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Effects of larval energetic resources on life history and adult allocation patterns in a caddisfly (Trichoptera: Phryganeidae)

JASON E. JANNOT[1,2,5], EVE BRUNEAU[2,4] and SCOTT A. WISSINGER[2,3] [1]Department of Biological Sciences, Purdue University, West Lafayette, U.S.A., [2]Rocky Mountain Biological Laboratory, Crested Butte, U.S.A., [3]Department of Biology, Allegheny College, Meadville, U.S.A., [4]Department of Environmental Science, Barnard College, Columbia University, New York, U.S.A., [5]BEES section, Department of Biological Sciences, Illinois State University, Normal, U.S.A.

Abstract. 1. How populations respond to environmental change depends, in part, on the connection between environmental variance during early life stages and its effect on subsequent life-history traits. For example, environmental variation during the larval stage can influence the life histories of organisms with complex life cycles by altering the amount of time spent in each stage of the life cycle as well as by altering allocation to life-history traits during metamorphosis.

2. The effects of larval energetic resources on developmental timing, adult mass, fecundity, mating success, and allocation to adult body structures (thorax, abdomen, wings) were examined in an aquatic caddisfly (*Agrypnia deflata* Milne, Trichoptera: Phryganeidae). Larval energetic reserves were manipulated by removing larval cases just prior to pupation. In the first experiment, cases of all individuals were removed just prior to pupation; experimental individuals were required to build a new case whereas control individuals were allowed to re-enter their case without building. In the second experiment, energy differences were maximised between the two treatments by supplementing the larval diet of the control group and removing cases and not supplementing the diet of the experimental group.

3. Male and female development time, adult mass, and female fecundity were not influenced by case removal or diet supplementation. In contrast, allocation to adult body parts indicated a trade-off between abdominal and thoracic mass among case-removal females, suggesting that, under larval resource stress, females adjust resource allocation during metamorphosis to alleviate potential negative impacts on clutch size. In addition, latency to copulation increased when cases were removed, indicating larval resource stress could influence male mating success.

4. This study suggests that, under larval energetic stress, the negative impacts on female reproduction might be mitigated by re-allocating resources during metamorphosis, whereas male allocation strategies might not be as flexible as female strategies.

Key words. Allocation, caddisfly, clutch size, complex life cycle, life-history, metamorphosis, Phryganeidae.

Introduction

Population regulation of organisms with complex life cycles (e.g. insects, marine invertebrates, amphibians, fishes) can result from processes operating during any life stage or combination of life stages (Wilbur, 1980). Unfortunately, most studies of

Correspondence: Jason E. Jannot, BEES section, Department of Biological Sciences, Illinois State University, Normal, IL 61790, U.S.A. E-mail: jjannot@ilstu.edu

species with complex life cycles usually only consider one stage of the life cycle (Pechenik *et al.*, 1998). Only recently have researchers examined the connection between early stage experiences and subsequent life-history outcomes (Boggs, 1997; Pechenik *et al.*, 1998; Blouin & Brown, 2000; Flanagin *et al.*, 2000; Peckarsky *et al.*, 2001; Searcy & Sponaugle, 2001; Phillips, 2002; De Block & Stoks, 2005; Vonesh, 2005). The potential for lasting effects of juvenile experience on subsequent life stages is being recognised as an important aspect of the evolutionary ecology of organisms with complex life cycles (Phillips, 2002).

Environmental variation during the juvenile stages can influence the realised life histories of organisms with complex life cycles by altering the amount of time spent in each stage of the life cycle as well as by altering allocation to life-history traits during metamorphosis (Wilbur, 1980; Nylin & Gotthard, 1998; Pechenik *et al.*, 1998; Vigliola & Meekan, 2002; Boggs, 2003; Gimenez, 2004). One of the most significant environmental conditions that most organisms must face at some time in their life is variation in food supply. Variation in food supply can lead to changes in both current and future resource allocation patterns. How organisms alter resource allocation in response to variation in energetic resources is not well understood (Boggs, 2003).

