

Interactive effects of larval host and competition on adult fitness: an experimental test with seed beetles (Coleoptera: Bruchidae)

S. M. VAMOSI†

Department of Biological Sciences, University of Calgary, 2500 University Drive N.W., Calgary, AB, Canada T2N 1N4

Summary

1. Resources and intensity of competition encountered during development can have significant consequences for adult fitness, yet their effects are rarely considered simultaneously. Furthermore, it is often assumed that these factors affect adult fitness only indirectly through their effects on body mass. Here, I examined the direct effects of larval host type and intensity of competition on mass at emergence and fecundity in two species of bruchid beetles (*Callosobruchus* spp.).

2. There was no effect of competition treatments on mass at emergence of *C. chinensis* females reared in Adzuki or Mung Beans. Controlling for body mass, there was a significant effect of competition treatment on number of eggs laid by *C. chinensis* females that had been reared on Mung Beans, with those reared with a competitor laying significantly fewer eggs than females that had been reared in the absence of competition. Competition had a highly significant effect on mass at emergence of *C. maculatus* females reared in Mung Beans. In the absence of a significant effect of competition on mean mass at emergence in Adzuki Beans, females reared with two competitors laid significantly fewer eggs than did females reared with either one or no competitors.

3. For certain combinations of bruchid species and resource type, thus, females laid fewer eggs for a given mass at emergence if they had been subject to competition during their larval phase. These results reveal subtle differences in the responses of closely related species with similar life histories to resources and competition during development, calling into question current generalizations about the direct effects of competition on fitness.

Key-words: Body size, *Callosobruchus*, clutch size, fecundity, oviposition

Functional Ecology (2005) **19**, 859–864
doi: 10.1111/j.1365-2435.2005.01029.x

Introduction

Environmental conditions encountered during development can have significant effects on adult fitness (Abrams & Rowe 1996; Mayntz, Toft & Vollrath 2003). The impacts of early life foraging decisions are especially significant for organisms that do not feed as adults. Quality of resources encountered and presence of competitors are two factors that are thought to be particularly important for elaboration of secondary sexually selected characters and investment in reproductive effort (e.g. Credland, Dick & Wright 1986; Grether, Hudon & Millie 1999; McGraw *et al.* 2002). Although a number of studies have documented the effects of resources and competition on fecundity in

isolation (e.g. Averill & Prokopy 1987; Colegrave 1993; Timms 1998; Allen & Hunt 2001; Bhattacharya & Banerjee 2001; Ojeda-Avila, Woods & Raguso 2003), these factors are rarely considered simultaneously. Instead, the relationship between body mass at maturity and fecundity is typically determined in the absence of competition or on a single resource type. To determine the effects of competition on fitness, for example, females subject to competition would be weighed after emergence and their fecundity would be estimated using the relationship derived in the absence of competition. This approach will yield meaningful estimates only if the direct effects of competition (or larval host type) are on body mass at maturity. However, competition and larval host type may have independent effects on fecundity; if this is the case, their effects may be underestimated using this approach (see Fig. 1 in Colegrave 1993). Given the number of studies

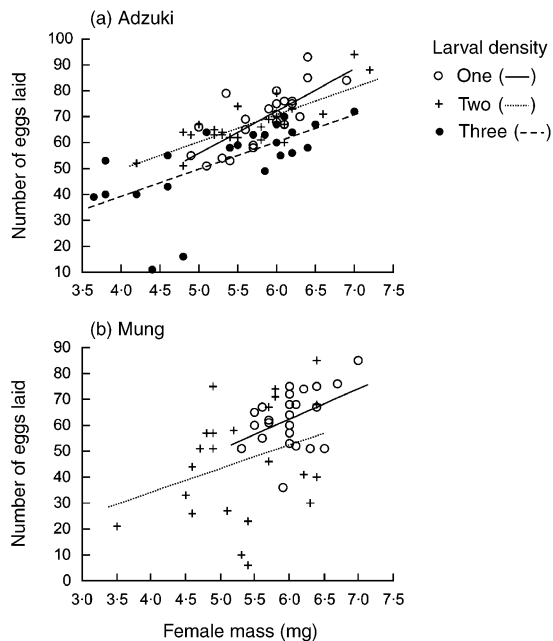


Fig. 1. Relationship between female mass at emergence (mg) and number of eggs laid for *C. maculatus* females reared on Adzuki (a) or Mung (b) Beans. Females reared on Adzuki Beans were reared alone (○ solid line; larval density of one egg per bean), with another larva (+ dotted line; larval density of two eggs per bean), or with two other larvae (● dashed line; larval density of three eggs per bean). Females reared on Mung Beans were reared alone or with another larva.

that implicitly assume that developmental conditions affect adult fitness only through their effects on body mass, it is critical to verify this assumption for a variety of competition and larval host conditions.

