*Biological Journal of the Linnean Society*, 2008, **95**, 495–504. With 5 figures

# Diet and a developmental time constraint alter life-history trade-offs in a caddis fly (Trichoptera: Limnephilidae)

JASON E. JANNOT[1,3]*, SCOTT A. WISSINGER[2,3] and JEFFREY R. LUCAS[1]

[1]*Department of Biological Sciences, Purdue University, West Lafayette, IN 47901, USA*
[2]*Biology Department, Allegheny College, Meadville, PA 16335, USA*
[3]*Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, CO 81224, USA*

*Received 5 November 2007; accepted for publication 18 January 2008*

Environmental factors influence variation in life histories by affecting growth, development, and reproduction. We conducted an experiment in outdoor mesocosms to examine how diet and a time constraint on juvenile development (pond-drying) influence life-history trade-offs (growth, development, adult body mass) in the caddis fly *Limnephilus externus* (Trichoptera: Limnephilidae). We predicted that: (1) diet supplementation would accelerate larval growth and development, and enhance survival to adulthood; (2) pond-drying would accelerate development and increase larval mortality; and (3) the relationship between adult mass and age at maturity would be negative. Diet supplementation did lead to larger adult mass under nondrying conditions, but did not significantly alter growth or development rates. Contrary to predictions, pond-drying reduced growth rates and delayed development. The slope (positive or negative) of the female mass–age at maturity relationship depended on interactions with diet or pond-drying, but the male mass–age relationship was negative and independent of treatment. Our results suggest that pond-drying can have negative effects on the future fitness of individuals by increasing the risk of desiccation-induced, pre-reproductive mortality and decreasing adult body size at maturity. These negative effects on life history cannot be overcome with additional nutritional resources in this species. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **95**, 495–504.

ADDITIONAL KEYWORDS: aquatic insect – desiccation – growth – habitat permanence – metamorphosis – reproduction – survival – plasticity.

## INTRODUCTION

Natural selection often operates on variation in life-history traits, including variation in development, growth, and reproduction (Roff, 1992; Stearns, 1992). One developmental event that leads to life-history variation is the timing of the transition from growth to reproduction, which typically occurs at a species-specific size (linear or mass), stage, or age. The timing of this transition is influenced by both external environmental factors (e.g. seasonal time constraints, temperature, predation; Wilbur & Collins, 1973; Thompson, 1975; Thompson, 1978; Bronson, 1979; Winemiller, 1989; Reznick, Bryga & Endler, 1990; Schoenly, Beaver & Heumier, 1991; Nylin & Gotthard, 1998; Benoit, Pepin & Brown, 2000; Lytle, 2001; Altwegg, 2002; De Block & Stoks, 2003) and internal developmental events (e.g. developmental thresholds, hormone regulation, circadian rhythms; Nijhout, 1975; Denver, 1997; Gotthard, Nylin & Wiklund, 2000; Day & Rowe, 2002; Donohue, 2002; Plaistow *et al.*, 2004). The timing of the transition determines adult size and age at maturity because a longer juvenile developmental period usually results in a larger size at maturity. Both size and age at maturity have important consequences for the lifetime reproductive success of individuals (Stearns, 1992; Roff, 2002).

*Corresponding author. Current address: BEES Section, Department of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA. E-mail: jjannot@ilstu.edu

A considerable body of life-history theory has been directed at predicting both the timing of the transition from growth to reproduction, and the trade-offs associated with shifts in that timing (Wilbur & Collins, 1973; Stearns & Koella, 1986; Werner, 1986; Ludwig & Rowe, 1990; Rowe & Ludwig, 1991; Abrams *et al.*, 1996; Hentschel, 1999). For example, environmental factors, such as food quantity/quality or developmental time constraints (e.g. seasonal constraints, habitat ephemerality), can alter the timing of the shift from growth to reproduction (Stearns & Koella, 1986; Ludwig & Rowe, 1990; Rowe & Ludwig, 1991; Abrams *et al.*, 1996; Day & Rowe, 2002). For aquatic organisms with complex life cycles that span aquatic and terrestrial habitats (e.g. aquatic insects, amphibians), time constraints associated with habitat-drying can significantly influence the timing of the growth–reproduction transition (Ludwig & Rowe, 1990; Rowe & Ludwig, 1991; Rudolf & Rödel, 2007). Both theoretical and empirical studies of developmental time constraints suggest that rapid development to avoid pre-reproductive mortality results in reduced adult body size (Newman, 1989; Ludwig & Rowe, 1990; Reques & Tejedo, 1997; Johansson & Rowe, 1999; Laurila & Kujasalo, 1999). Empirical studies of developmental time constraints typically report a positive correlation between size and age at maturity (i.e. organisms that extend growth and metamorphose at a later age are larger than those that mature early because of a time constraint) (Semlitsch & Wilbur, 1988; Newman, 1989; Ludwig & Rowe, 1990; Denver, Mirhadi & Phillips, 1998; Doughty & Roberts, 2003). The decreased size at metamorphosis that results from early maturation has important fitness costs in terms of adult survival, fecundity, and subsequent adult growth (Altwegg & Reyer, 2003).

By contrast, the effects of resource levels on the transition between growth and reproduction typically lead to a negative correlation between size and age at maturity (i.e. organisms with high quality/quantity of resources mature at a younger age and are larger than those with low quality/quantity of resources) (Leips & Travis, 1994; Morey & Reznick, 2004; Wissinger *et al.*, 2004). This negative relationship can arise either because of fluctuations in resources *per se* or as a result of density-dependent competition for resources (Travis, 1984; Scott, 1994; Brady & Griffiths, 2000; Morey & Reznick, 2004). Regardless, the effect of variation in per capita resource levels should lead to the opposite relationship between age and size at maturity than is observed for time-constrained development.

