sink habitat will not occur unless traits that confer a large fitness advantage arise frequently in the sink habitat (Holt and Gomulkiewicz 1997). Hence, ancestral development in temporary habitats may have selected for high activity rates, and current dispersal from sources to sinks may prevent local adaptation to conditions such as the presence of fish predators in the sink habitat.

Conclusions and speculation

In summary, naïveté to introduced predators, an inability to detect predator cues, a weak trade-off between foraging and predation risk, or conflicting selection pressures among habitat types may explain the lack of appropriate antipredator traits in *C. f. hageni*. The available literature and data from this study support the hypothesis that *Callibaetis* species have evolved primarily in fishless habitats, where there has been simultaneous selection for high activity imposed by sit-and-wait predators and habitat impermanence (Sih 1987, Wellborn et al. 1996). Additionally, the fixed behavior and development of *Callibaetis* suggest that high rates of dispersal from (fishless) source habitats to sinks (with trout) may have prevented the evolution of traits adaptive to the sink habitat (Holt and Gaines 1992), despite the large difference in fitness between habitat types (Caudill 2002). A complete understanding of these results will require knowledge of the phylogenetic relationships among the Baetidae, and behavioral responses to both native and nonnative fish and invertebrate predators, as well as a better understanding of how predators and dispersal interact to influence fitness and trait evolution in regional populations.

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