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Sex-specific life-history responses to seasonal time constraints in an alpine caddisfly

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ABSTRACT

Hypotheses: (1) Facultative species that occur in permanent and temporary streams can be locally adapted to their stream of origin or exhibit life-history plasticity. (2) Temporary stream populations respond to environmental cues signalling stream drying whereas permanent stream populations do not. (3) Sex-specific selection pressures imposed by seasonal time constraints imply that males prioritize early maturation whereas females maximize body size at maturity.

Organism: Permanent and temporary stream populations of the alpine caddisfly *Allogamus uncatus* (Trichoptera) in the Val Roseg, Switzerland.

Methods: We used a common garden experiment to test whether males and females from both stream types differed in their life-history response to combined changes in photoperiod (ambient vs. late) and hydroperiod (constant vs. drying).

Results: Caddisflies exhibited life-history plasticity, although responses varied by time constraint cue and sex. Both sexes shortened development time in the late photoperiod treatments, but neither sex showed a stronger developmental response when exposed to both time constraint cues. Males emerged earlier and at a smaller size than females, and permanent stream males responded to stream drying. Females from both populations increased growth rate in the combined stress treatment, but only permanent stream females responded to hydroperiod stress with decreased growth rate and size at emergence. Temporary stream insects did not emerge earlier than permanent stream insects.

Keywords: aquatic insect, hydroperiod, photoperiod, plasticity, protandry, temporary stream, Trichoptera.

INTRODUCTION

Seasonal environments impose time constraints on the life histories of many organisms. For example, many insects must reproduce before the onset of winter and amphibians must metamorphose prior to pond drying (Johansson *et al.*, 2001). Age and size at maturity are important and often highly plastic life-history variables that are closely linked with fitness

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(De Block and Stoks, 2005a). Accelerating maturity in response to seasonal time constraints comes at a cost of a shorter period available for growth, typically resulting in a smaller size at maturity and reduced fecundity (Johansson and Rowe, 1999). Life-history theory often assumes this trade-off between development time and body size – that is, early development and small size (Stearns, 1992; Roff, 2002). However, plasticity in growth rate may account for observed inconsistencies with these trade-off predictions (Nylin, 1992; Abrams *et al.*, 1996; Nylin and Gotthard, 1998). Instead of early development and small size, several models predict early development and a larger size at maturity when growth rate is increased or decoupled from development (Stearns and Koella, 1986; Day and Rowe, 2002).

Seasonal time constraint theory explains how individuals maximize fitness by maturing according to state-dependent mechanisms. The shift from larval stage to reproductive stage depends on an individual's state and the time remaining in the season for reproduction (Rowe and Ludwig, 1991; Lytle, 2002). States can include internal variables (e.g. body mass) as well as environmental variables (e.g. photoperiod and hydroperiod). Furthermore, the effects of environmental state variables on an organism's life-history response may be sex-specific (Houston and McNamara, 1992; Crowley, 2000; De Block and Stoks, 2003). Because the relationship between fitness, age and size at maturity differs between the sexes, males and females experience different selective pressures. For males, optimal time to and size at maturity will depend on the strength of selection for protandry [early male emergence (Fagerström and Wiklund, 1982)] and competitive ability or mating advantage (Thornhill and Alcock, 1983). Females, however, are assumed to be less time constrained during development than protandrous males, and selection should favour the fecundity advantage of large size (Fischer and Fiedler, 2001; Roff, 2002).