Although the effects of time constraints and resource levels on the relationship between age and size at maturity have been studied separately, few studies have addressed their interactive effects on age and size at metamorphosis (Johansson *et al.*, 2001; Morey & Reznick, 2004) despite the fact that variation in resource level and the impact of time constraints jointly influence most organisms with complex life cycles. The present study aimed to examine the interactive effects of time constraints and resource levels on size and age at maturity in the caddis fly *Limnephilus externus* Hagen (Trichoptera: Limnephilidae). Larvae of this species are detritivores that inhabit shallow permanent and semi-permanent ponds and wetlands where drying constrains development in some years (Berte & Pritchard, 1986; Pritchard & Berte, 1987; Wissinger, Brown & Jannot, 2003). Although larvae feed predominantly on vascular plant detritus, they frequently supplement their diet with benthic algae and invertebrate animal material depending on availability (S. A. Wissinger, unpublished data). Both algae and animal material have higher caloric and protein content than detritus (Bowen, Lutz & Ahlgren, 1995). The ponds at our study site are nutrient-poor (Wissinger & Whiteman, 1992), and previous studies suggest that the quality of food, rather than the quantity of detritus, is likely to limit growth rates (Wissinger *et al.*, 1996). Thus, depending on the habitat, larval development in this species is likely to be affected jointly by both variation in food resources and by drying time constraints. In this experimental study, we compared larval development and growth under permanent hydroperiods versus simulated drying in semi-natural conditions (outdoor mesocosms). We predicted that larvae should accelerate development to escape desiccation-induced mortality, thus maturing earlier and at smaller sizes than larvae in nondrying conditions. Simulated pond-drying should force rapid larval development and have serious fitness consequences, either directly by inducing pre-reproductive mortality, or indirectly by reducing adult body size. Caddis fly adult size can have a strong effect on female fecundity and male mating success (Honek, 1993; Andersson, 1994; Petersson, 1995; Hoffmann, 1998; Wissinger *et al.*, 2004; Jannot, Bruneau & Wissinger, 2007). We also manipulated larval diets by adding a high protein food supplement that has been shown to increase larval growth in a related species of caddis fly (Wissinger *et al.*, 2004). We predicted that individuals whose diet included this high-protein food supplement should grow faster and mature earlier than individuals fed ambient diets. We predicted that diet and pond-drying should interact such that a food supplement would allow individuals to shorten the larval growth period in the face of drying, but without a large reduction in adult body size, compared with time-constrained larvae exposed to ambient diets.

## MATERIAL AND METHODS

We conducted the experiment from 23 June to 23 August 2003 using 16 outdoor mesocosms (1.75-$m^2$ cattle tanks originally set up in 1999) at the Rocky Mountain Biological Laboratory (RMBL), Colorado, that were inoculated with substrate, detritus, invertebrates, and emergent vegetation from a nearby pond. Water in the mesocosms was from snow melt and rain. The mesocosms did not contain any vertebrate predators. Invertebrate predators of *L. externus* (e.g. beetles, hemipterans) were removed prior to the beginning of the experiment and no large predators of any type were observed during the experiment. Experimental larvae were obtained from the resident population in the mesocosms. We used this population of *L. externus* because the nearby source population went locally extinct during an early drying event in 2002. Both the mesocosms and the source pond from which this population was originally obtained in 1999 experience partial or complete drying most years. Thus, our experimental population, similar to many of the natural populations of this species, has a history of exposure to drying conditions (Berte & Pritchard, 1986; Wissinger *et al.*, 2003).

Prior to the experiment, all resident *L. externus* larvae were removed from each of the experimental mesocosms and aggregated into a single pool of experimental animals. We randomly assigned mesocosms to one of four replicated treatments (four treatments by four replicates/treatment = 16 mesocosms): drying hydroperiod + ambient diet (detritus only), permanent hydroperiod + ambient diet, drying hydroperiod + supplemented diet (detritus + supplement), or permanent hydroperiod + supplemented diet. Forty larvae were added to each mesocosm in proportion to the natural instar distributions at the time of set up (23 June: two second instars, 35 third instars, thee fourth instars; for sizes, see Supporting Information, Table S1). Mesocosm depths were equalized across all tanks on the first day of the experiment (Table S2). The mesocosm experiment ran for 25 days.

The dietary supplement of freeze-dried freshwater tubificid worms (Wardley's Tubifex fish food) has a comparable caloric and nutrient content to other invertebrates in caddis fly diets (Cummins & Klug, 1979; Wissinger *et al.*, 2004). Larvae rapidly found and aggressively competed for this dietary supplement (J. E. Jannot & S. A. Wissinger, pers. observ.); thus, we dispersed the supplement evenly around the mesocosm to reduce unnatural encounter rates among larvae. On days 5, 8, and 16, we added 4 g of diet supplement to the eight mesocosms assigned diet supplementation (approximately 22 mg dry mass of food per $cm^2$). This level of food supplementation is similar to that previously shown to result in increased larval growth rates in a related caddis fly species (Wissinger *et al.*, 2004).

To simulate drying, we reduced the total water depth by approximately 15 cm on days 6 and 18 in the eight drying treatments (Table S2). Observations on natural rates of pond-drying over multiple years at our study site indicate that our drying treatment was within the natural range of drying rates. Although our drying treatment approximated changes in water volume and temperature regime that occur as ponds dry in nature, it does not control for changes in solute concentration that would occur in naturally drying ponds (Juliano & Stoffregen, 1994).

