Developmental trade-offs in caddis flies: increased investment in larval defence alters adult resource allocation

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Developmental trade-offs in resource allocation across life-history stages and between different body parts are predicted by life-history theories. However, there is very little empirical evidence that these occur. We investigated these trade-offs in caddis flies by experimentally manipulating larval case construction and thereby silk expenditure. Case building diverts protein resources away from larval stores, which are of major importance to adult development in species with little or no adult feeding. We induced fifth-instar *Odontocerum albicorne* to build new cases and examined the consequences for the morphology of the resulting adults. Rebuilding did not alter larval food consumption or the date of entering pupation, but shortened the duration of the pupal period. Adults that had been induced to expend more silk as larvae had lighter thoraces and smaller wings than the controls, but their abdomens did not differ significantly in mass or nitrogen content. These results suggest a trade-off between larval silk production and the pattern of resource allocation within the adult. The maintenance of the abdomen is likely to preserve reproductive potential, while the reduction in thoracic and wing investment will have negative consequences for flight and associated activities, and possibly for adult longevity.

Keywords: larval silk expenditure; adult morphology; resource allocation

1. INTRODUCTION

The concept of trade-offs between traits is a central component of life-history theory. Given that the resources available to individuals are generally finite, increased allocation of resources to one trait will be at the expense of those allocated to other competing traits (Stearns 1992). In addition to the trade-offs that occur during the lifetime of the individual, for example between activities related to survival and reproduction, trade-offs may occur during development in the allocation of resources between different body parts within the individual itself. The existence of such developmental trade-offs and the ways in which they are constrained by developmental mechanisms have important consequences for the evolution of morphology (Trumbo 1999). Furthermore, in species that go through a number of life-history stages, increased expenditure of finite resources during one life-history stage may have profound consequences for the pattern of allocation of resources to different body parts during subsequent stages.

There are a number of different approaches to the study of life-history trade-offs and experimental manipulations of the phenotype can give valuable insights into the nature of particular trade-offs and their functional significance (Partridge 1992; Roff 1992; Stearns 1992). While the concept that different parts of the organism may be in competition with each other for resources

during development is well-established, this has proved very difficult to demonstrate experimentally (Nijhout & Emlen 1998; Trumbo 1999). Hormonal manipulations that influence the growth trajectories of particular organs or organ systems, thereby altering the resources available to other developing body parts, have recently proved a very useful tool in studying developmental trade-offs and the underlying endocrine regulatory mechanisms (Ketterson & Nolan 1992; Sinervo 1993; Zera *et al.* 1998). However, the complexity of endocrine interactions and the existence of compensatory feedback loops can make interpretation of the results difficult (Zera *et al.* 1998).

A complementary approach is to alter the resources available to organisms prior to organ formation and examine the effect on subsequent development (Sinervo 1993). Holometabolous insects, where organ development takes place in a closed system (the pupa), provide an excellent opportunity for studying developmental trade-offs if the resources available to the larva at pupation can be manipulated. Furthermore, altering the demands of particular activities during the larval stage and examining the effects on the adult provides the additional opportunity of examining trade-offs in the allocation of resources between life-history stages.

Caddis flies are holometabolous insects in which there is a distinct larval stage in fresh water, followed by pupation and the emergence of a free-flying, largely non-feeding, adult reproductive form (Hickin 1967). Many species of caddis fly build portable cases of organic and/or inorganic material, held together with silk secreted by the

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larva. The main function of these cases is protection from predators (Otto & Svensson 1980), usually fish and aquatic invertebrates. Such case building requires a relatively high investment by the larva in silk production. Otto (1974) estimated that this amounted to *ca.* 12% of the total larval energy content in the case-building caddis *Potomophylax cingulatus* and silk synthesis costs have also been found to be significant in various other silk-producing taxa (Prestwich 1977; Griffiths 1980; Dudgeon 1987; Jakob 1991; Berenbaum *et al.* 1993).