Holometabolous insects are a good model system for studying the influence of larval food variation on adult resource allocation because resources acquired during the larval stage are used to make adult body parts (e.g. flight muscles, wings, abdomens, eggs) (Boggs, 1981; Karlsson & Wickman, 1989; Gage, 1995; Karlsson, 1995; Stevens *et al.*, 1999, 2000). Some insects depend entirely on larval resources for adult structures (Boggs, 1981). In many insect species, adult body size decreases in response to larval food stress (Nylin & Gotthard, 1998; Boggs, 2003). Reduced size could significantly decrease the probability of survival, fecundity (Wickman & Karlsson, 1989; Ernsting *et al.*, 1993; McPeek & Peckarsky, 1998; Nylin & Gotthard, 1998; Taylor *et al.*, 1998; Wissinger *et al.*, 2004), and male mating success (Thornhill & Alcock, 1983; Gage, 1995; Choe & Crespi, 1997; Gage, 1998; Peckarsky *et al.*, 2002). Thus, current data suggest that larval conditions could significantly influence adult insect life history.

In two experiments on the aquatic caddisfly *Agrypnia deflata* Milne (Trichoptera: Phryganeidae), larval energetic resources were manipulated to determine the effect of larval conditions on developmental timing, adult mass, female fecundity, male mating success, and allocation to adult body structures (thorax, abdomen, wings). Larval energetic reserves were manipulated by removing larval cases just prior to pupation. *Agrypnia deflata* larvae construct cases from silk and plant materials (Wissinger *et al.*, 2004). Case construction is costly because it requires resource expenditure in the form of silk production (Stevens *et al.*, 1999, 2000). Therefore, case building should: (1) extend development time; (2) reduce adult mass, female fecundity, and male mating success; and (3) alter allocation patterns among adult body parts. In the first experiment (2001), final instar larvae were used to determine if costs associated with case removal influenced adult structures when all individuals were prevented from feeding. In the second experiment (2003), all animals were provided with an ambient diet (detritus) and given one of two treatments: case removal or diet supplementation (high-energy, animal-derived food).

Methods

Larvae and pupae of *A. deflata* develop exclusively in ponds with permanent hydroperiods (Wissinger *et al.*, 2004). Wissinger *et al.* (2004) provide a complete description of the life cycle of *A. deflata* at the study site [Mexican Cut Nature (MCN) Preserve, Gothic, Colorado, U.S.A.]. The diet of *A. deflata* at the MCN Preserve is unknown at this time; however, other caddisflies of the genus *Agrypnia* appear to be omnivores, becoming increasingly predatory in the final larval instars (Wiggins, 1998). The larvae spin a cylindrical case of silk with pieces of substrate and vegetation as protection. At the MCN Preserve, larval *A. deflata* have been observed to vacate their cases in response to antagonism by conspecifics and predators (the salamander *Ambystoma nigrinum*; J. E. Jannot, E. Bruneau & S. A. Wissinger, pers. obs.) as has been reported in other phryganeid caddisflies (Wiggins, 1998). Thus, case loss and reconstruction probably occurs naturally in the populations studied. At the end of the larval period, larvae burrow into the sediment and undergo pupation, which lasts approximately 2 weeks (Wissinger *et al.*, 2004). Adults emerge during early July; males emerge earlier than females (i.e. protandry) and males are smaller than females. Eggs are laid shortly after mating (late July). Larvae hatch during late summer, reach the third instar by the end of September, and then bury themselves in the sediment to overwinter (Wissinger *et al.*, 2004).