Three times during the experiment (days 13, 18, and 23), we collected and counted the larvae and pupae from each mesocosm. No pupae were observed until day 18; thus, we did not miss the onset of metamorphosis. On each sampled date, we returned larvae to the mesocosms and retained pupae for rearing inside a field laboratory at the RMBL. To monitor emergence, each pupa was transferred to a round, plastic pupation chamber (area = 100.3 $cm^2$) with either 3 cm if water (permanent treatment) or 1 cm of water (drying treatment). Pupae were transferred to mesh-covered pupation chambers because mesocosms were open to the environment and, therefore, emerging winged adults would have been lost otherwise. Pupation chambers were moved to a covered outdoor field laboratory (Weatherport) where each mesh-covered chamber was exposed to natural air temperature fluctuations and monitored daily for the emerging adult.

To ensure that the number of adults collected from the experiment was maximized, we removed all remaining larvae from the cattle tanks on day 25 and placed them in separate open-top rectangular microcosms (bottom area = 0.05 $m^2$). We added detritus (ambient diet food) to all microcosms, and diet supplement to supplemented treatments every 2–3 days (*ad libitum*). We maintained water levels at 3 cm depth in the permanent treatments and at 1 cm depth in the drying treatments. We checked each rectangular microcosm daily for pupation and transferred pupae to pupation chambers. We checked pupae daily for emergence. Pupae cut themselves out of their cases and swam to the surface to eclose. Emerging pupae (i.e. pharate adults) were unable to climb out of the water to complete eclosion because the plastic pupation chamber did not provide a foothold for emergence. Therefore, these pupae were removed from the chamber, gently patted dry, and placed in a dry container with a mesh top. Pharate adults eclosed within 24 h (eight females, 15 males; fully eclosed adults: 74 females, 75 males). Adults were preserved in a solution of 75% EtOH + 5% glycerin, dried at 50 °C for

24 h, and then dissected into each body part [head, thorax, wings (fore and hind), abdomen, and legs], and each body part weighed separately to the nearest 0.01 mg (all wings weighed together; all legs weighed together). On 28 August 2003 (Julian day 239), the larval portion of the experiment was halted at which point all but 21 larvae from the drying-hydroperiod, ambient-diet treatment had pupated or died.

### Statistical analysis

For all analyses, we examined residual and normal quantile plots of the dependent variables to check for homogeneity of variances and normality. Analyses were carried out using means from each mesocosm. Initially, we placed all factors and interactions in each model and then excluded nonsignificant factors ($P > 0.05$) during subsequent runs of the model. All statistical analyses were conducted with SAS/STAT software, Version 9.1 (SAS Inc.). Females are distinctly larger than males in this species (Wissinger *et al.*, 2003); therefore, we analyzed the sexes separately.

We used factorial analysis of variance (ANOVA) to examine the treatment effects (diet, hydroperiod, diet × hydroperiod) on growth rate and survival to adulthood. Survival was calculated as the mean number of fully eclosed adults from each tank. Growth rate was calculated as: [$\log_{10}$(adult dry mass, mg) – $\log_{10}$(initial mean dry mass, mg)]/number of days from the beginning of the experiment to emergence. Initial dry mass was estimated using the masses of 29 larvae randomly chosen and preserved on the first day of the experiment (mean ± SE: 3.82 ± 0.50 mg). Average growth rate was calculated for each sex in each tank. The tank average was used in the analysis.

To examine differences in emergence rate (= number of individuals successfully emerging over time), we used repeated-measures ANOVA (SAS PROC mixed, first-order autoregressive model; random effect = tank-by-time nested within diet-by-hydroperiod) with cumulative percent emergence (arcsine transformed) as the dependent variable and time (Julian day), diet, and hydroperiod as independent variables. The larval portion of the experiment was halted on Julian day 239; therefore, the cumulative emergence data ends on this date.

We used factorial analysis of covariance (SAS PROC GLM) to determine whether mass at metamorphosis depended on time to pupation (number of days from beginning of the experiment to pupation), pupal days (number of days from pupation to emergence), hydroperiod, diet, and the interactions between these variables. We $\log_{10}$-transformed adult dry mass to normalize the data and homogenize variances and analyzed the sexes separately.

We monitored temperature in the mesocosms because shallower water could lead to greater average temperature and greater ranges in temperatures in drying relative to permanent hydroperiods. We used factorial ANOVA to examine whether temperature means [(daily maximum °C + daily minimum °C)/2 averaged over 3 days within tanks] and average temperature range (daily maximum °C – daily minimum °C averaged over 3 days within tanks) correlated with diet and hydroperiod treatments.

## RESULTS

### Survival, growth, and development

Survival to reproductive age (i.e. larvae + pupae survival) was significantly reduced by drying ($F_{1,13} = 12.55$, $P = 0.004$; Fig. 1), and there was a weak, but nonsignificant effect of diet on survival (diet: $F_{1,13} = 2.36$, $P = 0.15$). There was no significant diet × hydroperiod interaction effect on survival ($F_{1,12} = 0.04$, $P = 0.85$).

Drying reduced larval growth rates in both sexes (males: $F_{1,12} = 25.47$, $P = 0.0003$; females: $F_{1,12} = 15.57$, $P = 0.002$; Fig. 2). There was a weak but nonsignificant effect of diet on growth rate in both sexes (males: diet, $F_{1,12} = 1.17$, $P = 0.30$; diet × hydroperiod interaction, $F_{1,11} = 0.26$, $P = 0.62$; females: diet, $F_{1,12} = 0.40$, $P = 0.54$; diet × hydroperiod interaction, $F_{1,11} = 1.09$, $P = 0.32$).

