Effects of early growth conditions on body composition, allometry, and survival in the ladybird beetle *Harmonia axyridis*

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Abstract: During both the larval and adult stages, the ladybird beetles *Harmonia axyridis* (Pallas, 1773) feed primarily on aphids, populations of which may fluctuate dramatically in time and space. *Harmonia axyridis* were reared under three resource treatments: high, low, and improving. We predicted that beetles experiencing consistently poor larval conditions would allocate limited resources to dispersal traits (by increasing relative wing surface area and fat storage), whereas larvae facing good or improving conditions were predicted to allocate preferentially to reproductive traits. As predicted, beetles reared at low food had lower wing loading and stored more fat than individuals reared at consistently high food. When conditions were initially poor but improved during development, body size was reduced relative to the high food treatment, though wing area scaled similarly. Allocation of fat and protein was dependent on both sex and treatment. Females in improving conditions stored less fat, and males less protein, relative to low food conditions. This is suggestive of a trade-off between reproduction and dispersal that is resolved differently between the sexes. Unexpectedly, adult survival under starvation was not appreciably affected by larval growth conditions, although males lived about 10 days longer, on average.

Résumé : Durant à la fois leurs stades larvaires et adultes, les coccinelles *Harmonia axyridis* (Pallas, 1773) se nourrissent principalement de pucerons dont les populations peuvent fluctuer de façon spectaculaire dans le temps et l'espace. Nous avons élevé des *H. axyridis* dans trois conditions expérimentales de ressources, favorables, médiocres et en amélioration. Nous avions prédit que les coléoptères qui connaissent des conditions larvaires médiocres devraient allouer leurs ressources limitées aux traits reliés à la dispersion (augmentation de la surface relative des ailes et accumulation de lipides), alors que les larves en conditions favorables ou en amélioration devraient les allouer de préférence aux traits reliés à la reproduction. Comme prédit, les coléoptères élevés dans des conditions alimentaires médiocres ont une charge alaire réduite et accumulent plus de lipides que les individus gardés continuellement en conditions alimentaires favorables. Lorsque les conditions sont médiocres au début et s'améliorent au cours du développement, la taille du corps est réduite par rapport à ce qui s'observe dans les conditions alimentaires favorables, bien que la surface alaire se développe de la même façon. L'allocation des lipides et des protéines dépend à la fois du sexe et des conditions expérimentales. Par rapport aux individus en conditions alimentaires médiocres, les femelles en conditions en amélioration stockent moins de lipides et les mâles moins de protéines. Cela semble indiquer un compromis entre la reproduction et la dispersion qui est résolu différemment par les deux sexes. De façon inattendue, la survie des adultes dans les conditions de pénurie alimentaire n'est pas affectée de manière appréciable par les conditions de croissance des larves, bien que les mâles vivent en moyenne environ dix jours de plus.

[Traduit par la Rédaction]

Introduction

Poor juvenile growth conditions typically lead to delayed maturation at a smaller body (Berrigan and Charnov 1994; Day and Rowe 2002). Growth conditions may additionally affect body shape and composition independent of changes in overall size. For example, it is commonly observed that body condition is preserved at the cost of skeletal size in fish reared at low food (e.g., Ali et al. 2003), while in some insects growth in structural size preceded gains in mass following periods of low food (e.g., Strobbe and Stoks 2004; Dmitriew and Rowe 2005). Stress during development may also result in changes in body size with respect to the scaling relationships between various morphological traits and overall size (e.g., Stevens et al. 1999, 2000), which may also be sex-specific (e.g., Boggs and Freeman 2005; Dmitriew et al. 2007). Therefore, as much interesting and potentially important variation may exist within size classes as it exists among classes.

