



The ontogenetic switch between odonate life history stages: effects on fitness when time and food are limited

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During the course of ontogeny, odonates switch from being aquatic larvae to being terrestrial adults. Ontogenetic niche shift theory proposes that such shifts are adaptive and have evolved to maximize a growth rate (size) to mortality rate ratio. Individuals should therefore switch from one niche to the other at an optimal size or state. Since the majority of odonates are seasonal breeders, the extent to which the switch is optimal will depend upon the time and the resources available during postembryonic development. We collected a cohort of larvae that varied in how close they were to eclosion and reared them on either a high-nutrition or a low-nutrition diet. We then determined the relative influence of both time and nutritional constraints on survival and development rate, as well as the body size, size-corrected flight muscle mass and fat reserves of individuals at eclosion. Damselflies in both high- and low-nutrition treatments responded to a short development period by developing faster and reducing their body size, but did not change their proportional investment in fat reserves and flight muscle. Reduced larval nutrition resulted in decreased body size, flight muscle mass and fat reserves at eclosion. However, it had no effect on survival to eclosion, or development rate. We discuss these results in terms of the influence that time and nutritional constraints have on odonate development patterns and fitness.

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Odonates shift between two discrete habitats during the course of their ontogeny (Corbert 1980): the egg and larval stages are aquatic, but reproduction occurs within a terrestrial environment. While odonate life history stages have previously been studied independently (Corbert 1980; Finke et al. 1997), few studies have examined the interaction between stages (but see Harvey & Corbert 1985; Finke 1992, 1994; Johansson & Rowe, in press). Such studies are important since fitness will ultimately depend upon selection that operates within and between all life history stages.

Ontogenetic niche shifts are believed to have evolved as an adaptive response to maximize growth rates while minimizing mortality risks (Werner & Gilliam 1984; Werner 1986). Different niches will vary in both the size-specific rates at which resources can be accumulated and the size-specific mortality risk involved in doing so (Werner & Gilliam 1984; Werner 1986). Consequently, ontogenetic niche shift theory predicts that selection will favour individuals that switch between habitats in a way that minimizes the mortality rate to growth rate ratio

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(Gilliam 1982). Under this paradigm, selection should produce an optimal body size or state at which individuals switch from one niche to the other (Rowe & Ludwig 1991). However, the fixation of any switch point becomes more complicated if the time available to reach the selected body size/state is constrained (see Ludwig & Rowe 1990; Rowe & Ludwig 1991; Werner & Anholt 1993; Crowley & Hopper 1994; Rowe et al. 1994), as is the case in seasonally breeding animals. Here the size, or 'state' of the individual at the switch point is no longer the only factor involved since the time at which a specific size or state is attained will also have important fitness consequences (Ludwig & Rowe 1990; Rowe & Ludwig 1991; Rowe et al. 1994; Johansson & Rowe, in press).

In many odonates the breeding season is restricted to just 1 or 2 months of the year (Corbert 1980). Natural selection alone may be responsible for the evolution of complex mechanisms that use photoperiod and temperature to regulate the development rate of larvae, such that emergence occurs at the correct time of year and is synchronized (see Corbert 1980). However, sexual selection may potentially hijack such mechanisms if they directly influence the relative fitness of the individual. Little is known about how the date of emergence relates to fitness in odonates. However, emergence periods,

particularly in temperate regions, are often characterized by sharp seasonal peaks (see Corbert 1980) and are sometimes skewed to the left (Tsubaki et al. 1997), suggesting that there is directional selection for early eclosion. Koenig & Albano (1987) found that lifetime reproductive success was correlated with early eclosion in *Plathemis lydia*; however, the reason for this was not determined. In species in which the breeding season is restricted and emergence is relatively synchronous, early eclosing individuals may have more time available to reproduce (Johansson & Rowe, in press). Moreover, individuals hatching at the beginning of the season will be amongst larvae of the same size and competitive ability for the whole developmental period, prior to reproducing the following season. In contrast, larvae hatching at the end of the season will have less time to develop and must compete with larger larvae that have been developing for longer. The presence of large larvae not only decreases the feeding rate (McPeck & Crowley 1987; Convey 1988) and the development rate of smaller larvae (Gribbin & Thompson 1990), it also increases the risk of cannibalism (Wissenger 1988; Johnson 1991; Anholt 1994; Ryazanova & Mazokhinporshnyakov 1995). Consequently, the reproductive value of offspring may decline as the season progresses, suggesting there may be strong selection for early eclosion and reproduction.