Emergence rate was significantly delayed in drying relative to permanent treatments ($F_{1,13} = 6.14$, $P = 0.03$; Fig. 3). Diet had no effect on emergence rate ($F_{1,13} = 0.05$, $P = 0.83$). In permanent tanks, an average of 80% of the individuals emerged within a 15-day period (Julian days 210–225), irrespective of diet. By contrast, during this time period, only 20–30% of the individuals in the drying hydroperiod emerged (Fig. 3). By the end of the experiment

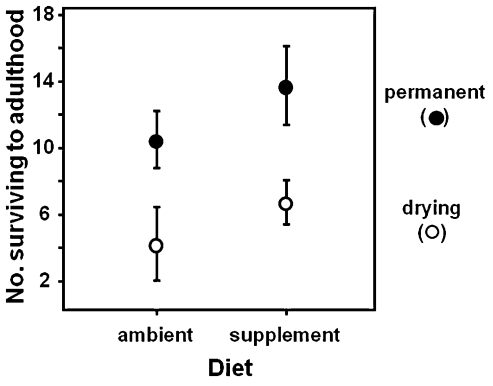


**Figure 1.** Mean ± SE number of larvae that survived to adulthood as a function of diet and hydroperiod (sexes combined) (dry ambient, $N = 3$; all others, $N = 4$).

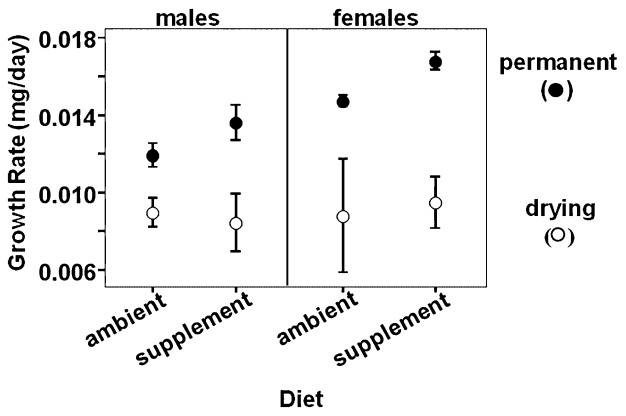


**Figure 2.** Mean ± SE growth rates as a function of diet and hydroperiod for males and females (dry ambient, $N = 3$; all others, $N = 4$).

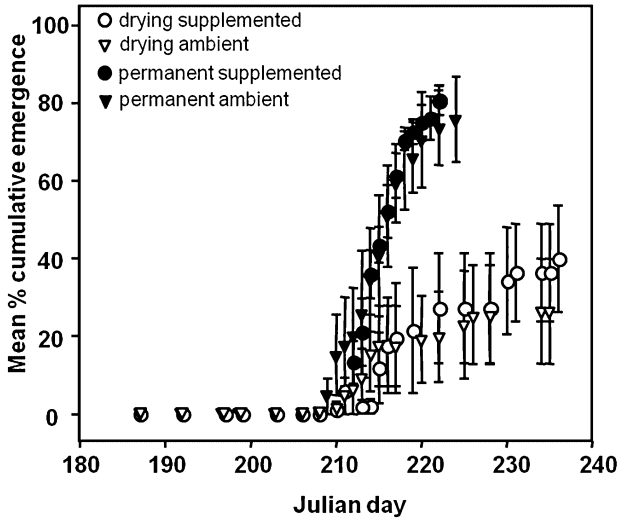


**Figure 3.** Mean ± SE percent cumulative emergence as a function of time, hydroperiod, and diet (drying ambient, $N = 3$; all others, $N = 4$).

(Julian day 239), approximately 60% of the drying hydroperiod individuals still had not emerged (Fig. 3).

Adult males that received a diet supplement during larval development were significantly heavier than those that did not ($F_{1,10} = 9.30$, $P = 0.01$; Fig. 4). Drying had no significant effect on male mass ($F_{1,10} = 0.62$, $P = 0.45$). Across all treatments, males exhibited a negative response between mass and age at maturity: males with a shorter time to pupation (less time as larvae) were significantly heavier than males that took a longer time to reach pupation ($F_{1,10} = 8.40$, $P = 0.02$; Fig. 4). The number of days as a pupa did not influence male mass at emergence ($F_{1,10} = 1.38$, $P = 0.27$).

Unlike males, female mass was influenced by three separate interactions. First, there was a diet by hydroperiod interaction ($F_{1,7} = 10.58$, $P = 0.01$; diet: $F_{1,7} = 16.30$, $P = 0.005$; hydroperiod: $F_{1,7} = 8.19$, $P = 0.02$). Females in the permanent-supplemented diet treatment were larger than females from the permanent-ambient diet treatment, but diet had no effect on female mass under drying conditions (Fig. 5). Second, the relationship between time to pupation and body mass differed for larvae in drying and permanent treatments ($F_{1,7} = 9.83$, $P = 0.02$; Fig. 5). There was a significant positive relationship between female mass and time to pupation among females in permanent conditions (Fig. 5, dashed line), but a non-significant relationship in drying treatments (Fig. 5). Finally, the relationship between time to pupation and body mass differed between females with and without a dietary supplement ($F_{1,7} = 24.46$, $P = 0.002$; Fig. 5). Females that pupated later were smaller than those that pupated earlier under ambient food conditions (Fig. 5, solid line), but there was no difference for females that were given a food supplement. The number of pupal days did not influence female mass at emergence ($F_{1,7} = 2.18$, $P = 0.18$).

The average daily temperature range was greater in drying (mean ± SE: 31.90 ± 2.22 °C, $N = 8$) than in permanent treatments (17.95 ± 2.32 °C, $N = 8$; $F_{1,15} = 17.62$, $P = 0.0008$). However, the daily average temperatures did not differ between drying and permanent treatments ($F_{1,15} = 0.52$, $P = 0.48$; drying ambient mean °C ± SE =18.89 ± 5.85; drying supplemented mean °C ± SE = 19.96 ± 4.13; permanent ambient mean °C ± SE = 18.61 ± 5.85; permanent supplemented mean °C ± SE = 21.31 ± 4.13).