Disturbance regimes (e.g. dry vs. wet periods) can interact with seasonal time constraints in shaping life-history strategies. For example, many species of insects and amphibians occur in both permanent and temporary aquatic habitats, and may experience different selection pressures imposed by hydroperiod (Williams, 1996). When disturbance regimes (in this case habitat drying) are relatively predictable, populations inhabiting temporary habitats may have adapted to emerge before the height of the harsh season or long-term average date of drying (Lytle, 2002). Alternatively, populations of temporary habitats may be prone to local extinction and persist by re-colonization from other subpopulations, resulting in source–sink metapopulation dynamics (Hanski, 1998; Caudill, 2003; De Block and Stoks, 2004). This contribution of individuals (i.e. gene flow) from other subpopulations should favour the spread of generalist, plastic genotypes rather than locally adapted specialists (Sultan and Spencer, 2002). More specifically, if colonizing individuals originate from permanent aquatic habitats and temporary aquatic habitats that did not completely dry, then life-history plasticity in response to hydroperiod should be evolutionarily favoured (De Block *et al.*, 2005).

Maximizing fitness using optimal emergence strategies requires that organisms be able to assess both the time in the season and their internal state. Many organisms use environmental cues to determine their proximity to an approaching time horizon (Altwegg, 2002; Frisch and Santer, 2004), and insects are capable of assessing their internal state (e.g. body size) via stretch receptors or other means (Nijhout, 1994). Photoperiod (day length) affects life-history timing in many organisms, being the primary seasonal cue for insects (Nylin and Gotthard, 1998). Experiments manipulating day length found either a development time/size trade-off (Gotthard, 1998; Johansson *et al.*, 2001) or a coupled response where individuals metamorphosed earlier and larger due to plasticity in growth rate or development (Wiklund *et al.*, 1991; Gotthard *et al.*, 1999; Margraf *et al.*, 2003). Studies investigating sex-specific responses to developmental time constraints caused by shorter day lengths (Leimar, 1996) or increased temperature (Fischer and Fiedler, 2000, 2001) found that protandrous males experienced a trade-off between development time and size, whereas females reduced development time but maintained large body size.

Habitat duration (hydroperiod) is probably the most important time constraint cue for organisms with complex life cycles inhabiting temporary water bodies (Denver *et al.*, 1998). Most amphibian studies on the effects of hydroperiod (pond drying) found individuals responded to falling water levels by metamorphosing earlier and at a smaller size (Denver *et al.*, 1998; Laurila and Kujasalo, 1999; Altwegg, 2002; Lane and Mahony, 2002). Although temporary aquatic habitats are ubiquitous, there have been surprisingly few manipulative studies testing the effects of hydroperiod on aquatic insect life-history traits. One study conducted on mosquito larvae showed that females exhibited a development time/size trade-off in response to habitat desiccation cues, but males did not (Juliano and Stoffregen, 1994). De Block and Stoks (2005b) found that damselfly larvae reared in artificial temporary ponds had slower development and growth than larvae reared in permanent ponds, and suggested that deteriorating growth conditions associated with pond drying may decouple trade-offs under time stress. Whether populations in temporary aquatic habitats are locally adapted or exhibit plasticity remains unresolved. Two recent studies using damselflies from permanent and temporary ponds showed little population differences in life-history responses, although male and female responses differed for some traits (De Block and Stoks, 2004, 2005b).

Temporary streams are common features of alpine floodplains, and are an ideal model system to investigate aquatic insect life-history responses to habitat duration. Alpine flood plains experience cycles of expansion and contraction, resulting in a mosaic of stream habitats that vary in water permanence (Robinson *et al.*, 2003). While some fauna are endemic to temporary streams, many species are facultative and occur in both permanent and temporary streams, allowing adaptive strategies to be compared. Invertebrates in temporary streams can survive via a drought-resistant life-history stage (e.g. terrestrial adult) or by larval migration to adjacent permanent habitats such as remnant pools (Delucchi and Peckarsky, 1989). Migration to remnant pools may not be a long-term solution, however, as these pools also can disappear in streams that go completely dry.