Small odonates may develop at a faster rate than larger individuals (Lutz 1968, 1974; Pickup & Thompson 1990; Johansson & Rowe, in press), leading to the suggestion that time-constrained larvae might develop faster by reducing their size (Murdoch 1971; Benke & Benke 1975; Koenig & Albano 1987; Pickup & Thompson 1990). Koenig & Albano (1987) first suggested that such a trade-off might explain the seasonal decline in body size commonly observed in many odonate populations (Penn 1951; Banks & Thompson 1985; Michiels & Dhondt 1989; Gribbin & Thompson 1990; Anholt 1994). Recent models (Ludwig & Rowe 1990; Rowe & Ludwig 1991; Leonardsson 1991; Houston et al. 1993; Werner & Anholt 1993; Abrams et al. 1996) and an experiment on the damselfly *Lestes congener* (Johansson & Rowe, in press) have shown that, aside from reducing body size, individuals may reduce development time by increasing foraging effort. Similarly, time-constrained individuals may switch earlier to a second habitat in which resources can be accumulated faster (Ludwig & Rowe 1990; Leonardsson 1991; Rowe & Ludwig 1991). Odonate larvae are typically inactive sit-and-wait predators (Corbert 1980; Johnson 1991), whereas immature adults are active flying predators. Consequently, we would predict that time-constrained individuals could accumulate resources faster as an adult. In species in which males are nonterritorial, body size is typically unrelated to fitness (Anholt et al. 1991) and can therefore be reduced to speed up development. However, in females and species in which males are territorial, a small body size will reduce not only development time, but also the capacity to accumulate flight muscle, fat reserves and eggs, and may therefore decrease fitness (see Anholt et al. 1991). An alternative may be to maintain body size and instead reduce the proportional investment in both flight muscle mass and fat reserves at eclosion.

Before any seasonally correlated change in odonate traits or behaviour can be seen as adaptive, it is first necessary to exclude alternative, nonadaptive explanations. As more eggs hatch, competition for food will increase and become asymmetric, and the time available to obtain resources will decrease. If resources become limited as the season progresses we might expect a seasonal decline in body size (Penn 1951; Banks & Thompson 1985; Michiels & Dhondt 1989) and an increase in foraging effort, independent of any effect of time constraints. Johansson & Rowe (in press) showed that in *L. congener* body size decreases and foraging effort increases over the season independent of any effect of larval nutrition. However, since nutrition effects were only controlled for, rather than being manipulated, it is not possible to gauge the relative influence that season and larval nutrition have in determining the size and the state at which individuals switched from one ontogenetic niche to the next. This is important if we are to understand both the seasonal patterns that we observe in the field and the adaptive significance of odonate ontogenetic niche shifts.

We examined the switch between aquatic larva and terrestrial adult in the territorial damselfly *Calopteryx splendens xanthostoma*. Male reproductive success depends upon fat reserves which are positively correlated with body size (Plaistow & Siva-Jothy 1996). Consequently, there is likely to be an advantage for large males in this species. We therefore predicted that all individuals should eclose with reduced flight muscle mass and fat reserves compared with those of mature adults. Moreover, we predicted that body size, the proportional investment in flight muscle fat reserves and ultimately development time should decline as the season progresses and individuals become increasingly time constrained. We used both field observations and a laboratory manipulation of larval nutrition to separate the effects of season and larval nutrition on the traits measured.

METHODS

Study Species

Calopteryx s. xanthostoma is part of the *Calopteryx splendens* species complex, which is common throughout Europe. In *C. s. xanthostoma* eggs are laid into the stems of the freshwater angiosperm *Ranunculus penicillatus* between the end of June and the middle of August. Egg development takes ca. 14–18 days (Siva-Jothy et al. 1995). Larvae overwinter within the final three instars and eclose as 'teneral' adults the following summer. Emergence is fairly synchronous, with the majority of individuals eclosing within 4 weeks of the beginning of the season (S. Plaistow, unpublished data). The immature stage lasts ca. 2 weeks, during which time immature adults feed away from the breeding sites. At the end of the immature stage, males arrive at the breeding sites and try to defend patches of *R. penicillatus*, the limited resource that females use as an oviposition substrate (Plaistow 1997b).

Field Observations

Seasonal change in body size

In 1995 we caught, individually marked (with enamel numbers on their wings), and measured males between the first (24 June 1995) and the 58th day (21 August 1995) of the reproductive season. To determine whether male body size declined throughout the season, we recorded the day on which the male was first seen. We measured size as forewing length (± 0.01 mm), using digital callipers (Mitutoyo 600-880 TM).