It is often supposed that simple reductions in overall body size are nonadaptive consequences of resource restriction during development, particularly since these effects are also often accompanied by delays in maturation (Day and Rowe 2002). However, this is not necessarily the case, particularly if the conditions experienced during development predict the conditions likely to be encountered by the adult form. For example, in addition to reducing time to maturation, small body size may reduce maintenance costs and improve locomotor efficiency of the adult (Blanckenhorn 2000; Reim et al. 2006). Likewise, changes in allocation to body parts (all-

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ometry) and to specific storage molecules may reflect highly specific adaptations of an animal to an anticipated environment. Recent studies suggest that diet received during development can affect the proportional allocation of resources to specific components of body mass, including fat and protein content and relative wing size (e.g., Ojeda-Avila et al. 2003; Boggs and Freeman 2005; Stoks et al. 2005).

In predaceous and herbivorous insects, there is evidence that populations faced with a food shortage or declining conditions when juveniles tend to develop adult phenotypes suited to dispersal, and that investment in these dispersal traits typically comes at a cost to investment in reproductive traits (Roff 1986). For example, high population density, which signals potential declines in resource quality or availability, triggers wing development in aphids (reviewed in Braendle et al. 2006), and winged aphids tend to have reduced gonad size and greater storage of lipids (Dixon et al. 1993). This is an example of an environmentally induced polyphenism, but an analogous phenomenon is observed in the sand field cricket (*Gryllus firmus* Scudder, 1902), populations of which contain two genetically distinct morphs (winged and flightless) having different dispersal capabilities and maximum reproductive rates (e.g., Zera and Denno 1997). The winged morph is favoured under poor or declining conditions, and allocates proportionally more to triglyceride fat, which is the primary flight fuel in insects, including beetles (Auerswald et al. 1998; Zera et al. 1999; Gäde et al. 2006). Wingless individuals allocate more resources to reproduction and thus contribute far more to the next generation than do winged individuals when food is abundant (Zhao and Zera 2002).

The diet of the Asian multicoloured ladybird beetle (*Harmonia axyridis* (Pallas, 1773)) in North America (Coleoptera: Coccinellidae) consists primarily of aphids (Hemiptera: Aphidae) during both the larval and adult stages (Koch 2003). Aphid populations may be highly ephemeral, with population levels fluctuating rapidly, often in response to predation by the ladybirds themselves. Activity, oviposition rate, and dispersal behaviour are strongly influenced by the densities of local aphid populations (With et al. 2002; Evans 2003). However, females frequently oviposit in the vicinity of declining aphid populations, or produce egg clutches that hatch before prey populations have peaked, so that hatchlings often encounter growth-limiting conditions (e.g., Evans 2003). Therefore, *H. axyridis* is under strong selection to cope with rapidly changing resources during both larval and adult stages. The ability of *H. axyridis* to disperse long distances contributes to their success in exploiting patchy resource distributions, even in comparison with other aphidophagous coccinellids (With et al. 2002). However, reproductive rate and dispersal ability may be in conflict for limited resources. While all ladybirds have functional wings, dispersal ability in insects in general is thought to depend both upon wing loading (wing area relative to body mass) and upon the quantity of triglycerides stored prior to eclosion (Beenakkers 1969; Auerswald et al. 1998; Vogel 2003).

To test the hypothesis that larval diet affects resource allocation in eclosing adults, we compared body shape and proportion of body mass composed of lipids and protein among groups of adult *H. axyridis* that had experienced one of three food treatments during larval development. A high-food group was fed a large ration of aphids daily from hatch to eclosion. Low-food larvae were fed an equivalent ration, but only every 2nd day, and larvae in the “improving” condition treatment were fed every 2nd day for the first 8 days posthatch, and daily thereafter. We predicted that when food was low, dispersal traits would be favoured, including higher relative fat storage and increased relative wing area than in the high or improving treatments. When conditions begin to improve, we predicted that adults would invest additional resources into reproduction, rather than in the dispersal traits described above. Each trait was also analysed for sex effects, since males and females maximize fitness in different ways (e.g., flight may be more important among mate-searching males). Between eclosion and reproductive maturity, there is additional opportunity to compensate for mass, though structural size is fixed as in all insects. Previous experiments in damselflies do suggest that compensation for structural size is prioritized in damselflies, but mass gain after eclosion was not measured in this group (e.g., Strobbe and Stoks 2004; Dmitriew and Rowe 2005). We tested the hypothesis that there is further potential for compensation in mass during the adult stage by comparing rates of mass gain during the teneral period among treatment groups in *H. axyridis*.