## DISCUSSION

The present study was designed to test the interaction between pond-drying and larval diets on size and age at maturity in a caddis fly. Based on previous studies, we predicted that: (1) the threat of drying should accelerate the development of caddis fly larvae at a cost to adult body size; (2) diet would result in increased rates of growth and development; and (3) the cost of early metamorphosis-small body size imposed by drying conditions would be ameliorated by increasing the quality of larval diets (i.e. diet supplemented individuals exposed to drying would emerge relatively early with little or no penalty in terms of adult size).

### Larval diet and adult body size

In agreement with the above predictions, the adult mass of newly-metamorphosed caddis fly adults in treatments with a high-protein supplement were larger than those in ambient food treatment (Pritchard & Berte, 1987; Nylin & Gotthard, 1998; Wissinger

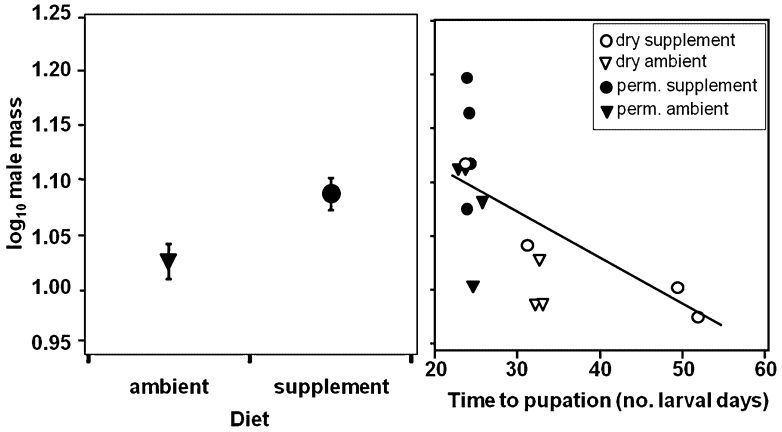


**Figure 4.** Male mass at metamorphosis ($\log_{10}$ mg) as a function of diet (each point = least-squares means ± SE; ambient, $N = 7$, supplemented, $N = 8$) and time to pupation [number of days; each point = 1 mesocosm; line represents all points: $\log_{10}$ mass = 1.21 – (0.005 × days)].

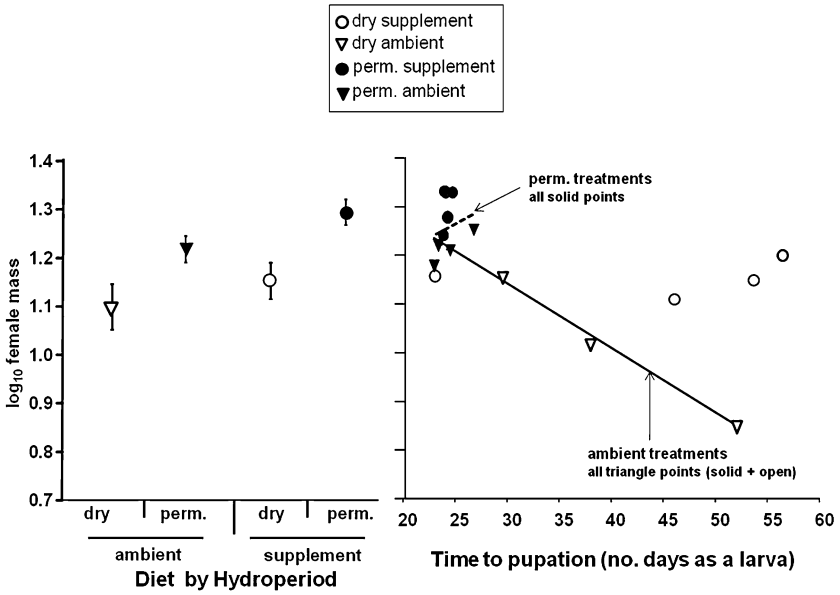


**Figure 5.** Female mass at metamorphosis ($\log_{10}$ mg) as a function of diet by hydroperiod (perm., permanent; each point = least-square means ± SE; drying ambient, $N = 3$, all other, $N = 4$) and time to pupation [dashed black line/all solid symbols = permanent treatment: $\log_{10}$ mass = 0.48 + (0.03 × days); solid black line/all triangle symbols = ambient diet: $\log_{10}$ mass = 1.55 – (0.01 × days)].

*et al.*, 2004). An increase in mass at metamorphosis should have a positive effect on fitness, given that adult female body size in caddisflies is positively correlated with realized fecundity and male body size is correlated with mating success (Honek, 1993; Andersson, 1994; Petersson, 1995; Hoffmann, 1998; Wissinger *et al.*, 2004; Jannot *et al.*, 2007). That a relatively small amount of high protein supplement can result in an increase in adult mass is consistent with the notion that the diet of detritivorous insects is nutritionally incomplete, and helps to explain why the larvae of many if not most aquatic detritivores supplement their diets with algae and/or animal material (Anderson, 1976; Mihuc, 1997; Wissinger *et al.*, 2004).

### GROWTH-DEVELOPMENT TRADE-OFFS IN DRYING PONDS

Despite an increase in adult mass in response to dietary supplementation, the predicted diet × time constraint interaction (Johansson *et al.*, 2001) was not observed (i.e. diet and pond-drying appear to

affect the mass–age at maturity relationship independently). Among males, the effect of diet on adult mass was independent of the effect of time to pupation on adult mass. Among females, supplementation of larval diets mitigated the negative effects of drying on female mass. However, the time to pupation was always longer under drying conditions compared with permanent conditions, irrespective of diet. For example, supplemented females exposed to drying conditions had to spend longer as a larva to attain an adult mass approximately similar to females in ambient diet permanent conditions (Fig. 5). These results differ from theoretical and empirical studies in which temporary habitat species accelerate development in the face of time constraints and typically pay a cost in terms of reduced adult size (Nylin & Gotthard, 1998).