Experiment 2001: Agrypnia deflata *larvae reared individually*

In July 2001, 100 fifth (final) instar larvae were collected and each head capsule width (size) measured. Each larva was randomly assigned to one of two treatments: case removal or control. Each of the 50 case-removal individuals had their larval case removed and were placed in a 16 oz. plastic cup for 24 h that contained pond water and case-building material (mainly fresh and dead *Carex* and *Isoetes* plants; see Wissinger *et al.*, 2004). During this time, individuals built a new case. Case removal forced larvae to expend energy (in the form of silk) and induced a pre-metamorphic reduction in internal resources. Late in the final instar, many insects, including caddisflies, enter a pre-pupal stage characterised by a cessation of feeding (Wiggins, 1998). By removing cases during this pre-pupal period, internal resources should decrease because feeding has stopped for the remainder of the pupal period. Each of the 50 control individuals was allowed to re-enter their case immediately after removal; thus no case construction was necessary. Control individuals were placed in cups for 24 h as described for the treatment group above. Two control individuals built new cases after handling and were placed into the case removal group. Head capsule widths did not differ between the two groups (control mean $\pm$ 1 SD: 1.92 ± 0.10 mm, $n = 48$; case removal: 1.93 ± 0.10 mm, $n = 52$; two-tailed t-test assuming equal variance: $t = -0.19$, $P = 0.85$).

On the following day, all individuals were placed in individual rearing chambers in their native pond. Chambers were constructed from nylon window mesh (≈ 20 cm × 20 cm) rolled into a tube and held together by duct tape and cable ties. Each chamber was then attached to Styrofoam insulation and floated on the surface of the pond such that the top half of each chamber was above the water line to allow the terrestrial adult to emerge. Screen cages allowed water to flow through; however cages were well above the pond substrate and therefore larvae had no access to detrital food sources. Chambers were monitored every 2–3 days for emergence. Adults were collected and immediately preserved in 75% ethanol and 5% glycerin. Adults were dissected to obtain the following body parts: head (antennae, eyes, mouthparts), legs, thorax (exoskeleton + flight muscle mass), wings (fore and hind), and abdomen. Female abdomens were dissected to count eggs. All body parts were dried at 50 °C for 24 h and weighed to the nearest 0.01 mg.

Experiment 2003: Agrypnia deflata *larvae reared in groups*

In June 2003, an additional experiment was conducted on *A. deflata* from a second, nearby population by modifying the 2001 protocol to maximise the difference in larval resources levels between treatments. A complete set of controls could not be set-up for the experiment in 2003 (see below). Nonetheless, the 2003 experiment did provide valuable information supporting the 2001 experiment.

Twenty 0.25 m^2 cages were placed along the shore of the pond. Cage bottoms were open to the substrate and cage edges were sealed with clay. Each cage was cleaned of all large macroinvertebrates (beetles, caddisflies, Hemiptera) and stocked with 11 *A. deflata* larvae (10 fifth instar and one fourth instar; all chosen randomly) from a pool of 250 larvae collected from the pond. Instar proportions were stocked in the experiment to mimic natural density, age, and size structure. Larvae were counted 5 days after initial stocking and additional larvae were added when necessary to maintain a constant density (11 larvae per cage).

The 20 cages were assigned randomly to two treatments: case removal or diet supplementation. Initial larval size did not differ between treatments (mean head capsule width ± 1 SE: case-removal individuals = 1.91 mm ± 0.03; diet-supplemented individuals = 1.87 mm ± 0.03). Two grams of diet supplement (Wardley's Tubifex fish food: crude protein 50%; crude fat 5%) was added to the 10 diet supplement cages every 2–3 days. To monitor pupation and capture adults, all individuals were moved from the pond cages to microcosms (plastic box: 0.17 m^2 bottom area; one microcosm per cage = 20 microcosms) 15 days after initial set-up (8 and 9 July), which coincides with the normal pupation period in the pond (Wissinger *et al.*, 2004). Each microcosm was filled with 5 cm of detritus and approximately 5 cm of pond water.

On 10 July, the larvae in the diet-supplemented treatment were removed from their case and allowed to re-enter their case immediately after removal; however larvae in the case-removal treatment were removed from their case and required to build a new case. Thus, case-removal individuals incurred a resource reduction (i.e. case building) prior to metamorphosis. Each individual was placed in a separate 16 oz. plastic cup as described for the 2001 experiment. Diet-supplemented individuals were returned to their microcosm after 24 h. Case-removal larvae that had not rebuilt their cases within a week of removal were excluded from the experiment. Individuals that successfully rebuilt a new case (usually ≈ 24–48 h) were returned to their respective microcosm. Every other day pupae were removed from the microcosms and placed into individual pupation chambers with 5 cm water. Pupation chambers were checked daily for emergence.