Finally, we measured the effect of larval growth conditions on adult longevity under food stress. Given the highly variable resource levels experienced by ladybird beetles in the wild (e.g., Koch 2003), resistance to periods of resource restriction is expected in this group. However, previous results suggest that poor conditions during early larval development lead to reduced starvation resistance late in life, although compensatory growth during the final instar eliminated any differences in mass or size by eclosion (Dmitriew and Rowe 2007). It has been hypothesized that early developmental conditions determine an individual’s performance in the future depending upon the conditions encountered by adults (e.g., Monaghan 2008). If it is the case that plasticity matches the individual to its future environment depending upon food availability during the larval stage, adult survival under resource stress could actually be greater in the low-food group than that of beetles reared at high or increasing food level.

Materials and methods

Adult *H. axyridis* were collected from Charlottesville, Virginia. On 16 January, males and females were paired randomly and allowed to mate. Following successful copulation, males were removed from each Petri dish and females were provided with about 10 large aphids daily to commence producing eggs. Larvae hatched from eggs produced by these females were used in the experiment.

On 22 January, we collected newly hatched larvae, which were placed individually in small (6 cm diameter) Petri dishes and randomly assigned to one of the three feeding treatments (*high*, fed daily; *low*, fed every 2nd day; *improving*, fed every 2nd day until day 8, and daily thereafter). Larvae were reared at room temperature (21 °C) under 24 h light. Each Petri dish contained a piece of cotton soaked in a solution of 10 g organic cane sugar per 100 mL of water. All larvae were weighed and pronotum widths measured following the second molt, which corresponds approximately to day 8 (the timing of the diet switch) at high food. Larvae were then transferred to a fresh 10 cm diameter Petri dish. During the first instar, each larvae was provided with small pea aphids (*Acyrthosiphon pisum* (Harris, 1776)) at each feeding, after which larvae were provided with 150 mg of aphids at each feeding (approximately 8–10 adult aphids) until pupation. At eclosion, individuals were again weighed and pronotum width measured. Within 24 h of eclosion to the adult stage, a subset of beetles was killed by freezing and stored at –20 °C. The remaining, live adults were placed individually in a fresh 10 cm diameter Petri dish and fed a ration of 8–10 aphids daily (mean mass 150 ± 10 mg) for a further 10 days. This was done to ensure that all animals were reproductively mature. Adults were then weighed to assess teneral mass gain and mated randomly with an individual from laboratory stock. Survival during food stress was tracked from this point forward, after which beetles were starved and provided with water (no sugar) only.

Within 1 week of freezing, photographs of aspects of body size were made using a digital camera (Leica DFC280) mounted on a dissecting microscope (Leica MZ6), and measures were taken from these digital images with NIH ImageJ (available from the National Institutes of Health at http://rsb.info.nih.gov/ij/, accessed 4 February 2009). Linear measures included head and pronotum width. Wing area was estimated as the area enclosed by four landmarks (Fig. 1): the second axillary sclerite, the apical end of the costal vein, the apical end of the radial vein (or radial fold), and the apical end of the anal fold (or first anal vein). Wing area was linearized by taking the square root prior to analysis by ANCOVA, with dry mass as the covariate to account for the positive correlation between wing size and overall body size.