Common garden experiments are a powerful tool used to assess environmental sources of variation associated with phenotypic variation observed in nature (Sears and Angilletta, 2003). Here, we used small, artificial ‘pools’ as common garden experimental habitats to assess stream insect life-history responses to changes in environmental conditions, and to simulate the physico-chemical environment of remnant pools during drying. As water levels fall, remnant pools are characterized by changes in habitat size, dissolved oxygen concentrations (from changes in water temperature and wind-induced aeration) and water chemistry (Williams, 1996). Our study investigated sex-specific life-history responses to the combined effects of two seasonal time constraint cues (photoperiod and hydroperiod) of an alpine caddisfly (Insecta: Trichoptera) inhabiting permanent and temporary streams. We tested the following predictions: (i) both sexes respond to shorter day length and habitat duration by shortening development time, and show the strongest response when exposed to both cues; (ii) the consequences of a shorter development time on adult body size differs between sexes relative to the strength of selection for protandry in males and large size in females; and (iii) temporary stream insects should emerge earlier than permanent stream insects if populations are locally adapted.

METHODS

The limnephilid caddisfly *Allogamus uncatus* (Brauer) occurs between 600 and 2600 m above sea level (a.s.l.) in the mountains of the Balkan Peninsula, Carpathians and Central Europe, including the Eastern Alps (Botosaneanu and Malicky, 1978). Larvae occur in pools of springs and small, slow-flowing rithral streams, and along the margins of alpine lakes, feeding on shed leaves, detritus and biofilms. The species is univoltine with terrestrial adults present from September through mid-October, and over-winters in the egg stage (H. Malicky, personal communication).

Third instar larvae ($n = 160$) were collected on 14 July 2003 from a permanent and a temporary stream (~2100 m a.s.l.) in the Val Roseg, Switzerland (46°29′28″N, 9°53′57″E). The permanent stream has relatively constant water levels, although low water occurs in years with minimal rainfall and high temperatures. The temporary stream dries or experiences considerably reduced water levels each year. During 2000–2003, this stream dried twice, resulting in the death of larvae that had not completed development prior to drying (L. Shama and C.T. Robinson, personal observation).

Larvae were transported to the laboratory and allowed to acclimate for 7 days in 10-litre aerated aquaria in a temperature-controlled room (12°C) with light conditions of L16 : D8 (24 h L/D cycle). Larvae were provided with conditioned alder leaves (*Alnus viridus*) collected near the study streams for food *ad libitum*. On 21 July, larvae were randomly assigned to experimental treatments (see below). Two larvae each were placed in individual plastic boxes (350 ml; 15 cm long by 7.5 cm wide by 5 cm high; $n = 80$) aerated with an airstone, and containing coarse sand, two small stones and 1.0 g of alder leaves. As sex cannot be determined for larval caddisflies, we randomly assigned two individuals per box and assessed sex at the end of the experiment using genital morphology of emerged adults. Initial larval mass was measured on a subset of 20 individuals from each source stream population. Larval mass (= dry mass) was determined by drying individuals for 48 h at 50°C and then weighing them to the nearest 0.01 mg.

The experiment consisted of eight treatments ($n = 10$ per treatment) in a $2 \times 2 \times 2$ factorial randomized design: two source streams (permanent vs. temporary), two photoperiods (ambient vs. late) and two hydroperiods (constant vs. falling). Photoperiod regimes were applied using plant growth lights (36W Biolux lamps, Osram AG, Winterthur, Switzerland) with programmable digital timers mounted within separate shelves shielded with black, photography-grade cardboard. The ambient photoperiod regime started on 21 July (~L15 : D9) and was adjusted daily to simulate the natural progress of the light cycle. The late photoperiod regime was set for 1 September (~L13 : D11), and adjusted daily from that date. Water level was either constant (maintained daily at 350 ml) or falling (water removed). For the latter, water was maintained at 100% volume (350 ml) from days 1 to 5, 75% from days 6 to 10, 50% from days 11 to 15, 33% from days 16 to 20, and then maintained at 25% from day 21 on. Water used during acclimation and the experiment was collected weekly from an alpine stream near the Val Roseg. Water in each box was changed every 10 days. Temperature was maintained at 12 ± 0.5°C throughout the experiment, verified hourly using temperature loggers (Stowaway XTI, Onset Corporation, USA) mounted within the experimental shelves.