Flight muscle mass and fat reserves

Immature and adult males were collected every few days from a site on the River Vidourle in southern France (43°52'N, 04°03'E). All samples were collected over the same period, between 15 July and 9 August 1994. Since teneral males were rarely sighted in the field, we collected only recently eclosed individuals (i.e. with very pale wing spot pigmentation) to obtain a measure of immature male flight muscle mass and fat reserves as close to eclosion as possible. Males were killed by chilling followed by decapitation. The methods used to measure the flight muscle mass (mg) and the fat reserves (mg) of immature and adult males were the same as those in [Plaistow & Siva-Jothy \(1996\)](#). However, the values of flight muscle mass (mg) and fat reserves (mg) were not corrected for size for the comparison since the relationship between 'dry fatless mass' (the measure of size used) and flight muscle mass and fat reserves differs for adult and immature males (see [Marden 1989](#)). We did not limit our collection to preterritorial males ([Plaistow 1997a](#)). As a result, the mean measure of adult male fat content will be an underestimate because some males will have used up a proportion of their stored fat reserves in acquiring a territory (see [Plaistow & Siva-Jothy 1996](#)). Consequently, the mean proportion of fat in immature males will be a conservative estimate.

Laboratory Larval Nutrition Experiment

We collected larvae of the subspecies *C. s. xanthostoma* from the same site on the river Vidourle on 21 September 1995, and 40 larvae of the subspecies *C. s. splendens* from a site in Derbyshire (52°51'N, 1°28'E) on 6 October 1995. All larvae were fed chironomid, *Chironomus plumosus*, larvae ad libitum, until the beginning of the experiment. On 8 October 1995, individual larvae were isolated in plastic pots (250 ml) with a fine, water-permeable mesh on the back and the front. We sorted the larvae into pairs ($N=35$) of the same size and subspecies. Food manipulations commenced on 10 October 1995. One larva from each pair was placed in a 'high'-nutrition treatment and the other in a 'low'-nutrition treatment. Both treatments were housed in the same flowing water system, maintained with natural fluctuation in both daylight and temperature. In the high-nutrition treatment larvae were given chironomids ad libitum every 48 h. In the low-nutrition treatment they were given chironomids ad libitum for 48 h in every 96-h period. Therefore

individuals in the high-nutrition treatment encountered food at about twice the rate of those in the low-nutrition treatment. In both treatments, uneaten chironomids and frass were removed and discarded every 48 h. We also checked the larvae for the presence of exuviae every 48 h. If present, the date of the moult was recorded and the exuvium removed. As final-instar larvae approached eclosion, we placed a mesh cage, 25 cm high, over the pot to isolate newly eclosed teneral adults. We checked final-instar larvae twice a day to determine the date and time of eclosion.

Date of F-2 moult

Since we collected larvae from the field, we could not determine date of hatching or total development time of all individuals. As an alternative, we used the date of the F-2 moult (the date of moult into the prepupal instar) as a measure of time of season.

Survival to eclosion

We scored individuals as either 'survivors' or 'non-survivors'. Survivors included all individuals that eclosed into a teneral adult and would have been capable of flight once the exoskeleton had hardened.

Body size, flight muscle mass and fat reserves at eclosion

Males were killed by chilling followed by decapitation. Body size at eclosion was defined as an individual's dry fatless body mass (see [Plaistow & Siva-Jothy 1996](#)). Flight muscle weight and fat content were measured as in [Plaistow & Siva-Jothy \(1996\)](#). Since fat reserves and flight muscle mass increase with body size (see [Marden & Rollins 1994](#)), we corrected all measures of flight muscle mass (mg) and fat reserves (mg) for size. They are expressed as residuals from a regression of the trait over dry fatless body mass.

Development rate

Development rate was defined as the length of time (days) between moulting into the F-2 larval instar and eclosing as an adult. Individuals that had already passed into the F-2 moult at the time of collection were omitted from analysis.

Statistical Analysis

To test deviations from normality, we used the Kolmogorov-Smirnov (Liliefors) test and to test homogeneity of variance we used F_{\max} tests ([Sokal & Rohlf 1995](#)). In cases where data deviated from normality and would not fit a normal distribution after transformation, non-parametric statistics were used. In all cases the tests were two tailed and, where multiple tests were necessary, we used a Bonferroni correction to eliminate the possibility of type 1 statistical errors ([Sokal & Rohlf 1995](#)). All statistical analyses were carried out using SYSTAT ([Wilkinson 1988](#)).

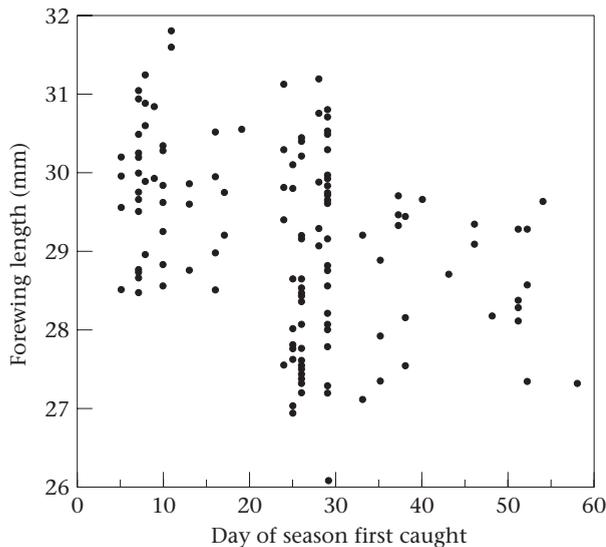


Figure 1. The relationship between the size (forewing length) of field-caught males and season. Day 1 of the season was 24 June 1995, day 58 was 21 August 1995.