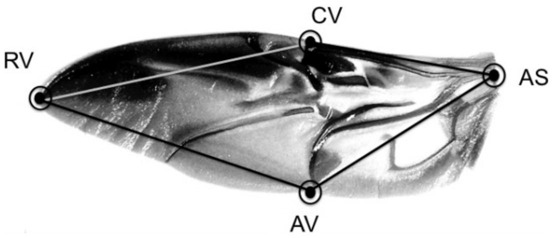
Beetles were then placed immediately in a drying oven at 60 °C for 48 h to completely dehydrate samples and dry mass was measured to the nearest 0.1 mg using a Mettler Toledo XS105 scale. Fat and protein content were determined as per Plaistow and Siva-Jothy (1996) and Marden (1989). Fat was extracted using chloroform redux in a Soxhlet apparatus for 8 h, after which beetles were dried as before and reweighed. Fat mass was estimated as the change in dry mass before and after fat extraction. Subsequently, individuals were placed in a 0.1 mol/L solution of KOH for 24 h, which caused protein to dissolve. Beetles were then dried a third time and weighed to provide the total protein content (dry fatless mass – dry mass following the KOH treatment).

Results

Growth and survival of larvae

Of the original 480 larvae, only 410 larvae survived to eclosion. During the initial food-treatment period (first 8 days after hatching), a greater proportion of larvae receiving food every 2 days (low and improving treatments) died than did larvae fed daily (12% and 5.0% mortality, respectively; $\chi^2_{[1]} = 5.47$, $P < 0.05$). Mortality rates thereafter were significantly higher when feeding rates were kept low until eclosion, although higher mortality persisted even in the improving treatment (11% (low), 5.5% (improving), and 1.2% (high); $\chi^2_{[2]} = 12.9$, $P < 0.01$). The low food treatment caused a significant reduction in mass and delay in time to the second molt for larvae in the low and improving treatments relative to the high food treatment ($P < 0.01$ for all analyses). Individuals reared at high food emerged earlier, heavier, and with a larger mean pronotum width than both the improving and low food treatments (ANOVA: Table 1, Fig. 2). There was evidence of compensatory growth in the improving treatment, where growth rate of mass was significantly increased relative to that of larvae reared at high food between day 8 and eclosion, (Tukey's post hoc HSD: improving > high > low). In terms of structural body size, there was a significant effect of treatment on rate of growth (Table 1, Fig. 2), with larvae in the improving treatment growing at a higher daily rate, though the difference between the improving and the high food treatments was not significant according to a Tukey's post hoc HSD test (improving = high > low).

Fig. 1. Schematic of wing measurements of Asian multicoloured ladybird beetles (*Harmonia axyridis*). Wing area is estimated from the quadrilateral enclosed by the four landmarks indicated. AS, second axillary sclerite; CV, apical end of the costal vein; RV, apical end of the radial vein (or radial fold); AV, apical end of the anal fold (or first anal vein).



Body composition and wing size at eclosion

In the subset of beetles for which body composition was analysed, fat and protein content were positively correlated with total dry mass (fat: $R^2 = 0.38$, $F_{[1,163]} = 99.6$, $P < 0.0001$; protein mass: $R^2 = 0.45$, $F_{[1,163]} = 133.9$, $P < 0.0001$). Thus, we included dry mass as the covariate when comparing the effects of treatment on fat and protein content using ANCOVA (Table 2, Fig. 3). In females, there was a significant interaction effect between treatment and dry mass for both fat and protein content. All females allocated a greater proportion of overall mass to fat as size increased; however, this effect was strongest in the low food treatment. For protein, the results are somewhat more complicated but suggest that animals in the low food treatment increase allocation at the lowest rate of all three treatments. Among males, fat content relative to body size was similar in the high and improving treatments, while protein content was relatively lower in the latter group. There was no interaction effect between treatment and total dry mass.

Wing area increased with dry mass ($F_{[1,151]} = 102.6$, $P < 0.0001$), and females had relatively larger wings than males ($F_{[1,151]} = 89.3$, $P < 0.0001$). However, this relationship depended on treatment. As predicted, adults reared on low food had a larger wing area for a given mass than under high or improving conditions ($F_{[2,151]} = 5.06$, $P = 0.0075$). All interaction effects were nonsignificant (all $P > 0.05$).