We assessed the following traits for each individual: sex, development time, growth rate and mass at emergence. Development time was measured as: (1) total development time (from experiment day 1 to adult emergence), (2) estimated time to pupation (number of pupae per treatment was recorded on days 10, 20 and 30), and (3) estimated pupation duration (total development time minus mean time to pupation). Mass at emergence (= dry mass) was determined by drying adults for 48 h at 50°C and then weighing them to the nearest 0.01 mg using an electronic microbalance. Growth rate was calculated as ln(dry mass) divided by time to pupation. The effects of treatments on the three response variables (total development time, growth rate and mass at emergence) were first analysed as a multivariate analysis of variance (MANOVA), with subsequent separate four-way analyses of variance (factors: sex, source stream, photoperiod, hydroperiod) on box means (significance threshold $P \leq 0.05$). Individuals were used as replicates for boxes from which one male and one female emerged (MF; $n = 12$). While using individuals as replicates inflates the error degrees of freedom by 12, excluding the MF boxes did not change the outcome of any analyses. Therefore, we retained the MF individuals to maintain adequate sample sizes in each treatment. No four-way interactions were significant and were therefore removed from the final models. All statistical analyses were performed using SPSS (Version 11.0).

RESULTS

Of the initial 160 larvae, 102 emerged as adults. Twenty-four larvae died due to pump or airstone failure, and 20 pupae failed to emerge due to fungal infections. Of the remaining 14 dead larvae, 8 died in ambient photoperiod/constant water treatments, 5 died in ambient photoperiod/falling water treatments, and one larva died in the late photoperiod/constant water treatment. Mortality was evenly distributed among larvae from each source stream population, suggesting that laboratory conditions did not differentially affect either population. Furthermore, it is unlikely that larval mortality occurred due to cannibalism between the two individuals per box. We have successfully reared adults from larval densities as high as eight individuals per box with no deaths due to cannibalism (L. Shama and C.T. Robinson, unpublished data).

The MANOVA showed that sex, source stream and time constraint cues had a significant effect on the three life-history responses. The interaction between source stream and hydroperiod affected the sexes differently, as shown by the significant three-way interaction term (Table 1). We also detected a significant three-way interaction between source stream, photoperiod and hydroperiod. Subsequent univariate analyses showed that larvae reared under the late photoperiod (indicating a later date in the growth season) had shorter total development times than those reared in the ambient photoperiod, and males had shorter development times than females (Table 2). Estimated time to pupation was shorter in the late photoperiod (mean = 20.88 ± 0.50 days) than in the ambient photoperiod (25.19 ± 0.69 days), but estimated pupation duration was shorter in the ambient photoperiod (24.99 ± 0.54 days) than in the late photoperiod (27.32 ± 0.33 days). In other words, insects in the late photoperiod pupated earlier, but spent a longer time as pupae than insects in the ambient photoperiod. Larvae from permanent and temporary stream sources did not differ significantly in total development time (Fig. 1 a,b). However, time to pupation was shorter for permanent stream insects (22.03 ± 0.60 days) than temporary stream insects (23.77 ± 0.67 days), and pupation duration was significantly longer for permanent stream insects (27.03 ± 0.38 days) than temporary stream insects (25.60 ± 0.43 days; ANOVA: $F_{1,63} = 4.58$; $P = 0.036$). In other words, permanent stream insects pupated earlier, but spent a longer time as pupae than temporary stream insects.