In insects such as caddis flies, where adult feeding is minimal, the formation of the adult and its subsequent condition will depend on the amount of stored reserves acquired by the larva. Therefore, resources that are diverted into larval defence, such as case building, will not be available for use by the adult. Nitrogen is an important resource in this respect. It is a major constituent of silk (Craig 1997), it is absent from the adult diet even if some feeding does occur and muscle, eggs (vitellogenin) and spermatophores (lipoprotein) are all high in nitrogen (Boggs 1981). In holometabolous insects, allocation to either adult soma or reproduction occurs during pupation and is fixed. The amount of resources available for reproduction is approximately equivalent to the amount of resources allocated to the abdomen at eclosion (Boggs 1981), while the amount allocated to soma is equivalent to that allocated to the rest of the body, which is mainly the thoracic flight muscles (Karlsson & Wickman 1989).

To determine the effect of increased demands at the larval stage on the pattern of resource allocation in the developing adult, we experimentally manipulated the demands of case building in the mineral case-building caddis fly *Odontocerum albicorne* (Scopoli 1763). Since it is important to establish the extent to which the organism responds by any changes in resource acquisition as well as resource allocation, we monitored the food intake of the larvae from the manipulation until pupation. Resources allocated to defence were measured as the amount of silk contained within larval cases. The allocation of resources to the somatic and reproductive body components of the adults was examined in recently emerged individuals, in terms of both mass and nitrogen.

2. METHODS

Larval *O. albicorne* are found in rivers with gravel and sand substrates and are omnivorous scavengers (Elliott 1982). The case is composed of sand grains, and silk is applied as 'mortar' and braces between grains (Wallace *et al.* 1990), giving a very strong end-product (Otto & Svensson 1980). The larval growing period is relatively long. Eggs hatch in the autumn and adults emerge in late summer and live for only a short period of time.

Seventy-seven fifth-instar *O. albicorne* larvae were collected on 18 May and 2 June 1997 from a small burn in Milngavie, Glasgow and transported to the University Field Station, Rowardennan, Loch Lomond. Individual larvae were removed from their cases, blotted dry, weighed and randomly assigned to either the control or experimental group. There was no difference in the weights of larvae allocated to each group at the start of the experiment; however, as is typical of this species (Elliott 1982), male larvae were significantly smaller than females

(general linear model (GLM): sex $F_{1,43}=186.71$, $p < 0.001$ and group $F_{1,43}=1.25$, $p > 0.05$). Controls were placed back into their original cases, whereas experimentals were not, thus obliging them to rebuild. A few larvae in both the control and experimental groups died shortly after collection, escaped or did not complete development; these were excluded from further analysis and, thus, sample sizes vary accordingly. The proportion lost did not differ between control and experimental groups.

Animals were housed singly in small plastic pots (diameter 82 mm $\times$ height 57 mm) with gauze lids, which were placed in a small outdoor flume (270 cm $\times$ 126 cm $\times$ 32 cm). Sand from the collection site was added to each pot for use as building material and as a substrate to facilitate easy movement. Once all experimental animals had rebuilt a new case (three days), four frozen blood worms were provided as food for individuals of both groups. Every few days all the pots were checked to record how much food had been eaten. Uneaten food items were removed and fresh worms added.

Larvae were considered to be in pupation once they had closed off the opening of their case with a small stone. Once larvae entered pupation, they were removed from the flume and placed individually into numbered cells of plastic trays in another tank that had water flowing through it and were covered by a net to catch newly eclosed adults. Adults emerged overnight and were collected from the net at some stage the next day. They were then frozen and the remaining empty pupal cases were retained for further analysis.

Frozen adults were weighed and their right forewing length was measured using a microscope with an eyepiece micrometer. Heads, legs and wings were removed and the remaining thoraces–abdomens were dried to a constant weight at 60 °C, separated and then weighed. Nitrogen content, which is a good measure of protein content (Gnaiger & Bitterlich 1984), was measured by flash combustion of dried thoraces and abdomens in a Carlo Erba 1106 elemental analyser. All larval and pupal cases were freeze-dried, weighed and combusted using a bomb calorimeter. The remaining sand grains were then weighed and the silk content of the case calculated by subtraction. To comply with the requirements of the statistical tests used, all data were log transformed.