Adult mass gain and survival

There were no treatment effects on mass gain over the 10 days prior to mating ($F_{[2,234]} = 1.89$, $P = 0.15$) and no

Table 1. Results of ANOVA on time from hatching to eclosion, adult size metrics, and larval growth rates (change in size/time) of Asian multicoloured ladybird beetles (*Harmonia axyridis*).

		Larval growth rate						Adult traits									
		Pronotum width*			Mass			Time to eclosion			Pronotum width			Mass			
Source	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	
Treatment	2	0.6	35.8	<0.0001	217.3	13.9	<0.0001	794.5	427.9	<0.0001	0.61	18.5	<0.0001	46 830.1	23.0	<0.0001	
Sex	1	0.9	9.5	0.0022	301.7	38.7	<0.0001	3.81	4.1	0.044	0.9	56.4	<0.0001	78 715.7	77.4	<0.0001	
Treatment × sex	2	0.05	0.12	0.89	3.24	0.21	0.81	0.94	0.51	0.6	0.05	1.55	0.21	3 173.8	1.56	0.12	
Error	404																

Note: SS, sums of squares.

*Growth rate of pronotum error df is 393 because of the missing data at the second molt.

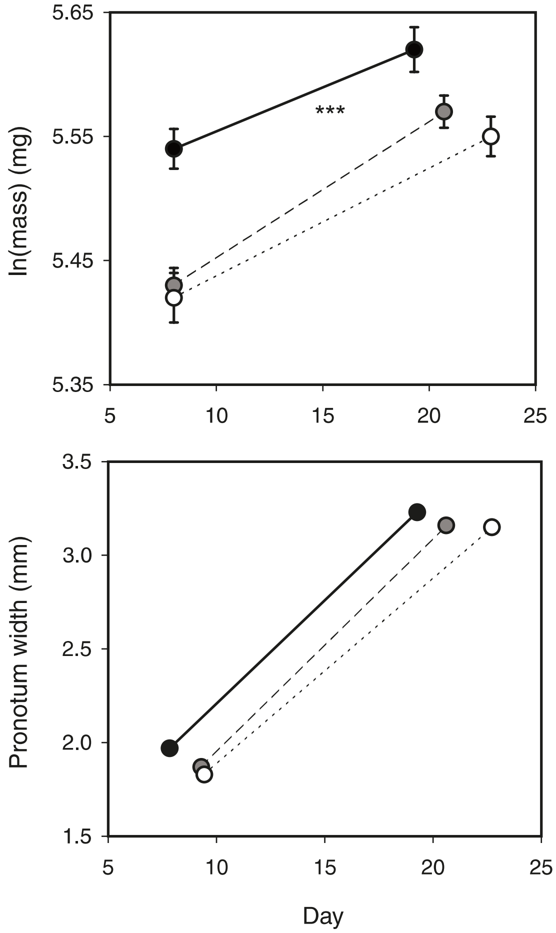


Fig. 2. Larval growth trajectories for male and female Asian multicoloured ladybird beetles (*Harmonia axyridis*) reared under three food treatments. Data for males and females are pooled for simplification and there are no interaction effects between sex and treatment. Upper figure: ln(mass) is measured at day 8 and at eclosion; *** indicates significantly higher rate compared with high and low food treatments. Lower figure: pronotum width is measured within 24 h of the second molt and again at eclosion. Symbols represent individual treatments (solid, high food; shaded, improving food; open, low food). Error bars indicate ±1 SE; if the bars are not visible, they are smaller than the symbol.