To observe mate selection behaviour, 22 mating trials were conducted with 11 females from each treatment. During each trial one female was housed with two males, one from each treatment, in a 250-ml glass dish covered with mesh. Matings typically occurred in the late morning (10.00–12.00 hours), and trials were conducted inside near a window to provide natural light. Latency to copulation and length of copulation were recorded using a stopwatch. If copulation did not begin after 3 h, the mating trial was considered unsuccessful and stopped (12/22 trials). After the copulating pair de-coupled (1–3 h), the copulating male was preserved in 75% ethanol. Non-copulating males were kept alive for subsequent trials. The fertilised female was transferred to a 250-ml container with 10 cm water, a small piece of mesh for oviposition substrate, and a mesh cover. The number of oviposited eggs was counted under a dissecting microscope. Females were preserved in 75% ethanol after 48 h irrespective of oviposition status. All adults were collected, preserved, dissected (including eggs), dried, and weighed as described for the 2001 experiment (above).

Data and statistical analyses

In both years, time to maturity (number of days from experimental set-up to emergence), total adult body mass (sum of all body parts), head mass, leg mass (all legs combined), wing mass (all wings combined), abdominal mass, thoracic mass, and clutch size (egg number) were measured. For the mating trials (only conducted in 2003), female live mass (mass at the time of the trial) was used in the analysis; all other reported masses are dry masses.

For all analyses, residual and normal quantile plots of the dependent variables were inspected to check for homogeneity of variances and normality. The data were normalised and variances were equalised by $\log_{10}$ transforming total adult mass. Per cent abdominal mass (= abdominal mass/total mass), per cent thoracic mass (= thoracic mass/total mass), per cent wing mass (= wing mass/total mass) and per cent legs and head mass [= (leg mass + head mass)/total mass] were arcsine transformed. Each body part mass was converted to a percentage to control for differences in total adult mass among individuals. Leg and head masses were combined because these traits comprised <20% of the total adult mass. Egg counts were square-root transformed. All statistical analyses were conducted with SAS® statistical software (version 9.1 for Windows, 2002–2003).

In 2001, each individual was reared separately and therefore could be counted as an independent observation; thus MANOVA

(SAS® PROC GLM) was used to examine the effect of sex, treatment (case removal or control), and the sex-by-treatment interaction on time to maturity and total adult body mass. MANOVA was also used to examine how resource allocation to different adult body parts expressed as a percentage of total body mass changed as a function of sex, treatment, and the sex-by-treatment interaction. ANOVA (SAS® PROC GLM) was used to examine how the number of eggs produced by a female changed as a function of treatment, female mass, and the treatment-by-female mass interaction.

In 2003, individuals were reared in groups (cages); thus each sex was analysed separately to avoid pseudo-replication. For each sex, MANOVA (SAS® PROC GLM) was used to examine the effect of treatment (case removal or control) on time to maturity and total adult body mass. For each sex, MANOVA was used to examine how resource allocation to different adult body parts expressed as a percentage of total body mass changed as a function of treatment. ANOVA (SAS® PROC GLM) was used to examine how the number of eggs produced by a female changed as a function of treatment, female mass, and the treatment-by-female mass interaction. In each analysis, correct degrees of freedom were set by nesting cage within treatment in the MANOVA statement (e = option) or by nesting cage within treatment-by-female mass interaction in the ANOVA (TEST statement of PROC GLM).

Fisher's Exact Test was used to test for a treatment effect on the probability of mating or mating preference. ANOVA was used to examine the effect of female live mass, treatment, and male treatment on latency to mate and copulation duration.

Results

Adult body mass and time to maturity

Males and females differed in the adult mass–time to maturity relationship in 2001 (Tables 1 and 2). However, treatment (in both years) and the sex-by-treatment interaction (2001 only) did not influence the mass–time relationship (Tables 1 and 3).