RESULTS

Field Observations

Seasonal change in body size

Male size (forewing length) declined progressively throughout the field season (Spearman's rank order correlation: $r_s = -0.332$, $N=135$, $P < 0.0001$; Fig. 1).

Flight muscle mass and fat reserves

The flight muscle mass of immature males caught soon after eclosion was significantly lower (63.2%) than that of adult males (unpaired t test: $t_{88} = 12.273$, $P < 0.0001$; Fig. 2a). Similarly, the fat content of young immature males was significantly lower (49.6%) than that of adult males (Mann-Whitney U test: $Z = -3.786$, $N_1 = 62$, $N_2 = 26$, $P = 0.0002$; Fig. 2b).

Laboratory Larval Nutrition Experiment

Reduced sample sizes prevented a fully factorial analysis of the results with larval nutrition treatment, subspecies and sex as factors. Of the 35 individuals that eclosed successfully 16 were male and 19 were female. Unpaired t tests revealed that sex had no influence on the variables measured in the experiment (Table 1). The data for males and females were therefore pooled for all subsequent analysis.

Date of F-2 moult

The frequency distribution of the dates that individuals moulted into the F-2 larval instar (starting with 11 October 1996 as day 1) deviated significantly from normality (Kolmogorov-Smirnov (Liliefors) test: $N=26$, $P=0.024$). Consequently a log transformation was required to normalize the data (Kolmogorov-Smirnov (Liliefors) test: $N=26$, $P=0.319$). There was no effect of

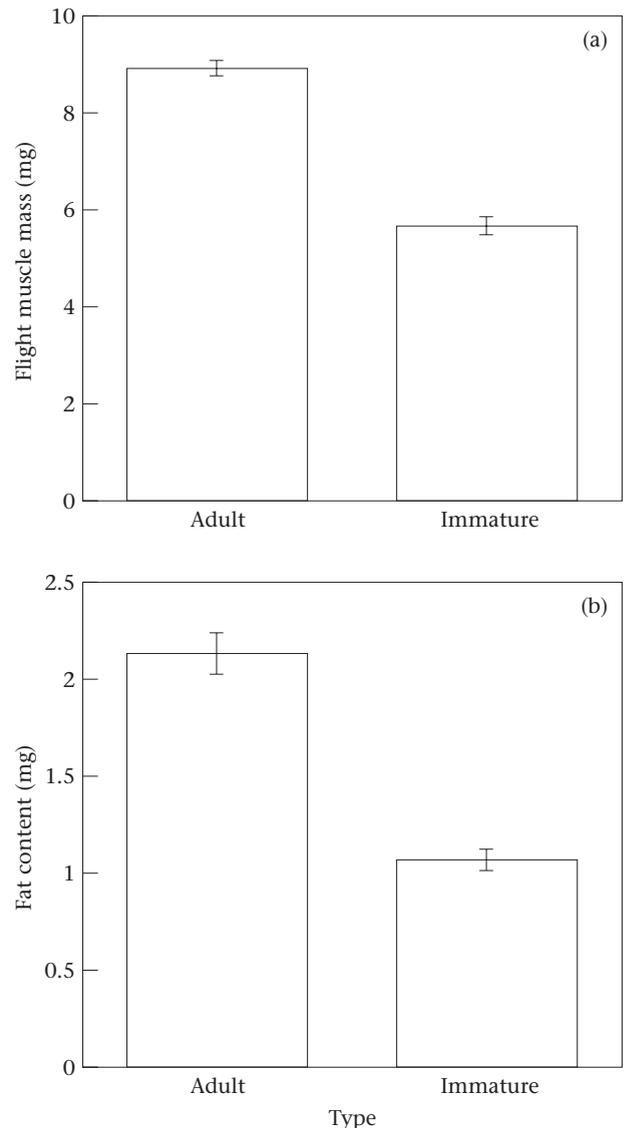


Figure 2. (a) Flight muscle mass (mg), and (b) fat content (mg) of adult and immature male *C. s. xanthostoma* collected from the River Vidourle in southern France. All samples were collected between 15 July and 9 August 1994.

nutrition treatment on the date of moult into the F-2 instar (two-way ANOVA: $F_{1,21} = 0.83$, $P = 0.372$); however, there was an effect of subspecies: larvae of *C. s. splendens* typically moulted into the F-2 instar earlier than *C. s. xanthostoma* larvae (two-way ANOVA: $F_{1,21} = 5.44$, $P = 0.030$). However, the interaction term between subspecies and larval nutrition treatment was not significant (two-way ANOVA: $F_{1,21} = 0.05$, $P = 0.942$) hence data for the two subspecies were pooled for all further analyses.