3. RESULTS

By the end of the experimental period, the cases of the control group were significantly heavier than the original cases removed from rebuilding larvae at the start of the experiment (case mass: control males 72.25 ± 5.92 mg, $n=12$; control females 109.00 ± 9.00 mg, $n=14$; experimental males 52.42 ± 3.31 mg, $n=19$; experimental females 91.21 ± 3.94 mg, $n=19$) (GLM: sex $F_{1,60}=72.09$, $p < 0.001$ and group $F_{1,60}=17.88$, $p < 0.001$; interaction not significant $F_{1,60}=0.05$, $p > 0.05$). This reflects the further building the larvae undertook as they grew, between the time of the start of the experiment and the time of entering pupation. Silk comprised a similar proportion of these cases (GLM on silk mass with case mass as covariate: covariate $F_{1,58}=10.73$, $p < 0.01$; sex $F_{1,58}=1.02$, $p > 0.05$ and group $F_{1,58}=0.94$, $p > 0.05$; interaction not significant $F_{1,58}=0.56$, $p > 0.05$). Control cases and rebuilt cases did not differ in mass at the point of adult emergence, which indicates larvae rebuild cases to a size consistent with their own body

Table 1. Mean case weights and silk contents of male and female pupal *O. albicorne* cases from a control group and a group that had to rebuild cases while fifth-instar larvae

(Figures in parentheses are standard errors.)

group	case mass (mg)	silk mass (mg)	% silk content
controls			
♂ (<i>n</i> = 12)	72.25 (5.92)	6.52 (1.09)	8.96 (1.26)
♀ (<i>n</i> = 14)	109.00 (5.02)	8.96 (0.71)	8.47 (0.82)
rebuilders			
♂ (<i>n</i> = 9)	75.22 (5.28)	5.40 (0.68)	7.17 (0.74)
♀ (<i>n</i> = 11)	125.91 (6.25)	7.07 (0.46)	5.70 (0.39)

size (table 1; GLM: sex $F_{1,42} = 58.05$, $p < 0.001$ and group $F_{1,42} = 3.00$, $p > 0.05$; interaction not significant $F_{1,42} = 1.47$, $p > 0.05$); however, the percentage, silk content was lower in the rebuilt cases in comparison (table 1; GLM on silk mass with case mass as covariate: covariate $F_{1,45} = 7.94$, $p < 0.01$; sex $F_{1,45} = 0.00$, $p > 0.05$ and group $F_{1,45} = 6.01$, $p < 0.05$; interaction not significant $F_{1,58} = 0.61$, $p > 0.05$). The total silk production by individuals in each group was taken as the silk content of the final case (controls) and the silk content of the rebuilt case plus that of the removed case (rebuilders). The total silk expenditure by larvae was significantly different between the treatment groups for both males and females, demonstrating the extent of the increased investment in silk required by the experimental group (it increased on average by 53% in males and 60% in females, figure 1; GLM: sex $F_{1,40} = 13.11$, $p < 0.001$ and group $F_{1,40} = 20.00$, $p < 0.001$; interaction $F_{1,40} = 1.00$, $p > 0.05$).

There was no change in resource acquisition by rebuilding larvae, as the mean amount of food eaten per day (table 2) did not differ between the treatment groups or sexes (GLM: sex $F_{1,57} = 0.10$, $p > 0.05$ and group $F_{1,57} = 0.21$, $p > 0.05$; interaction not significant $F_{1,57} = 0.31$, $p > 0.05$). There was also no difference between the groups or sexes in the mean date of pupation (table 2; GLM: sex $F_{1,57} = 2.17$, $p > 0.05$ and group $F_{1,57} = 1.00$, $p > 0.05$; interaction not significant $F_{1,57} = 0.06$, $p > 0.05$). The time spent in the pupal stage differed between males and females and was reduced in both to a similar extent in the experimental group (table 2; GLM: sex $F_{1,57} = 8.13$, $p < 0.01$ and group $F_{1,57} = 8.12$, $p < 0.01$; interaction not significant $F_{1,57} = 0.60$, $p > 0.05$).