Resource allocation

In 2001, allocation to adult body parts, expressed as a function of total adult mass, differed between the sexes and treatments (Table 4; Fig. 1). The treatment effect was driven largely by females, which shifted allocation from thoracic mass to abdominal mass under case removal compared with control conditions (Fig. 1). This trade-off is also expressed as a negative relationship between abdominal mass and thoracic mass (standardised correlation coefficients, Table 4). Males did not appear to shift allocation strategy as much as females when cases were removed and allocated more to thoracic mass and less to abdominal mass than females, contributing to the differences between sexes (Table 4; Fig. 1).

These results were supported in the 2003 experiment, where again, female abdominal and thoracic mass exhibited a negative correlation (standardised correlation coefficients, Table 5). Case-removal females shifted allocation from the thorax to the abdomen compared with supplemented females (Fig. 2). Males do not appear to shift allocation strategy under case removal or diet supplementation (Table 5; Fig. 2).

Female fecundity

In 2001, clutch size was positively correlated to female mass ($F_{1,22} = 14.20$, $P = 0.001$, $r^2 = 0.40$), but was not affected by treatment ($F_{1,22} = 0.45$, $P = 0.51$) or the female mass–treatment interaction ($F_{1,22} = 0.31$, $P = 0.58$). In 2003, female clutch size (oviposited + dissected) was not correlated with female mass ($F_{1,17} = 1.53$, $P = 0.23$), treatment ($F_{1,17} = 0.14$, $P = 0.71$), or the mass–treatment interaction ($F_{1,17} = 0.06$, $P = 0.81$).

Mating (2003 only)

Ten of 22 mating trials resulted in copulation; in four of the successful trials the female had her larval case removed. One

Table 1. MANOVA statistics for adult mass and time to maturity as a function of sex and treatment in the 2001 experiment.

					Standardised canonical coefficients	
Source	Pillai's trace	F	d.f.	P	Adult size	Time to maturity
Sex	0.15	3.72	2,41	0.03	0.92	1.02
Treatment	0.04	0.79	2,41	0.46	–0.71	0.45
Sex × Treatment	0.003	0.07	2,41	0.93	0.85	–0.27

Table 2. Adult mass (least-squared means) and time to maturity (least-squared means) and standard errors for females and males in 2001.

		±1 SE			
Sex	Adult mass (mg)	Upper	Lower	Time to maturity (days)	± 1 SE
Females	7.15	0.34	0.32	29.33	0.60
Males	7.87	0.41	0.39	30.78	0.67

Table 3. MANOVA statistics, conducted on females and males, separately, for adult mass and time to maturity as a function of treatment in the 2003 experiment.

						Standardised canonical coefficients	
Sex	Source	Pillai's trace	F	d.f.	P	Adult size	Time to maturity
Females	Treatment	0.03	0.30	2,17	0.74	0.78	–0.38
Males	Treatment	0.05	0.47	2,17	0.64	0.80	–0.25

Table 4. MANOVA statistics for resource allocation (mass of traits expressed as a percentage of body mass) as a function of sex and treatment in the 2001 experiment.

					Standardised canonical coefficients			
Source	Pillai's trace	F	d.f.	P	% abdomen	% thorax	% wing	% leg + head
Sex	0.51	9.78	4,38	<0.0001	1.07	–0.46	0.07	–0.31
Treatment	0.21	2.46	4,38	0.06	1.17	–0.49	0.17	–0.17
Sex × Treatment	0.12	1.31	4,38	0.29	1.01	–0.66	0.33	0.14

mating trial was dropped from the analysis because copulation did not occur until nearly the end of the 3-h waiting period (2 h 51 min; see Methods). All other successful trials took place within 30 min ($n = 9$). Neither male nor female treatment influenced the probability of mating or mating preference (Fisher exact test $P > 0.30$). For both sexes, the latency to copulate was longer for case-removal individuals than for diet-supplemented individuals (Table 6; Fig. 3). Female mass had no effect on latency to copulate (Table 6). Female mass, treatment, and copulating male treatment had no effect on copulation duration (female live mass: $F_{1,3} = 4.28$, $P = 0.13$; female treatment: $F_{1,3} = 2.06$, $P = 0.25$; male treatment: $F_{1,3} = 0.65$, $P = 0.48$).