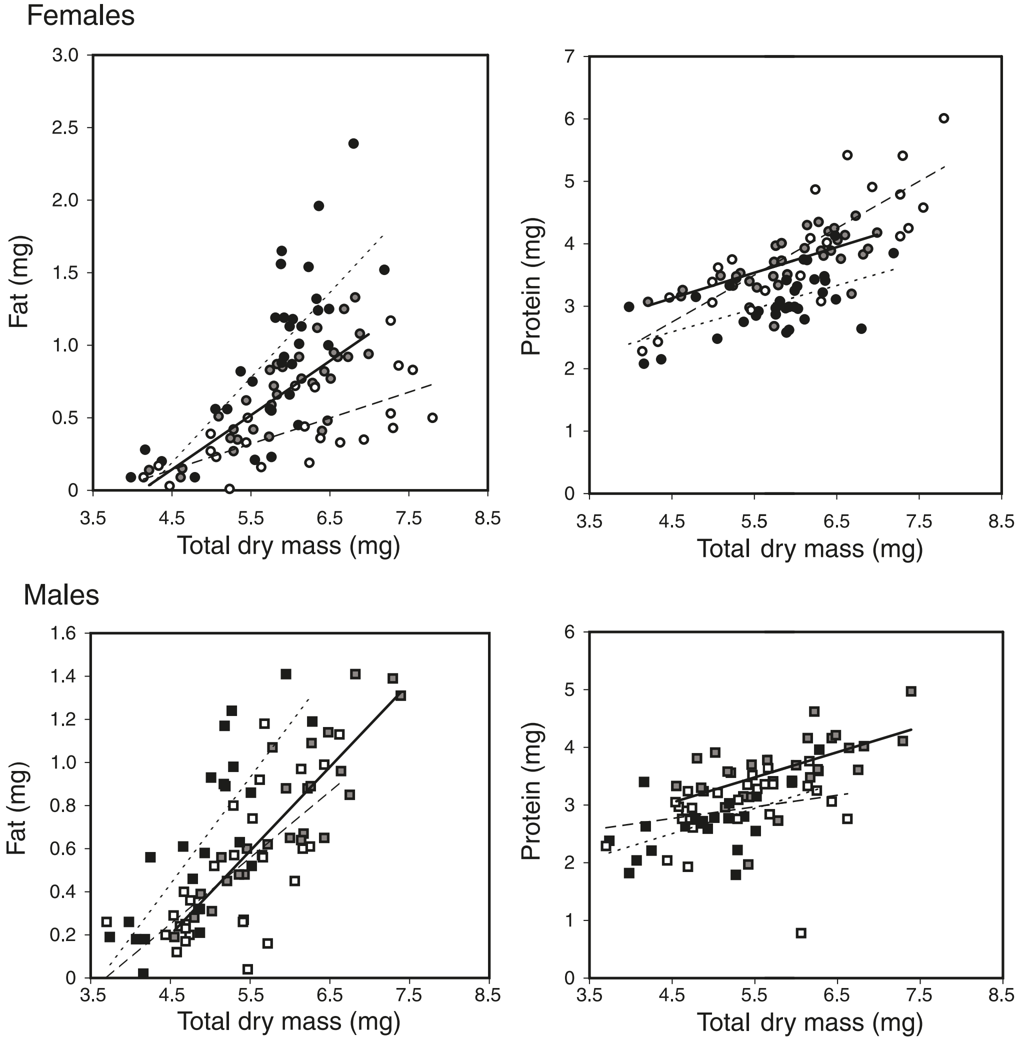
relationship between size at eclosion and mass gained ($P > 0.05$), although females gained more mass than males during this time ($F_{[2,234]} = 74.0$, $P < 0.0001$), indicating that there was no compensatory growth during this period. Overall, there was no treatment effect on mean longevity ($F_{[2,234]} = 0.59$, $P = 0.55$), but males lived 53 ± 1.2 days and females only 43 ± 1.1 days ($F_{[1,234]} = 45.0$, $P < 0.0001$). There was no interaction effect between sex and treatment ($F_{[2,234]} = 0.24$, $P = 0.79$). When the data were analysed using a survival analysis, in males similar curves were generated for all treatments (Wilcoxon test $\chi^2_{[2]} = 0.27$, $P = 0.87$). However, there was a significant effect of treatment on female survival (Wilcoxon test $\chi^2_{[2]} = 12.3$, $P = 0.02$), with those in the low food treatment having a higher median longevity than the other treatments (post hoc pairwise tests: low > improving = high).