Survival to eclosion

There was no difference in survivorship to eclosion between larvae in the high-nutrition treatment and larvae in the low-nutrition treatment (chi-square test: $\chi^2_1 = 0.238$, NS).

Table 1. A comparison of males and females reared in the larval nutrition experiment

Variable	Male	Female	P
Dry fatless body mass (mg)	18.130±0.960 (14)	17.579±0.790 (18)	0.659
Size-corrected flight muscle weight*	0.141±1.780 (14)	-0.016±0.180 (18)	0.539
Size-corrected fat reserves*	0.276±0.470 (14)	-0.228±0.410 (17)	0.420
Date of F-2 moult (log)†	0.525±0.058 (13)	0.479±0.079 (11)	0.635
Development time (days)	195.077±9.869 (13)	196.091±9.859 (11)	0.943

Values are $\bar{X} \pm SE$ (N).

*Residuals from a regression of the trait over dry fatless mass.

†Day 1 = 11 October 1996.

Body size, flight muscle mass and fat reserves at eclosion

The total flight muscle mass (mg) of adults eclosing from both nutrition treatments was positively correlated with their size (dry fatless mass) in *C. s. xanthostoma* (linear regression: $r^2=0.803$, $F_{1,9}=36.780$, $P=0.0002$) and *C. s. splendens* (linear regression: $r^2=0.837$, $F_{1,22}=112.720$, $P<0.0001$). A similar result was found for fat content (mg) in *C. s. xanthostoma* (linear regression: $r^2=0.88$, $F_{1,9}=73.711$, $P<0.0001$) and *C. s. splendens* (linear regression: $r^2=0.414$, $F_{1,22}=15.542$, $P=0.0002$). There was no difference in the homogeneity of slopes between subspecies for either the relationship between flight muscle mass (mg) and dry fatless mass (ANCOVA: dry fatless mass by subspecies interaction: $F_{1,31}=0.137$, $P=0.714$), or between fat content (mg) and dry fatless mass (ANCOVA: dry fatless mass by subspecies interaction: $F_{1,30}=1.931$, $P=0.175$). Consequently the data for the two subspecies were pooled. In all further analyses an individual's flight muscle mass and fat reserves are expressed as the residuals from the pooled relationships for all individuals independent of sex and subspecies (linear regression: flight muscle mass: $r^2=0.819$, $F_{1,33}=149.003$, $P<0.0001$; fat reserves: $r^2=0.637$, $F_{1,33}=57.805$, $P<0.0001$).

Individuals that moulted into the F-2 instar later in the season eclosed with a significantly reduced dry fatless mass, that is, a smaller body size (ANCOVA: date of F-2 moult (log): $F_{1,19}=7.503$, $P=0.013$; Fig. 3). The relationship between dry fatless mass and the date of F-2 moult (log) was the same for individuals eclosing from both the high- and the low-nutrition treatments (ANCOVA: nutrition treatment by date of F-2 moult (log) interaction: $F_{1,18}=3.505$, $P=0.078$; Fig. 3). There was no significant relationship between date of moult into the F-2 instar and either the size-corrected flight muscle mass of individuals at eclosion (ANCOVA: date of F-2 moult (log): $F_{1,19}=0.345$, $P=0.564$; Fig. 4a), or the size-corrected fat reserves of individuals at eclosion (ANCOVA: date of F-2 moult (log): $F_{1,16}=1.389$, $P=0.256$; Fig. 4b). Larvae in the high-nutrition treatment were significantly heavier (dry

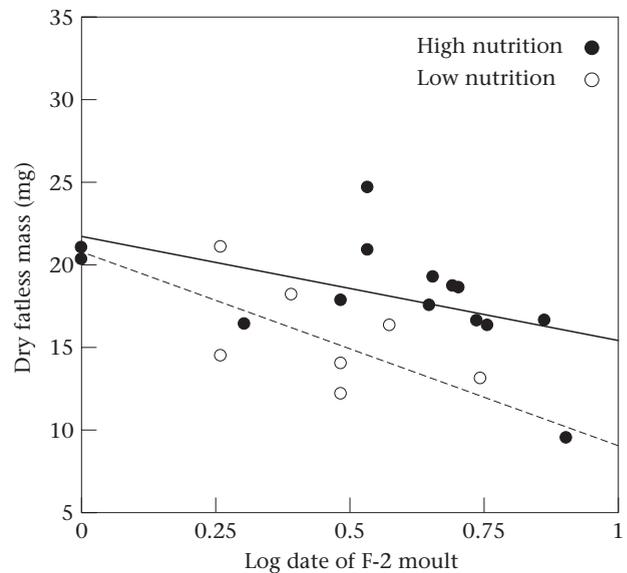


Figure 3. The relationship between the dry fatless mass at eclosion (mg) and the date that the individual moulted into the F-2 larval instar (log) for individuals eclosing from both the high- and the low-nutrition treatments. The solid regression line represents individuals from the high-nutrition treatment, and the broken regression line individuals from the low-nutrition treatment. The first individual in the study entered the F-2 larval instar on 11 October 1996. This date was defined as day 1 of the season. All subsequent moult dates were expressed as days relative to day 1.