There are at least two explanations for the disparity between our results and those previous studies. First, it is possible that *L. externus* is not developmentally flexible. This caddis fly mainly occurs in permanent habitats and long-duration temporary habitats where the selection pressures for rapid development are exerted only intermittently (Wissinger *et al.*, 2003). Although many amphibians exhibit flexibility in development rate, there is considerable variation in the extent of this variability among species depending on whether they typically inhabit relatively ephemeral or relatively permanent habitats (Merila, Laurila & Lindgren, 2004; Morey & Reznick, 2004).

An alternative explanation for the apparent absence of developmental flexibility in *Limnephilus* is that its responsiveness to the threat of drying is offset by deteriorating growing conditions associated with pond-drying. Most empirical studies in which species exhibit plasticity in development in response to the threat of drying have been conducted under laboratory conditions where other factors (temperature, ultraviolet radiation, etc.) were held constant (Newman, 1988; Newman, 1992; Reques & Tejedo, 1997; Denver *et al.*, 1998; Laurila & Kujasalo, 1999; Leips, McManus & Travis, 2000; Merila *et al.*, 2004; Shama & Robinson, 2006). By contrast, daily temperature fluctuations in our mesocosms exceeded 30 °C and were nearly two-fold greater than that observed in the permanent treatments. Fluctuations in our mesocosms were relatively small compared to fluctuations observed in ponds at our high elevation (+3000 m a.s.l.) study sites (Wissinger *et al.*, 1999). The conditions of clear water, intense solar radiation, and low humidity at our high elevation sites leads to rapid heating and evaporation of ponds during the day; and rapid cooling of air temperature at night contributes to decreased water temperatures overnight (Dillon, Frazier & Dudley, 2006). This combination of daytime heating and nighttime cooling leads to daily temperature cycles that become magnified in our shallow, drying ponds (Heath, 1975; Whiteman & Buschhaus, 2002). At low temperatures, such as those occurring at night at our sites, insects often decrease activity levels and foraging rates (Gotthard, 2001; De Block & Stoks, 2003; Van Doorslaer & Stoks, 2005). Modest increases in temperature can accelerate aquatic insect development (Ward & Stanford, 1982; Sweeney, 1984; Williams & Feltmate, 1992). At extremely high temperatures, metabolic rates increase, and digestion and growth efficiencies decrease (Gallepp, 1977; Iversen, 1979; Sweeney, 1984; Pritchard & Berte, 1987). Thus, it is possible that, at high elevations, suboptimal physiological temperatures both at night (too cool) and during the day (too warm) in drying habitats constrain the ability of caddisflies to increase their growth rates. Because growth is often coupled with development prior to metamorphosis (Robertson, 1963; Nijhout, 1975; Lounibos, 1979; Rowe & Ludwig, 1991; Lytle, 2001), a reduction in growth should increase the time to pupation.

This temperature–growth hypothesis is similar to the density effects observed in other insect (De Block & Stoks, 2005; Shama & Robinson, 2006) and amphibian (Brady & Griffiths, 2000) systems where deteriorating conditions during drying appear to decouple growth–development responses. These previous studies suggest that decreases in water volume were associated with decreases in growth rates, possibly because smaller volumes led to higher densities and increased competition for food (Brady & Griffiths, 2000; De Block & Stoks, 2005). Denver *et al.* (1998) also demonstrated that decreases in water volume resulted in decreased foraging activity of frogs. Similar density effects could be operating in our system; however, anecdotal evidence suggests that density effects might be less important than the temperature effects described above. Previous studies of this species provide little evidence for resource competition, even under densities higher than those in the present study (Wissinger *et al.*, 1996). In an experiment where a stream-dwelling caddis fly was exposed to decreasing water volumes, growth rates were similarly suppressed in drying versus permanent conditions even under very low intra-specific competition (two larvae per replicate) (Shama & Robinson, 2006). In summary, regardless of the underlying mechanisms, the results obtained in the present study suggest that physicochemical changes associated with pond-drying conditions in natural habitats might mask phenotypic plasticity in development responses. Future experimental studies that tease apart the effects of water temperature, water depth, and food levels as factors reducing growth rates in drying freshwater systems will be necessary to determine the degree to which developmental responses to

the threat of drying under laboratory conditions are realized under deteriorating conditions in the field.

## ACKNOWLEDGEMENTS

We would like to thank Carol Boggs, Richard Howard, Mark Jervis, Steven Juliano, Joel Trexler, and an anonymous reviewer for constructive suggestions that have improved earlier versions of this manuscript. J. E. Jannot would like to thank Steven Juliano for postdoctoral support during the completion of this manuscript. We thank the Rocky Mountain Biological Laboratory (RMBL) for access to field sites and laboratory space. Funding from Sigma Xi, the RMBL, and Purdue University supported J. E. Jannot. NSF DEB 0108931 provided financial support for S. A. Wissinger.

## REFERENCES

**Abrams PA, Leimar O, Nylin S, Wiklund C. 1996.** The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *American Naturalist* **147:** 381–395.

**Altwegg R. 2002.** Predator-induced life-history plasticity under time constraints in pool frogs. *Ecology* **83:** 2542–2551.

**Altwegg R, Reyer HU. 2003.** Patterns of natural selection on size at metamorphosis in water frogs. *Evolution* **57:** 872–882.

**Anderson NH. 1976.** Carnivory by an aquatic detritivore, *Clistoronia magnifica* (Trichoptera: Limnephilidae). *Ecology* **57:** 1081–1085.