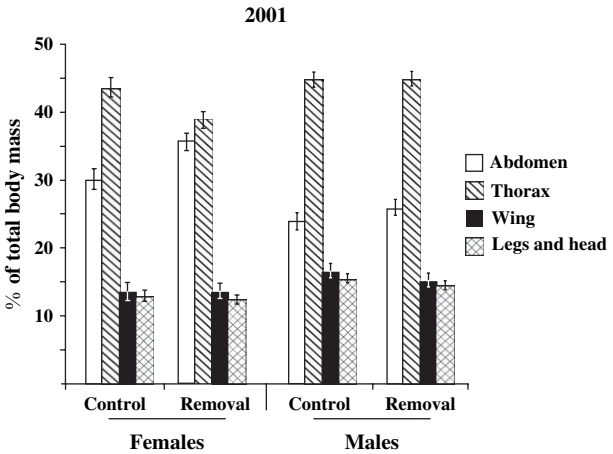

Fig. 1. Abdominal, thoracic, wing, and leg and head mass (least-squares means ± 1 SE), expressed as a percentage of total adult mass for males and females from each treatment (control and case removal) in the 2001 experiment.

Discussion

Adult mass and development time are probably not determined by resource levels late in the larval stage. Diet supplementation and case removal during the final larval stage, just prior to pupation, did not influence time to emergence and, surprisingly, did not directly influence adult mass or female fecundity. In contrast, allocation pathways involved in the trade-off between abdominal mass and thoracic mass might respond to changes in larval resource levels and remain plastic during pupation in females. Case removal appears to lengthen the latency to copulation relative to supplemented individuals.

Adult mass and time to maturity

In contrast to other case removal experiments on caddisflies (Stevens *et al.*, 1999, 2000), the adult mass–time to maturity relationship (i.e. emergence) in *A. deflata* is not influenced by case removal. Stevens *et al.* (1999) found that case removal reduced the amount of time spent in the pupal stage. By contrast, the data presented here imply that adult size and development time in *A. deflata* are probably not influenced solely by resource conditions during the final larval instar only. More likely, adult size and development time are a product of growth conditions experienced during the entire larval period. Growth rate throughout the entire juvenile period determines how quickly an individual achieves a minimum size necessary to successfully complete metamorphosis (Day & Rowe, 2002) and therefore determines the relationship between size and age at maturity. Individuals under high growth conditions achieve the minimum size early in development and have time to continue to grow beyond the minimum size. Individuals experiencing low growth conditions reach the size threshold later than high growth individuals and therefore must mature at the minimum size before the season ends. Not surprisingly, male and female *A. deflata* most likely

Table 5. MANOVA statistics, conducted on females and males, separately, for resource allocation (mass of traits expressed as a percentage of body mass) as a function of treatment in the 2003 experiment.

						Standardised canonical coefficients			
Sex	Source	Pillai's trace	*F*	d.f.	*P*	% abdomen	% thorax	% wing	% leg + head
Females	Treatment	0.51	3.82	4,15	0.02	17.71	–29.6	45.99	3.10
Males	Treatment	0.22	1.05	4,15	0.41	1.74	–34.5	37.49	–0.78

have different forms of this size–age relationship – males appear to emerge smaller and earlier than females.

Resource allocation

Similar to previous case removal studies (Stevens *et al.*, 1999, 2000), larval resource conditions did alter allocation patterns to female body parts. Female thoracic and abdominal mass showed consistent results across the two experiments: abdominal mass increased and thoracic mass decreased under case removal conditions. The net result in both experiments was that clutch size remained unaffected by case removal. One explanation for this pattern is that females adjusted allocation patterns by shifting resources away from the thorax and toward the abdomen during pupation to compensate for resource reduction and thereby mitigating any impact on clutch size. Both eggs and flight muscle (thorax) require a significant allocation of protein (Wheeler, 1996). Thus, when resources are limited, the development of eggs and flight muscle might compete for similar resource pools within an individual and produce a trade-off (Wheeler, 1996).