fatless mass) than larvae eclosing from the low-nutrition treatment (ANCOVA: $F_{1,19}=15.589$, $P<0.001$; Fig. 3). Moreover, even after correcting for size differences, teneral individuals that eclosed from the high-nutrition treatment had a significantly greater flight muscle mass than teneral individuals that eclosed from the low-nutrition treatment (ANCOVA: $F_{1,19}=6.785$, $P=0.017$; Fig. 4a). This pattern was the same for the size-corrected fat content of larvae eclosing from the high- and low-nutrition treatments (ANCOVA: $F_{1,16}=10.467$, $P=0.005$; Fig. 4b).

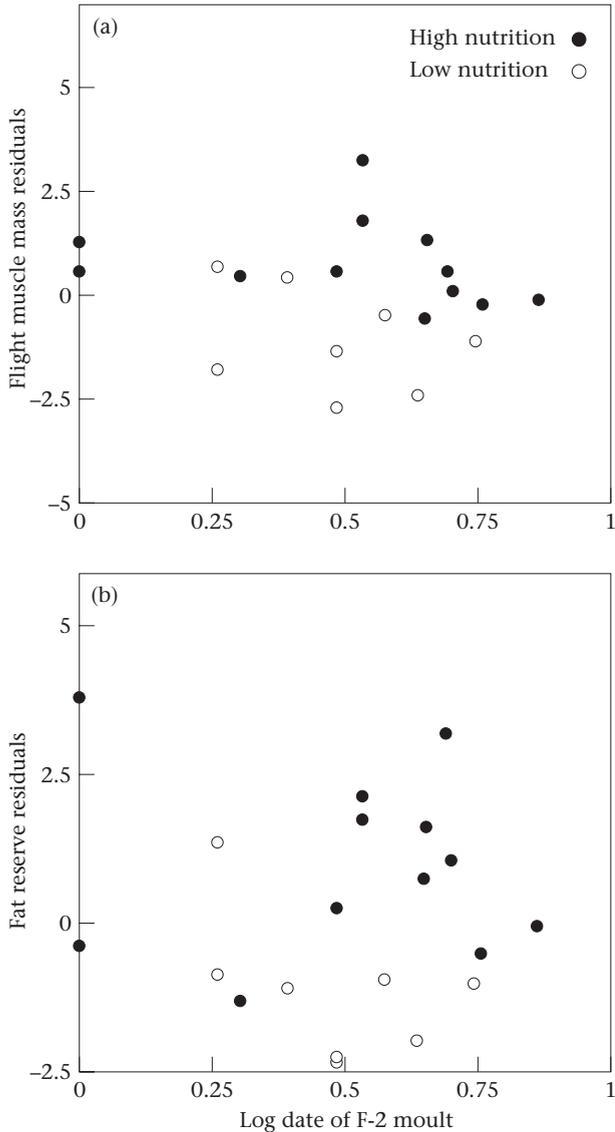


Figure 4. The relationship between the date an individual moulted into the F-2 instar (log) and (a) its flight muscle mass and (b) its fat reserves at eclosion for individuals eclosing from both the high- and the low-nutrition treatments. To correct for differences in body size, flight muscle mass is expressed as standardized residuals from a regression of flight muscle mass (mg) over dry fatless mass (mg) ($Y = -1.903 + 0.264X$; $r^2 = 0.819$, $F_{1,33} = 149.003$, $P < 0.0001$), and fat reserves are expressed as standardized residuals from a regression of fat (mg) over dry fatless mass (mg) ($Y = -1.921 + 0.389X$; $r^2 = 0.637$, $F_{1,33} = 57.805$, $P < 0.0001$).