**Andersson M. 1994.** *Sexual selection*. Princeton, NJ: Princeton University Press.

**Benoit HP, Pepin P, Brown JA. 2000.** Patterns of metamorphic age and length in marine fishes, from individuals to taxa. *Canadian Journal of Fisheries and Aquatic Sciences* **57:** 856–869.

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

**Bowen SH, Lutz EV, Ahlgren MO. 1995.** Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* **76:** 899–907.

**Brady LD, Griffiths RA. 2000.** Developmental responses to pond desiccation in tadpoles of the British anuran amphibians (*Bufo bufo, B. calamita* and *Rana temporaria*). *Journal of Zoology* **252:** 61–69.

**Bronson MT. 1979.** Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Ecology* **60:** 272–279.

**Cummins KW, Klug MJ. 1979.** Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* **10:** 147–172.

**Day T, Rowe L. 2002.** Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. *American Naturalist* **159:** 338–350.

**De Block M, Stoks R. 2003.** Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of Evolutionary Biology* **16:** 986–995.

**De Block M, Stoks R. 2005.** Pond drying and hatching date shape the tradeoff between age and size at emergence in a damselfly. *Oikos* **108:** 485–494.

**Denver RJ. 1997.** Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. *American Zoologist* **37:** 172–184.

**Denver RJ, Mirhadi N, Phillips M. 1998.** Adaptive plasticity in amphibian metamorphosis: response of *Scaphiopus hammondii* tadpoles to habitat desiccation. *Ecology* **79:** 1859–1872.

**Dillon ME, Frazier MR, Dudley R. 2006.** Into thin air: Physiology and evolution of alpine insects. *Integrative and Comparative Biology* **46:** 49–61.

**Donohue K. 2002.** Germination timing influences natural selection on life-history characters in Arabidopsis thaliana. *Ecology* **83:** 1006–1016.

**Doughty P, Roberts JD. 2003.** Plasticity in age and size at metamorphosis of *Crinia georgiana* tadpoles: responses to variation in food levels and deteriorating conditions during development. *Australian Journal of Zoology* **51:** 271–284.

**Gallepp GW. 1977.** Responses of caddisfly larvae (*Brachycentrus* sp.) to temperature, food availability, and current velocity. *American Midland Naturalist* **98:** 59–84.

**Gotthard K. 2001.** Growth strategies of ectothermic animals in temperate environments. In: Atkinson D, Thorndyke M, eds. *Environment and animal development: genes, life histories and plasticity*. Oxford: BIOS Scientific Publishers Ltd., 287–303.

**Gotthard K, Nylin S, Wiklund C. 2000.** Individual state controls temperature dependence in a butterfly (*Lasiommata maera*). *Proceedings of the Royal Society of London Series B, Biological Sciences* **267:** 589–593.

**Heath AG. 1975.** Behavioral thermoregulation in high altitude tiger salamanders, *Ambystoma tigrinum*. *Herpetologica* **31:** 84–93.

**Hentschel BT. 1999.** Complex life cycles in a variable environment: Predicting when the timing of metamorphosis shifts from resource dependent to developmentally fixed. *American Naturalist* **154:** 549–558.

**Hoffmann A. 1998.** Mating systems in Trichoptera: a little about the little known. In: Malicky H, Chantaramongkol P, eds. *Ninth International Symposium on Trichoptera*. Chiang Mai: Faculty of Science, Chiang Mai University, 133–139.

**Honek A. 1993.** Intraspecific variation in body size and fecundity in insects – a general relationship. *Oikos* **66:** 483–492.

**Iversen TM. 1979.** Laboratory energetics of larvae of *Sericostoma personatum* (Trichoptera). *Holarctic Ecology* **2:** 1–5.

**Jannot JE, Bruneau E, Wissinger SA. 2007.** Effects of larval energetic resources on life history and adult allocation patterns in a caddisfly (Trichoptera: Phyrganeidae). *Ecological Entomology* **32:** 376–383.

**Johansson F, Rowe L. 1999.** Life history and behavioral responses to time constraints in a damselfly. *Ecology* **80:** 1242–1252.

**Johansson F, Stoks R, Rowe L, De Block M. 2001.** Life history plasticity in a damselfly: effects of combined time and biotic constraints. *Ecology* **82:** 1857–1869.

**Juliano SA, Stoffregen TL. 1994.** Effects of habitat drying on size at and time to metamorphosis in the tree hole mosquito *Aedes triseriatus*. *Oecologia* **97:** 369–376.

**Laurila A, Kujasalo J. 1999.** Habitat duration, predation risk and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles. *Journal of Animal Ecology* **68:** 1123–1132.

**Leips J, McManus MG, Travis J. 2000.** Response of treefrog larvae to drying ponds: comparing temporary and permanent pond breeders. *Ecology* **81:** 2997–3008.

**Leips J, Travis J. 1994.** Metamorphic responses to changing food levels in 2 species of hylid frogs. *Ecology* **75:** 1345–1356.

**Lounibos LP. 1979.** Temporal and spatial distribution, growth, and predatory behavior of *Toxorhynchites brevipalpis* (Diptera: Culicidae) on the Kenya coast. *Journal of Animal Ecology* **48:** 213–236.

**Ludwig D, Rowe L. 1990.** Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* **135:** 686–707.

**Lytle DA. 2001.** Disturbance regimes and life-history evolution. *American Naturalist* **157:** 525–536.

**Merila J, Laurila A, Lindgren B. 2004.** Variation in the degree and costs of adaptive phenotypic plasticity among *Rana temporaria* populations. *Journal of Evolutionary Biology* **17:** 1132–1140.

**Mihuc TB. 1997.** The functional trophic role of lotic primary consumers: generalist versus specialist strategies. *Freshwater Biology* **37:** 455.

**Morey SR, Reznick DN. 2004.** The relationship between habitat permanence and larval development in California spadefoot toads: field and laboratory comparisons of developmental plasticity. *Oikos* **104:** 172–190.