These results could reflect a localised effect of competition between proximate characters – in this case, thorax and abdomen. Such an effect would occur if resource pools were localised within an individual and thus only particular organs competed with each other (Nijhout & Emlen, 1998). Competition among growing body parts for a common resource pool within individuals has a theoretical basis (Nijhout & Wheeler, 1996) which stems back to Darwin (Darwin, 1859). This study adds to the small, but growing, set of empirical data demonstrating competition among body parts (Nijhout & Emlen, 1998; Stevens *et al.*, 1999, 2000; Consoli & Vinson, 2004; Moczek & Nijhout, 2004; Dominguez & Casares, 2005; Tomkins *et al.*, 2005). At this point, it is unclear if competition-by-proximity or a direct trade-off is responsible for the thorax–abdomen relationship in female *A. deflata*.

Irrespective of the proximate nature of the trade-off between female abdomen and thorax, such a trade-off suggests that the construction of the flight apparatus (i.e. flight muscles = thorax) competes with oogenesis for limited energy reserves (e.g. protein); a trade-off which is common in a number of insect species (Wheeler, 1996). Assuming that abdomen size is a reasonably good estimate of egg production in caddisflies, as it is in other insects (Wickman & Karlsson, 1989), then the data from the present study indicate a trade-off between flight and reproduction in female *A. deflata*. The effect of a reduction in thoracic mass on dispersal and flight depends on if the flight machinery correlates positively with the behavioural propensity to fly. Limited available data support this assumption in some insects (Fairbairn, 1987; Fairbairn & Desranleau, 1987) and correlative data in caddisflies also support this assumption (Hoffsten, 2004). For example, in caddisflies, species with larger wings and thoraxes occupied more sites than species with smaller thoraxes (Hoffsten, 2004), suggesting that the flight muscles found in the thorax of caddisflies can influence dispersal ability. Variation in dispersal traits such as thorax size depends on the costs and benefits of dispersal relative to other life-history functions, and these costs and benefits are context dependent; that is, they depend on the environmental conditions

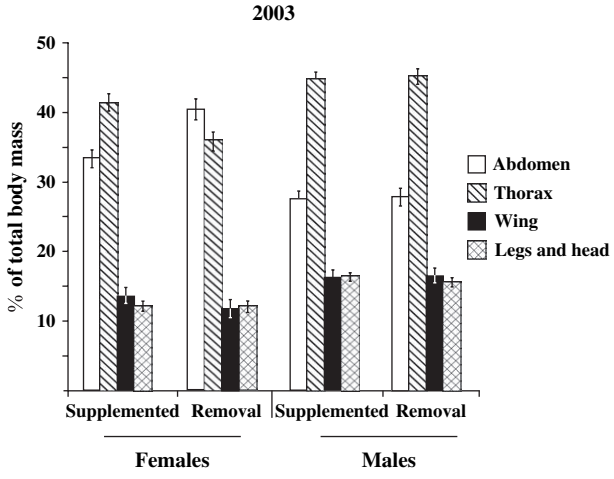

Fig. 2. Abdominal, thoracic, wing, and leg and head mass (least-squares means ± 1 SE), expressed as a percentage of total adult mass for males and females from each treatment (case removal and diet supplementation) in the 2003 experiment.

Table 6. ANOVA statistics for the latency to copulate (minutes) as a function of female live mass ($\log_{10}$), female treatment, and male treatment for the 2003 experiment.