Table 1. Summary of the multivariate analysis of variance of the effects of sex, source stream (permanent vs. temporary), photoperiod (ambient vs. late) and hydroperiod (constant vs. drying) on development time, growth rate and mass at emergence of *A. uncatus*

Source	Wilks' λ	d.f.	*F*	*P*
Sex	0.361	3,54	31.888	<0.001
Source stream (SS)	0.078	3,54	211.919	<0.001
Photoperiod (P)	0.014	3,54	1284.688	<0.001
Hydroperiod (H)	0.956	3,54	0.823	0.487
Sex*SS	0.933	3,54	1.292	0.287
Sex*P	0.799	3,54	4.533	0.007
Sex*H	0.919	3,54	1.588	0.203
SS*P	0.168	3,54	89.406	<0.001
SS*H	0.863	3,54	2.867	0.045
P*H	0.295	3,54	43.076	<0.001
Sex*SS*P	0.915	3,54	1.675	0.183
Sex*SS*H	0.855	3,54	3.046	0.036
Sex*P*H	0.889	3,54	2.242	0.094
SS*P*H	0.067	3,54	252.022	<0.001

Larvae reared under the late photoperiod had higher growth rates than those reared under the ambient photoperiod, and females had higher growth rates than males (Fig. 1c,d). Growth rates differed between the source streams, sexes, photoperiods and hydroperiods, as evidenced by the two significant three-way interaction terms (Table 2). Permanent stream larvae had reduced growth rates in the ambient photoperiod/falling water treatment (hydroperiod stress), but increased growth rates in the combined stress treatment (late photoperiod/falling water). Temporary stream females also had increased growth rates in the combined stress treatment, whereas temporary stream males did not respond to hydroperiod.

Mass at emergence was higher for females than males, and permanent stream adults were larger than temporary stream adults (Fig. 1e,f). Average initial larval mass was higher for permanent stream individuals (mean dry mass = 7.89 ± 0.73 mg) than temporary stream individuals (3.97 ± 0.59 mg). However, we could not determine the sex of larvae and so do not know if the initial mass of females was higher than that of males. We also found a significant three-way interaction between sex, photoperiod and hydroperiod for mass at emergence (Table 2). Permanent stream females had reduced mass at emergence under hydroperiod stress, whereas temporary stream females had increased mass at emergence in the combined stress treatment (Fig. 1f). For males, mass at emergence only differed between the two source streams.

DISCUSSION

Multiple state variables, both internal and environmental, can interact in determining life-history responses to seasonal time constraints. Larval *A. uncatus* caddisflies exhibited life-history plasticity, although responses varied according to time constraint cue and sex. First, as predicted, both sexes shortened development time in the late photoperiod