Table 2. Results of ANCOVA for effect of food treatment on fat and protein content in Asian multicoloured ladybird beetles (*Harmonia axyridis*) at eclosion.

		Fat			Protein content		
Source	df	SS	*F*	*P*	SS	*F*	*P*
Treatment	2	3.62	29	<0.0001	6.02	13.8	<0.0001
Sex	1	0.71	11.8	0.0008	1.47	1.54	0.0085
Treatment × sex	2	0.021	1.86	0.16	2.36	2.47	0.0041
Mass	1	13.12	203.1	<0.0001	16.6	16.6	<0.0001
Treatment × mass	2	1.21	9.51	0.0001	0.09	0.089	0.81
Sex × mass	1	0.0074	0.12	0.73	0.51	0.51	0.13
Treatment × sex × mass	2	0.17	1.37	0.26	1.94	1.94	0.013
Error	153						

Note: SS, sums of squares.

Fig. 3. Effect of larval food treatments on fat and protein content for females (upper figures; circles) and males (lower figures; squares) of Asian multicoloured ladybird beetles (*Harmonia axyridis*) relative to total dry mass at eclosion. Symbols represent individual treatments (solid, high food; shaded, improving food; open, low food).



Discussion

We have shown that larval growth conditions affect wing area and body composition independently of effects on body size in *H. axyridis*. Rather than maturing at progressively smaller sizes with proportional allocation to different tissues, newly eclosed ladybird beetles had body compositions specific to each set of growth conditions. These effects may reflect adaptive responses in patterns of resource allocation in ladybird beetles facing constant or changing conditions.

Beetles reared at consistently low food levels grew more slowly, delayed development, and matured at a smaller mean body size — effects that are typical of insects reared on a restricted diet (Berrigan and Charnov 1994; Day and Rowe 2002). When resources were temporarily restricted early in life, a partial compensatory response was observed following improvement of diet. The daily rate of mass gain was greater in the improving treatment than that of the high food treatment during the final two instars, even though both treatments received equal rations. However, acceleration of growth in terms of structural size was not statistically significant, although this has previously been shown in this species (e.g., Dmitriew and Rowe 2007).

Body composition at low food

As predicted, allocation to fat was greater among beetles reared at low food levels, which may be an adaptive response to survival and reproduction in poor conditions. Triglycerides are storage fatty acids and represent the main source of fuel for high-energy functions such as flight in many insects (Zhao and Zera 2002; Gäde et al. 2006; Klowden 2007). As a result, lipid content may predict dispersal ability (Beenakkers 1969; Van der Horst 2003; Gäde et al. 2006), as well as the ability to survive periods of food restriction (Ali et al. 2003; Rolff et al. 2004). Because phosopholipids (the other major component of total lipid content in insects) are only minimally soluble in the chloroform solvent used here, we are confident that our estimate of fat is closely representative of the actual triglyceride content in the beetles. By allocating a greater proportion of available resources to triglyceride fat, *H. axyridis* reared at low food levels may be improving both their dispersal ability and resistance to subsequent periods of starvation.

In ladybird beetle, long-distance dispersal flights allow reproductively quiescent adults to aggregate at overwintering sites. In the spring, a second dispersal event occurs among foraging beetles prior to reproducing (Evans 2003). During the reproductively active stage, short flights between resource patches occur in males searching for mates and females for oviposition sites (Evans 2003). Because the principal source of mortality in *H. axyridis* is starvation during the larval stage (Koch 2003), eggs deposited at sites in which aphid populations are abundant or are increasing are at a great advantage. While a similar increase in investment in lipid content might also be expected in ladybird beetles entering diapause rather than dispersing, we note that the temperature and photoperiod conditions used here were identical between treatments, and moreover, that high mating rates were observed in all treatments within 10 days of eclosion.