Source	Mean (±1 SE)	d.f	*F*	*P*
Female mass		1,3	1.50	0.31
Female treatment		1,3	14.83	0.03
Removal	20.10 (2.61)			
Supplemented	7.37 (1.44)			
Male treatment		1,3	21.26	0.02
Removal	18.89 (1.85)			
Supplemented	8.58 (1.58)			

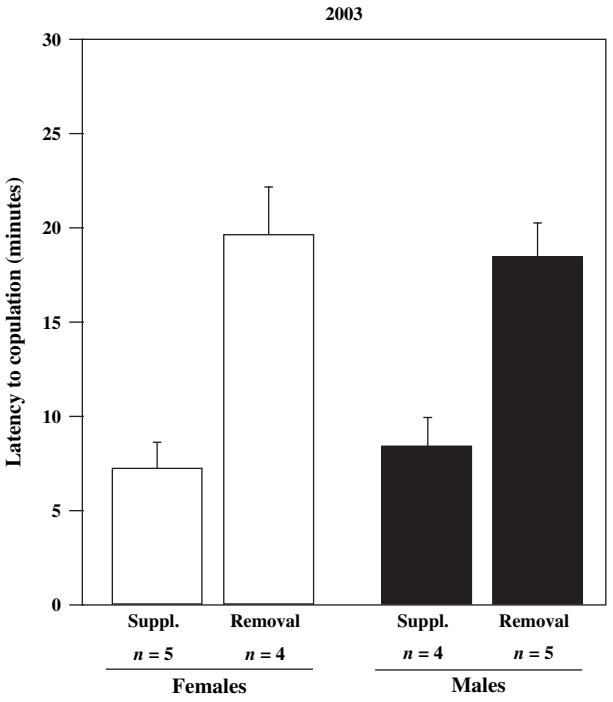

Fig. 3. The latency time until copulation in the 2003 experiment by treatment and sex (least-squares means ± 1 SE). Suppl., supplemented.

in which the flight architecture develops (Harrison, 1980; Bilton *et al.*, 2001). When energetic resources are scarce, female *A. deflata* at the MCN Preserve appear to place a premium on reproduction even if this comes at the cost of dispersal.

Mating

Female *A. deflata* probably mate shortly after emergence (Wissinger *et al.*, 2004). Latency to copulation was longer in case removal than diet-supplemented treatments. Immediately mating with the first mate encountered is optimal if there is a cost to searching for a new mate (Taylor *et al.*, 1998). Increasing the latency time to copulation could be disadvantageous if mate-searching costs are high. For example, increasing latency to first mating could increase the probability of dying prior to reproduction.

Surprisingly, male allocation strategies were not affected by larval energetic status. Why male allocation patterns were fixed as opposed to plastic is still unresolved. Although our knowledge of caddisfly mating behavior is limited (Hoffmann, 1998), at least in some species, larger male wings have been correlated with increased ability to carry females during copulation (Gullefors & Petersson, 1993; Petersson, 1995) and larger male accessory glands (Hoffmann, 1998), suggesting a link between male morphology and mating success. However, male *A. deflata* did not alter allocation strategies in this study, indicating either male morphology is not affected by larval conditions in this species, or the effects were masked by the experimental design (e.g. small sample size). These results suggest that allocation pathways of male *A. deflata* are significantly less plastic than females. Perhaps sexual selection on male flight architecture (i.e. wings, flight muscles) has selected against plasticity in these traits. Alternatively, condition-sensitive developmental mechanisms might be absent or not as sensitive in male *A. deflata* compared with females. Currently there is very limited information about the relationships between mating, male morphology, and male mating success in caddisflies. However, this study demonstrates that larval ecological conditions can produce effects on male mating behavior in *A. deflata*.

In conclusion, the results of the present study are consistent with other studies which demonstrate that competition among body parts can alter morphology and potentially constrain morphological evolution (Nijhout & Emlen, 1998; Stevens *et al.*, 1999, 2000; Consoli & Vinson, 2004; Moczek & Nijhout, 2004; Dominguez & Casares, 2005; Tomkins *et al.*, 2005). Resource conditions during the larval stage have the potential to influence allocation patterns during metamorphosis as well as mating success in *A. deflata*. Resource allocation during metamorphosis could provide individuals with a mechanism for responding to environmental change without sacrificing critical life-history traits.

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