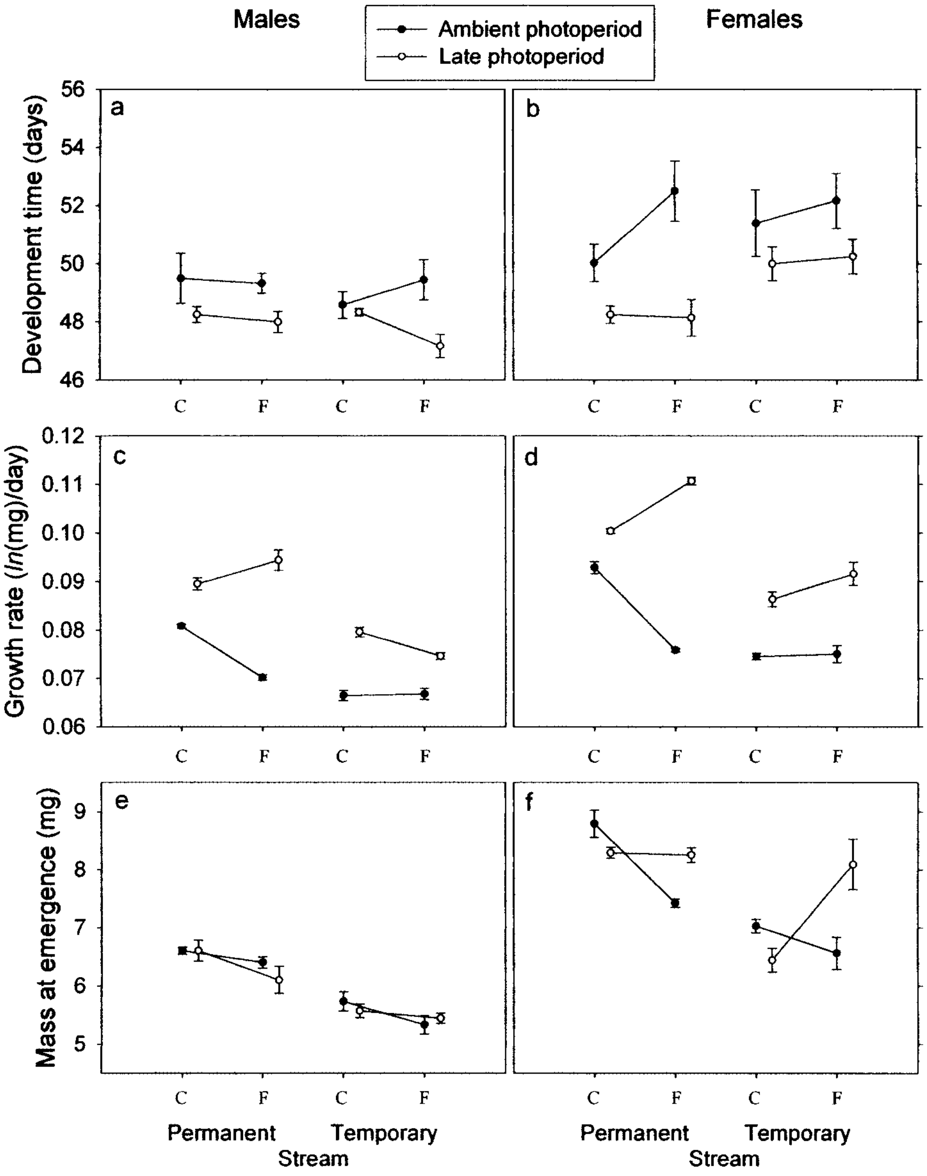

Fig. 1. The effect of source stream (permanent vs. temporary), photoperiod (ambient vs. late) and hydroperiod (C = constant; F = falling) on life-history variables in male and female *Allogamus uncatus*: (a, b) development time; (c, d) growth rate; (e, f) mass at emergence. Means are given ± 1 standard error.

(indicating a later date in the growth season), although neither sex showed a stronger developmental response when exposed to both time constraint cues. Second, males emerged earlier and at a smaller size than females. Both male and female growth rates were affected by photoperiod and hydroperiod cues, but only female mass at emergence differed among

Table 2. Summary of univariate analyses of variance of the effects of sex, source stream (permanent vs. temporary), photoperiod (ambient vs. late) and hydroperiod (constant vs. drying) on *A. uncatus* development time, growth rate and mass at emergence

		Development time		Growth rate		Mass at emergence	
Source	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Sex	1	10.59	0.002	87.01	<0.001	91.18	<0.001
Source stream (SS)	1	0.71	0.403	121.15	<0.001	35.85	<0.001
Photoperiod (P)	1	10.26	0.002	188.67	<0.001	0.49	0.487
Hydroperiod (H)	1	0.39	0.534	1.60	0.211	1.12	0.294
Sex*SS	1	2.34	0.132	0.32	0.576	0.53	0.472
Sex*P	1	1.03	0.315	3.57	0.064	1.38	0.245
Sex*H	1	0.67	0.416	1.13	0.293	0.50	0.482
SS*P	1	0.32	0.575	8.02	0.006	0.38	0.542
SS*H	1	0.13	0.718	2.31	0.134	3.96	0.051
P*H	1	1.90	0.174	23.02	<0.001	6.25	0.015
Sex*SS*P	1	0.36	0.551	0.05	0.828	0.07	0.796
Sex*SS*H	1	0.04	0.837	1.57	0.215	3.20	0.079
Sex*P*H	1	0.03	0.876	5.75	0.020	6.56	0.013
SS*P*H	1	0.001	0.971	22.75	<0.001	0.96	0.331
Error	56						
Total	71						

time constraint treatments. Finally, contrary to our prediction, temporary stream insects did not emerge earlier than permanent stream insects.