Development rate

Individuals that were late moulting into the F-2 instar spent less time within the final three instars (ANCOVA: $F_{1,23} = 5.254$, $P = 0.031$; Fig. 5) in both the high- and the low-nutrition treatments (ANCOVA: nutrition treatment by date of F-2 moult (log) interaction: $F_{1,22} = 1.817$, $P = 0.191$; Fig. 5). However, larval nutrition had no effect on the total time spent within the final three larval instars (ANCOVA: $F_{1,23} = 0.494$, $P = 0.494$; Fig. 6). Further analysis enabling a comparison within each of the three final instars also revealed no effect (one-way repeated

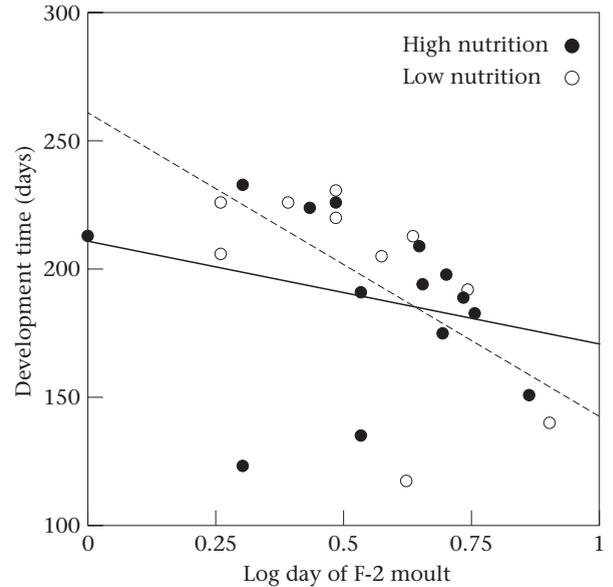


Figure 5. The relationship between the date that an individual moulted into the F-2 instar (log) and the number of days it spent within the final three larval instars, for larvae reared in the high-nutrition and low-nutrition treatments. The solid regression line represents individuals from the high-nutrition treatment, and the broken regression line individuals from the low-nutrition treatment.

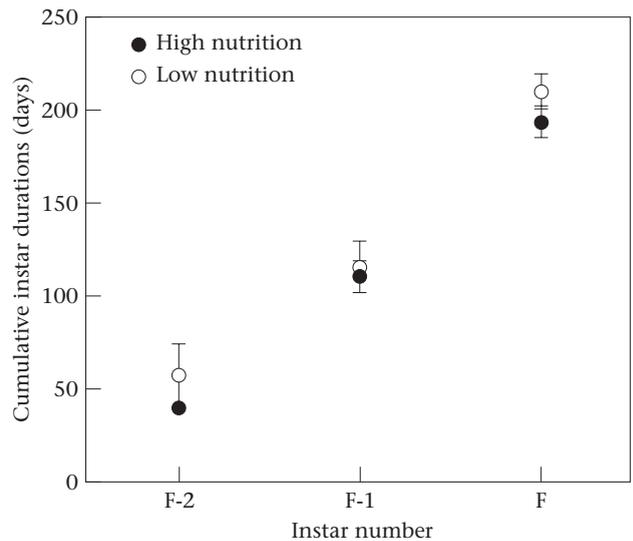


Figure 6. The cumulative time (days) spent within the final three larval instars for larvae reared in the high-nutrition and low-nutrition treatments. Values are $\bar{X} \pm \text{SEM}$.

measures ANOVA: $F_{1,26} = 0.126$, $P = 0.725$; Fig. 6). However, the duration of each instar increased as individuals approached eclosion (one-way repeated measures ANOVA: $F_{2,52} = 4.918$, $P = 0.011$; Fig. 6). The increases in successive larval instar durations were not significantly different for larvae developing in the high- and the low-nutrition treatments (one-way repeated measures ANOVA: nutrition treatment by instar number interaction: $F_{2,52} = 0.980$, $P = 0.382$; Fig. 6).

DISCUSSION

As in many other odonate species (Penn 1951; Banks & Thompson 1985; Michiels & Dhondt 1989; Gribbin & Thompson 1990; Anholt 1994) male body size declined with season in both the field and laboratory where competition effects were absent and feeding was controlled. These results support previous models (Ludwig & Rowe 1990; Rowe & Ludwig 1991; Werner & Anholt 1993; Crowley & Hopper 1994; Rowe et al. 1994), and empirical studies (Nylín et al. 1989; Nylín 1992; Carriere et al. 1996; Johansson & Rowe, *in press*) that suggest that at least part of the seasonal reduction in odonate body size arises from an adaptive trade-off between body size and development rate. Further evidence that selection favours early eclosion in odonates comes from our finding that, as predicted, field-collected immature male damselflies had substantially reduced levels of flight muscle mass (63.2%) and fat reserves (49.6%) compared with adults collected within the same year and over the same period. Female 'mass gain' was not examined. However, we suspect it will be equal to or greater than that of males since male and female body mass, flight muscle mass and fat reserves were the same at eclosion (Table 1), yet females are typically slightly heavier than males in the field (S. Plaistow, unpublished data).