The increased allocation of larval reserves to case building was associated with a change in adult morphology. In both control and rebuilding groups, females were larger than males. However, the forewings of adults in the rebuilding group were shorter in both sexes (figure 2*a,b*; GLM: sex $F_{1,39} = 215.87$, $p < 0.001$ and group $F_{1,39} = 4.39$, $p < 0.05$; interaction not significant $F_{1,39} = 0.30$, $p > 0.05$) and their thoraces lighter on average than those of the controls (figure 2*c,d*; GLM: sex $F_{1,40} = 105.64$, $p < 0.001$ and group $F_{1,40} = 7.33$, $p < 0.01$; interaction not significant $F_{1,40} = 0.27$, $p > 0.05$). The proportion of nitrogen in the thoracic tissue did not

Figure 1. Total silk produced by (a) male and (b) female *O. albicorne* larvae in a control group and a group forced to rebuild their fifth-instar larval cases. Silk was measured as the organic content of pupal cases (controls) and larval and rebuilt pupal cases (rebuilders). Data presented as means $\pm$ s.e. (sample sizes).

change (mean percentage nitrogen content of thorax: control males $11.10 \pm 0.26\%$, $n = 11$; control females $11.19 \pm 0.19\%$, $n = 14$; experimental males $11.48 \pm 0.14\%$, $n = 8$; experimental females $11.47 \pm 0.31\%$, $n = 11$) (GLM on thoracic nitrogen content with thorax mass as covariate: covariate $F_{1,39} = 146.27$, $p < 0.001$; sex $F_{1,39} = 5.64$, $p < 0.05$ and group $F_{1,39} = 0.40$, $p > 0.05$; interaction not significant $F_{1,39} = 1.81$, $p > 0.05$). Abdomens, on the other hand, did not differ in size between the groups (figure 2*e,f*; GLM: sex $F_{1,40} = 301.35$, $p < 0.001$ and group $F_{1,40} = 1.36$, $p > 0.05$; interaction not significant $F_{1,40} = 0.21$, $p > 0.05$). As with the thorax, the proportional nitrogen content of the abdominal tissue did not change (mean percentage nitrogen content of abdomen: control males $9.76 \pm 0.36\%$, $n = 11$; control females $9.04 \pm 0.19\%$, $n = 14$; experimental males $9.94 \pm 0.14\%$, $n = 8$; experimental females $9.39 \pm 0.31\%$, $n = 11$); (GLM on abdominal nitrogen content with abdomen mass as covariate: covariate $F_{1,39} = 333.19$, $p < 0.001$; sex $F_{1,39} = 2.31$, $p > 0.05$ and group $F_{1,39} = 0.27$, $p > 0.05$; interaction not significant $F_{1,39} = 0.00$, $p > 0.05$).

Table 2. Mean food intake, date of pupation and duration of pupal period of male and female *O. albicorne* larvae from a control group and a group that had to rebuild cases while fifth-instar larvae

(Dates are days after the start of the experiment. Figures in parentheses are standard errors.)

group	blood worms per day	pupation date	pupal duration
controls			
♂ (<i>n</i> = 15)	0.26 (0.03)	50.33 (2.76)	35.58 (0.74) ^a
♀ (<i>n</i> = 18)	0.36 (0.06)	47.17 (2.33)	38.81 (0.97) ^b
rebuilders			
♂ (<i>n</i> = 11)	0.33 (0.06)	53.09 (2.67)	33.88 (0.72) ^c
♀ (<i>n</i> = 11)	0.34 (0.06) ^d	48.43 (1.70)	35.55 (0.56)

^a *n* = 12; ^b *n* = 16; ^c *n* = 8; ^d *n* = 14.

4. DISCUSSION

The incorporation of silk into the larval case is vital for the defence of caddis fly larvae because silk allocation is positively correlated with larval security (Otto & Svensson 1980). Silk expenditure appears to be an important factor influencing life-history strategies in caddis flies. It has been suggested, for example, that increased investment in silk is responsible for the relatively smaller larval size at pupation of caddis species making relatively expensive mineral cases, compared to those species making cheaper organic cases (Otto 1982). The effect of intraspecific differences in larval silk expenditure has not hitherto been examined.