**Newman RA. 1988.** Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. *Evolution* **42:** 774–783.

**Newman RA. 1989.** Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. *Ecology* **70:** 1775–1787.

**Newman RA. 1992.** Adaptive plasticity in amphibian metamorphosis. *Bioscience* **42:** 671–678.

**Nijhout HF. 1975.** A threshold size for metamorphosis in the tobacco hornworm, *Manduca sexta* (L.). *Biological Bulletin* **149:** 774–783.

**Nylin S, Gotthard K. 1998.** Plasticity in life-history traits. *Annual Review of Entomology* **43:** 63–83.

**Petersson E. 1995.** Male load-lifting capacity and mating success in the swarming caddis fly *Athripsodes cinereus*. *Physiological Entomology* **20:** 66–70.

**Plaistow SJ, Lapsley CT, Beckerman AP, Benton TG. 2004.** Age and size at maturity: sex, environmental variability and developmental thresholds. *Proceedings of the Royal Society of London Series B, Biological Sciences* **271:** 919–924.

**Pritchard G, Berte SB. 1987.** Growth and food choice by 2 species of Limnephlid caddis larvae given natural and artificial foods. *Freshwater Biology* **18:** 529–535.

**Reques R, Tejedo M. 1997.** Reaction norms for metamorphic traits in natterjack toads to larval density and pond duration. *Journal of Evolutionary Biology* **10:** 829–851.

**Reznick DA, Bryga H, Endler JA. 1990.** Experimentally induced life-history evolution in a natural population. *Nature* **346:** 357–359.

**Robertson FW. 1963.** The ecological genetics of growth in *Drosophila*. 6. The genetic correlation between the duration of the larval growth period and body size in relation to larval diet. *Genetical Research, Cambridge* **4:** 74–92.

**Roff D. 1992.** *The evolution of life histories*. New York, NY: Chapman and Hall.

**Roff DA. 2002.** *Life history evolution*. Sunderland, MA: Sinauer Associates.

**Rowe L, Ludwig D. 1991.** Size and timing of metamorphosis in complex life-cycles – time constraints and variation. *Ecology* **72:** 413–427.

**Rudolf V, Rödel M-O. 2007.** Phenotypic plasticity and optimal timing of metamorphosis under uncertain time constraints. *Evolutionary Ecology* **21:** 121–142.

**Schoenly K, Beaver RA, Heumier TA. 1991.** On the trophic relations of insects – a food-web approach. *American Naturalist* **137:** 597–638.

**Scott DE. 1994.** The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* **75:** 1383–1396.

**Semlitsch RD, Wilbur HM. 1988.** Effects of pond drying time on metamorphosis and survival in the salamander. *Copeia* **4:** 978.

**Shama LNS, Robinson CT. 2006.** Sex-specific life-history responses to seasonal time constraints in an alpine caddisfly. *Evolutionary Ecology Research* **8:** 169–180.

**Stearns S. 1992.** *The evolution of life histories*. Oxford: Oxford University Press.

**Stearns SC, Koella JC. 1986.** The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40:** 893–913.

**Sweeney BW. 1984.** Factors influencing life-history patterns of aquatic insects. In: Resh VH, Rosenberg DM, eds. *The ecology of aquatic insects*. New York, NY: Praeger, 56–100.

**Thompson DJ. 1975.** Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *Journal of Animal Ecology* **44:** 907–916.

**Thompson DJ. 1978.** Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, Ischnura elegans. *Journal of Animal Ecology* **47:** 757–767.

**Travis J. 1984.** Anuran size at metamorphosis: experimental test of a model based on intraspecific competition. *Ecology* **65:** 1155–1160.

**Van Doorslaer W, Stoks R. 2005.** Growth rate plasticity to temperature in two damselfly species differing in latitude:

contributions of behaviour and physiology. *Oikos* **111:** 599–605.

**Ward JV, Stanford JA. 1982.** Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27:** 97–117.

**Werner EE. 1986.** Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* **128:** 319–341.

**Whiteman HH, Buschhaus NL. 2002.** Behavioral thermoregulation in amphibian larvae. In: Ploger B, Yasukawa K, eds. *Exploring animal behavior in laboratory and field*. New York, NY: Academic Press.

**Wilbur HM, Collins JP. 1973.** Ecological aspects of amphibian metamorphosis. *Science* **182:** 1305–1314.

**Williams DD, Feltmate BW. 1992.** *Aquatic insects*. Wallingford: CAB International.

**Winemiller KO. 1989.** Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **81:** 225–241.

**Wissinger SA, Bohonak AJ, Whiteman HH, Brown WS. 1999.** Subalpine wetlands in Colorado: habitat permanence, salamander predation, and invertebrate communities. In: Batzer DP, Rader RB, Wissinger SA, eds. *Invertebrates in freshwater wetlands of North America: ecology and management*. New York, NY: John Wiley and Sons, Inc., 757–790.

**Wissinger SA, Brown WS, Jannot JE. 2003.** Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A.). *Freshwater Biology* **48:** 255–270.

**Wissinger SA, Sparks GB, Rouse GL, Brown WS, Steltzer H. 1996.** Intraguild predation and cannibalism among larvae of the detritivorous caddisflies in subalpine wetlands. *Ecology* **77:** 2421–2430.

**Wissinger SA, Steinmetz J, Alexander JS, Brown W. 2004.** Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. *Oecologia* **138:** 39–47.

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

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Mean ± SE dry mass, case length, and case diameter for instars 2–4.
**Table S2.** Mean ± SE tank depths over time for each hydroperiod treatment. For the drying tanks, depths are given for pre- and post-removal. n.a., not applicable. Water was not removed on the first day of the experiment (day 0).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.