Trade-offs between age and size at maturity are expected among individuals under time stress, when growth rate is maximized rather than optimized. Combinations of time stress cues should generate even clearer trade-off patterns (Nylin and Gotthard, 1998; but see De Block and Stoks, 2005b). However, when growth rate is optimized and can vary adaptively, trade-offs between age and size are no longer expected (Abrams *et al.*, 1996). Contrary to classic life-history theory, *A. uncatus* did not trade-off early maturation against large size under the late photoperiod time constraint. Instead, sizes were similar in both photoperiods (despite a shorter development time in the late photoperiod), as a result of increased growth rates under time stress. Accelerated development in response to photoperiod cues indicating a later date in the season is adaptive, and our results add to the body of literature demonstrating this for insects (reviewed in Nylin and Gotthard, 1998). Selection for a flexible growth strategy in response to photoperiod cues enabled larvae to compensate for the shorter development period, and maintain large adult body size. This result is consistent with recent growth-development models (Day and Rowe, 2002) that predict a coupled response, where individuals metamorphose earlier and larger due to plasticity in growth rate (Wiklund *et al.*, 1991; Gotthard *et al.*, 1999), or growth rate is decoupled from development (Wissinger *et al.*, 2004).

Photoperiod is the primary seasonal cue for insects; however, habitat drying is the most important environmental factor affecting larval survivorship for insects (and amphibians) with aquatic larvae and terrestrial adults (Denver *et al.*, 1998). Where photoperiod provides a reliable cue for the proximity of the seasonal time horizon, habitat drying is a more stochastic time constraint, both in incidence and the speed of onset (Altwegg, 2002). Aquatic organisms with complex life cycles should then prioritize habitat desiccation risk over late season emergence, even if this effort comes at a cost of smaller body size. Surprisingly, neither temporary nor permanent stream larvae shortened development time under the hydroperiod time constraint. Instead, larvae from both populations prioritized late season emergence. The absence of an adaptive developmental response to hydroperiod is consistent with other studies of aquatic insects (Delucchi and Peckarsky, 1989; De Block and Stoks, 2004, 2005b). However, this is in contrast with several studies on tadpoles that have demonstrated accelerated life history in response to pond drying (Denver *et al.*, 1998; Laurila and Kujasalo, 1999; Altwegg, 2002; Lane and Mahony, 2002; Morey and Reznick, 2004). The reasons for this difference in life-history response are unclear. Fixed high development rates do not explain the lack of a response in *A. uncatus*, as this species can accelerate development under late photoperiod cues. A possible explanation is that *A. uncatus* larvae were already at a developmental stage at the start of the experiment that was beyond a sensitivity threshold of the hydroperiod time constraint treatments (Twombly, 1996).

Clearer trade-offs between age and size at maturity are expected under the combined time stress of late season photoperiod and stream drying because growth rate should be maximized (Nylin and Gotthard, 1998). As previously discussed for photoperiod, *A. uncatus* also did not show a trade-off under the combined stress treatment because growth rates were optimized rather than maximized. High growth rates in the combined stress treatment decoupled the expected trade-off (De Block and Stoks, 2005b). Overall, growth rates were highest in the combined stress treatment (except for temporary stream males), which suggests that while photoperiod time stress may be the primary cue for increased growth rate, the additional stress of stream drying can further accelerate growth rate. Interestingly, growth rate responses to hydroperiod when larvae were not stressed by photoperiod (ambient photoperiod/drying) differed between the two populations. Temporary stream larvae did not show a growth rate response to hydroperiod, whereas permanent stream larvae had reduced growth rates under the hydroperiod stress. Also, permanent stream females emerged at their smallest size when stressed by hydroperiod. Although we see no obvious reason for this growth rate response by permanent stream larvae to hydroperiod stress, the reduction in female size at emergence (but not male size) likely reflects the larger difference in growth rate between hydroperiod treatments for females than males.