Rebuilt cases contained less silk at pupation than did the cases of control flies, indicating that case quality is reduced when cases are completely rebuilt in a matter of days, rather than over the course of the larval period. Despite this, overall silk expenditure was much greater in the experimental group. The consequent reduction in the size of the thorax and wings in the adults could have various potential consequences. Flight is the most energy-demanding activity performed by insects (Sartori *et al.* 1992). The thorax of holometabolous insects is mainly flight muscle (Petersson 1995) and a proportionally smaller thorax will sustain greater stresses during flight. Adult insects with a low flight-muscle ratio (thoracic mass/body mass) will have reduced flight ability (Marden 1989) and distance flown and manoeuvrability have been shown to be greater in Lepidoptera species with high flight-muscle ratios (Srygley & Kingsolver 1998). However, caddis flies are reluctant fliers and many species do not move far from the water body from which they emerged (Hickin 1967), so any effect of reduced thorax size and reduced muscle mass on flight performance may not be as important as other possible effects. Thoracic size has been found to be positively correlated with longevity in various Lepidopterans (Karlsson & Wickman 1989; Gage 1995). A reduction in longevity could have effects on realized fecundity, particularly in polygamous species. However, it may be that, for caddis flies that do not have a long life span and mate quite quickly after emergence (such as with *O. albicorne* used in this experiment), maintaining larval survival at the expense of adult life span may be more important. Other

Figure 2. (a,b) Wing length, (c,d) dry thorax mass and (e,f) dry abdomen mass of adult male and female *O. albicorne* from a control group and a group forced to rebuild their cases during the fifth larval instar. Data presented as means $\pm$ s.e. (sample sizes).

species of caddis flies from temporary waters emerge as adults in spring or early summer (Hickin 1967) and undergo ovarian diapause for several months before they are able to lay eggs (Novak & Sehnal 1963). Any decrease in adult longevity would be expected to have much more important fitness consequences in these species, as they may suffer pre-reproductive mortality if adult life span was reduced.

Our finding that increased larval silk production shortened the duration of the pupal stage in the experimental group is probably because the time taken for tissue reorganization is mass dependent. The resultant adult morphology, in which thorax size but not abdomen size was reduced, could be a consequence of developmental constraints. Developmental pathways may be spatially constrained, such that the resources released from the breakdown of larval structures enter into discrete resource

'pools', each of which are designated for the building of specific body parts only (Trumbo 1999). These resource pools may be composed of the breakdown products of anatomically close structures in the larva and they may only give rise to body parts in similar areas to those where they originated. In this study, silk glands will have been depleted after rebuilding the case; this may explain why the thoraces and wings were smaller, but not the abdomens in manipulated individuals, as silk glands also arise in the anterior part of the body. Alternatively, the constraint may be temporal, with resources liberated from the breakdown of larval structures only available to be incorporated into adult tissues that develop soon afterwards. Nijhout & Emlen (1998) found that removing the imaginal discs that give rise to the hindwings in *Precis coenia* larvae (Lepidoptera: Nymphalidae) caused an increase in resource allocation to the forewings, forelegs and thorax, but not the abdomen or head of the adults. This also would suggest the existence of compartmentalized pools of resources during pupation.

Alternatively, the maintenance of abdomen size may represent a strategic preservation of reproductive potential in the face of diminished resources with which to form the developing adult. Allocation patterns have been found to be adjustable within holometabolous species depending on the predicted adult needs. Gage (1995) found that larval males of the moth *Plodia interpunctella* could alter allocation to abdomens or thoraces depending on larval densities. At high larval densities—and therefore high adult densities—sperm competition is high and males allocate more to reproduction (testes size). At low densities, males allocate more to migratory and mate finding ability (i.e. the thorax) and, consequently, live for longer. Karlsson & Wickman (1989) found that directly developing individuals allocated less resources to their thoraces than hibernating (i.e. longer-lived) individuals in the Lepidopteran *Polygonia c-album*.

Differences between individuals in case-building requirements do occur in the wild, since case loss in larval caddis flies occurs under certain adverse conditions. For example, some species leave their cases as a result of strandings after spates (K. Hall and J. Lancaster, personal communication) or leave them during times of respiratory stress (Otto 1982) and build new cases. The timing of case loss in relation to the timing of pupation may be crucial. Our experiment was conducted in fifth-instar larvae, relatively close to pupation; thus, the time available to compensate for the increase cost was relatively short. Increased investment in larval defence comes at the expense of adult thoracic size and protein content, which presumably means reduced muscle mass. Abdomen size, however, is preserved. The results of this study provide an empirical demonstration of trade-offs that have long been speculated, but rarely demonstrated empirically (Trumbo 1999).

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