The rapid accumulation of more than half the reserves required for reproduction supports our hypothesis that 'mass gain' during the immature stage may represent an adaptive 'early' ontogenetic niche shift. An alternative, but not mutually exclusive, explanation is that selection for increased body size alone is responsible. There is some evidence that larger larvae are more susceptible to predation in the aquatic niche (Morin 1984; Dixon & Baker 1988). If this is the case, there may be upper limits to the size a larva can attain, so restricting further growth in the larval environment. This may then have led to further growth and mass gain in the adult environment, where size may be less restricted. However, this alternative hypothesis seems less likely since it does not explain why body size declined throughout the season (Figs 1, 3). Laboratory-reared larvae that were late moulting into the F-2 larval instar (i.e. time constrained) spent fewer days within the final three instars (Fig. 5), and eclosed at a smaller body size (dry fatless mass; Fig. 3). However, we found no evidence that they adjusted their proportional investment in flight muscle and fat reserves (Fig. 4a,b), as we had predicted. This could be because all individuals are already strongly selected to maximize their development rate and therefore eclose with the bare minimum of muscle and fat reserves necessary for flight and survival at eclosion (Marden 1989). The apparent lack of ability to regulate investment in both flight muscle and fat reserves is surprising since, if they could do this, individuals that hatched early in the season might be able to reduce time costs and the risk of predation during the immature phase considerably (see Anholt 1992). That they do not suggests that the optimal investment in flight muscle and fat reserves may be predetermined and cannot be used to adjust development rate in response to seasonal cues.

Larvae reared on a low-nutrition diet eclosed as significantly smaller (dry fatless mass) individuals than larvae reared on a high-nutrition diet (Fig. 3). Furthermore, even after correcting for differences in body size, larvae reared within the low-nutrition treatment eclosed with significantly smaller flight muscle mass (Fig. 4a) and fat reserves (Fig. 4b) than larvae reared within the high-nutrition treatment. In contrast, there was no difference in the survival or development rate of larvae from the high- and the low-nutrition treatments (Fig. 5). The extent to which individuals relax life history parameters in response to stresses such as nutritional deficiencies supposedly represents an adaptive response that maximizes net fitness (Calow & Woolhead 1977; Collins 1980; Simmons 1987). This leads to the prediction that life history parameters that are strongly related to fitness should be maintained at a relatively constant level, while those that are less important in determining fitness should be allowed to vary (Collins 1980). In the populations of calopterygid damselflies examined in this study, development rate appears to be the major determinant of fitness and is maintained at the expense of body size and investment in flight muscle and fat reserves. Our results suggest that in calopterygids development rate varies seasonally because early-hatching individuals allocate more time to each instar than individuals that are time constrained. The growth rate within each instar (the rate at which resources are accumulated) appears to depend upon the diet that the individual receives, as well as the time available to obtain nutrition prior to moulting into the next instar. Larvae that are able to accumulate a full quota of resources within an instar probably increase their body size to a large degree in the following moult. However, larvae that do not obtain a full quota of resources may be forced to increase their body size to a lesser degree, depending upon the quota of resources they were able to obtain. In short, this means that all time-constrained larvae will most likely reduce their body size since the time available to obtain resources within each instar is reduced. This perhaps explains why time-constrained *L. congener* had reduced growth rates even though the level of food available was controlled and consumption was the same in both time-constrained and early hatching larvae (Johansson & Rowe, *in press*). The relative extent to which individuals sacrifice growth rate for development rate may then vary within a season depending on how close they are to the breeding season and how much food is available.

In contrast to our results, previous studies have found that some odonates reduce both development rate and growth rate when larval nutrition is decreased (Lawton et al. 1980; Baker 1982; Wissenger 1988; Pickup & Thompson 1990). Some of the differences observed in laboratory studies may arise from variation in the severity of experimental food reductions. However, we suggest that the duration of the emergence period will have the most important effects on larval development. For example, in the libellulid dragonflies *Libellula lydia* and *Libellula luctuosa*, development is asynchronous, the emergence period is not restricted and breeding occurs all summer. Consequently, selection favouring faster

development is weakened. [Wissinger \(1988\)](#) found that when food availability was reduced in these species larvae tended to maintain size but let development rate fluctuate by as much as five-fold. Thus, in species in which the emergence period is long, all larvae may be able to obtain sufficient resources to eclose at the naturally selected optimal body size. Consequently variation in body size at eclosion is likely to be small and body size should therefore have little influence on mating success. However, in species in which the emergence period is restricted, time constraints may force many larvae to eclose at a suboptimal size. In these species the variance in body size at eclosion is likely to be higher, and body size may be correlated with mating success. Our understanding of how body size relates to fitness in odonates is at best unclear ([Finke et al. 1997](#)). We suggest that a greater consideration of the relationship between the duration of the emergence period and the optimal body size at eclosion may prove useful in clarifying this relationship.

In conclusion, our results have gone some way to demonstrating that selection pressures acting within one odonate life history stage strongly influence individual and offspring traits in other life history stages: understanding this relationship is critical for understanding how fitness is determined.

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