A drying stream is a complex environment. As conditions are likely to vary from stream to stream, insects must be capable of detecting a cue common to all drying streams or be able to respond to multiple cues (Denver *et al.*, 1998). The precise mechanism by which *A. uncatus* responds to stream drying remains unresolved. Stream drying may affect metamorphosis of insects via changes in several factors associated with decreasing water volume, such as increasing concentrations of dissolved solutes, increasing water temperature, and an increase in interactions among conspecifics (Juliano and Stoffregen, 1994). In an additional experiment, we found that concentrations of dissolved solutes were significantly higher in falling water treatments than in constant water, whereas temperature did not differ between the two hydroperiods (L. Shama and C.T. Robinson, unpublished data). It has been suggested that increasing solute concentrations enhances microbial growth, which could lead to an increase in insect growth rates (Juliano and Stoffregen, 1994). While this may explain the higher growth rate of larvae in the late photoperiod/drying treatment, it does not explain why permanent stream larvae should have reduced growth rates in the ambient photoperiod/drying treatment. Furthermore, while elevated stream temperature likely contributes to accelerated maturity and growth rate (Delucchi and Peckarsky, 1989), it was not necessary for a response to hydroperiod in our experiments (see also Denver *et al.*, 1998; Laurila and Kujasalo, 1999). Also, it is unlikely that insect density affected *A. uncatus* in this experiment. There were only two individuals per box, and including density as a factor in the analyses did not affect the outcome. Finally, the experiment was conducted in aerated 'pools' instead of flow-through artificial streams. While our 'pools' may not have mimicked a drying stream perfectly, the results are unlikely to be artefacts of atypical environmental conditions, as this species occurs in pools of slow-flowing streams. Also, many abiotic factors associated with drying, remnant pools (such as changes in habitat size, dissolved oxygen concentrations and water chemistry) that are likely to be used as cues were present in our study.

Facultative species that occur in permanent and temporary aquatic habitats may be either locally adapted to conditions of their origin stream or they may exhibit life-history plasticity in response to hydroperiod (Morey and Reznick, 2004). Contrary to our prediction, temporary stream insects did not emerge earlier than permanent stream insects. Stream drying does not appear to exert sufficient selection pressure to promote faster development in temporary streams (see also Delucchi and Peckarsky, 1989). There is still no evidence for local adaptation to habitat duration in insects (see also Juliano and Stoffregen, 1994; De Block and Stoks, 2004, 2005b). The absence of fixed faster development or higher plasticity in development rate in response to hydroperiod suggests that temporary stream populations may act as sinks, and persist via repeated colonization from source populations following local population extinction (Caudhill, 2003). In such a source–sink metapopulation system, gene flow from permanent stream sources (and temporary streams that did not completely dry) should be high, and should favour the spread of life-history plasticity in response to hydroperiod (Sultan and Spencer, 2002; De Block *et al.*, 2005). Previous studies have found only weak evidence for plasticity to hydroperiod (Juliano and Stoffregen, 1994) or populations responded to hydroperiod cues but in the seemingly wrong direction (De Block and Stoks, 2005b). Although we did not find an adaptive response in development time to hydroperiod stress, both populations did exhibit plasticity in growth rate in the combined time stress treatment, and responded in the appropriate direction. Our evidence for life-history plasticity (and not local adaptation) is consistent with the hypothesis of a source–sink metapopulation system. Clearly, more empirical studies are needed before we can generalize about aquatic insect responses to hydroperiod. Furthermore, given the (apparent) importance of gene flow for the persistence of temporary habitat populations, understanding of metapopulation dynamics would benefit from more population genetics studies that quantify the exchange of individuals between habitat types.

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