The hypothesis that ladybird beetles reared at low food levels are displaying a phenotype that favours dispersal is supported by the observation that wing area is relatively greater in beetles reared at low food. A greater wing area to body mass ratio reduces wing loading, which is likely to impact flight endurance in *H. axyridis*. For example, female ladybird beetles that are heavily gravid may actually be temporarily unable to fly owing to the excess mass (Evans 2003). Though we are aware of no studies on flight biomechanics of coccinellids specifically, the ability of insects to fly is strongly affected by the relationship between wing area and mass, an allometric relationship that is highly conserved within species and is under strong selection (e.g., Gilchrist et al. 2000; Frankino et al. 2005).

Body composition under improving conditions

Of all three treatments, females experiencing a switch to high conditions partway through development allocated to fat at the lowest rate and to protein at the highest rate as body size increased. This could be interpreted as preferential allocation to protein as the pool of available resources increases, which is in contrast to those females reared at consistently low food that appear to invest most heavily in fat content even as body size increases. Conversely, males experiencing improving resource availability stored less protein than at high food levels, though proportion of mass as fat was comparable with that of animals reared at high food levels.

The divergence of the responses of males and females to changing conditions could reflect sex-dependent strategies for beetles facing improving conditions after a period of poor growth. While female coccinellids may range widely as adults, upon reaching a high-quality patch they rapidly increase oviposition rate (Evans 2003). Rapid initiation of oviposition upon finding a waxing aphid population could reduce competition between larvae as patch use intensifies over time (Evans 2003). In such conditions, females may benefit more from initiating egg production than from storing resources for flight. As a result, protein deposition (in the form of vitellogenins) will be relatively high. Evidence of a trade-off between reproductive rate and flight in females is also found in studies of the coccinellid *Hippodamia convergens* Guérin-Méneville, 1842, in which female ovarian mass and flight activity are inversely correlated, while there was no such pattern for testes mass in males (Rankin and Rankin 1980). Unfortunately, our techniques do not allow us to discriminate between yolk protein and other proteins, but we are currently planning experiments to address this hypothesis.

Males, which generally maximize reproductive success via mating rate, are likely to benefit more from lipid reserves, which fuel mate-searching behaviour, than from increased protein content. In the laboratory, male mating rate in *H. axyridis* and other insects appears to be quite insensitive to hunger level (Ziegler 1991; Ortigosa and Rowe 2002; J. Perry, personal communication), suggesting that males may be heavily dependent on stored lipids for mate-searching flights.

Resistance to starvation

Overall, we found no effect of food treatment on adult survival during starvation in either sex, although males in all groups lived substantially longer. The independence of adult survival and food treatment are difficult to interpret in laboratory conditions, since the subjects could not undergo dispersal, thereby using up energy reserves. As a result, we may have overestimated longevity in this group. Future studies should explore the effect of larval growth conditions on the relationship between reproductive rate and longevity among females, and between dispersal and longevity in both sexes, with the expectation that these traits will trade-off with one another when energy reserves are limiting.

Summary

We have found that larval growth conditions affect maturation traits independently of overall size in *H. axyridis*, and the nature of these effects suggests that the response may be adaptive for newly eclosed adults encountering the same local conditions as larvae. Those reared on poor food emerged with large fat stores and reduced wing loading relative to control larvae reared at high food levels. These allometric effects are likely to improve dispersal ability. When larvae encountered improving growth conditions, sex-specific changes in both fat and protein content at eclosion occurred, which may reflect preferential allocation to egg production among females that are relatively resource restricted yet face abundant food as adults.

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