Bruchid beetles (Coleoptera: Bruchidae) have a number of features that make them ideal candidates for the study of the effects of early life conditions on adult fitness. First, larvae must complete their development, after hatching from the egg, inside a single legume seed chosen by their mother. Characteristics of the seed (e.g. toxicity of seed contents) and presence of other larvae have significant impacts on survival and growth (Janzen 1977; Fox *et al.* 1996). Second, bruchids typically do not need to feed as adults and, thus, rely on the nutrients obtained as larvae for reproduction. The absence of adult feeding allows for the quantification of the direct link between larval performance and adult reproductive success. Finally, because females glue their eggs, which are visible to the naked eye, to the outside of legume seeds it is possible to obtain accurate measurements of female lifetime fecundity (e.g. Credland *et al.* 1986; Fox 1993; Messina 1993). Accurate counts are further facilitated by short life spans (typically less than 7 days), with oviposition typically completed within a few days of mating.

The effects of larval competition and host type on female lifetime fecundity in *Callosobruchus maculatus* (F) have been considered separately in two previous studies. Females reared on Mung Beans (*Vigna radiata* (L.) R. Wilcz.) with competition (i.e. larval density of two per bean) tended to have lower emergence weight

than those reared without competition (i.e. larval density of one per bean), although no significant interaction between competition treatment and mass at emergence was detected (Colegrave 1993). In other words, females of a given mass tended to lay the same number of eggs regardless of whether they emerged from a bean with a larval density of one or two eggs per bean. More recently, Timms (1998) followed up on this investigation by considering the fecundity of females that had been reared in one of two different hosts, Cowpeas (*V. unguiculata* (L.) Walp.) or Mung Beans. To remove 'any confounding effects of larval competition' (Timms 1998, p. 480), all larval densities were reduced to one per bean. Larval host type had a direct effect on fecundity: although there was no difference in size at emergence (measured as left elytron length) between treatments, females reared in Mung Beans laid more eggs. While these studies provided potentially valuable insights into the effects of larval competition and larval host on female fecundity, the use of a single strain to address each factor in isolation of the other potentially limits the generality of their findings.

Here, I measure the fecundity of female bruchid beetles in two species, *C. maculatus* and *C. chinensis* (L.), in response to both larval competition and host type. The two species have comparable life histories, with the most conspicuous phenotypic difference expected *a priori* to affect their response(s) to larval rearing conditions being the smaller size of *C. chinensis*. To quantify the impacts of larval rearing conditions on fecundity, I reared larvae in one of two resource types and in the presence or absence of competitors. The results obtained suggest that the direct effects of competition and resource type on fecundity, independent of their effects on body mass at emergence, are not straightforward and that interactions between these factors need to be explicitly considered when considering the impacts of developmental conditions on female fitness.

Materials and methods

BEEBLE CULTURES

I conducted the experiment with the 'jC' strain of *C. chinensis* and the 'hQ' strain of *C. maculatus*. The jC strain was collected from Adzuki Beans (*Vigna angularis* (Willd.) Ohwi & Ohashi) in Japan in 1935 and the hQ strain was collected from imported Broadbeans from New Zealand in 1992 (M. Tuda, personal communication). Both strains have been cultured continuously on Adzuki Beans and exhibit scramble larval competition strategies. Stock cultures and experiments containers were reared in growth chambers at 28 ± 2 °C, $35 \pm 5\%$ r.h., and 12:12 h light : dark.

LARVAL COMPETITION EXPERIMENTS

To obtain adults from the different host types, a minimum of 200 adults was allowed to mate and lay eggs on

300 Adzuki or Mung Beans overnight. Because there is evidence that females can detect poor quality beans, I discarded beans with fewer than two eggs. Beans were haphazardly assigned to larval density treatments and their larval densities were reduced, by scraping off excess eggs with a scalpel, to one egg per bean for 80 beans, two per bean for 60 beans, and three per bean for 80 beans. Beans were incubated in individual 1.5 ml microcentrifuge tubes. After 20 days, beans were examined daily and any adults that had emerged were removed. Females were weighed and paired with a male haphazardly drawn from the same treatment. Twenty-four pairs of males and females were introduced into small containers with 100 Adzuki Beans. Females were allowed to lay eggs until they died. Adults were subsequently removed and the number of eggs laid on all the beans was counted.

STATISTICAL ANALYSES

Effects of competition treatment (i.e. different larval densities) on female mass at emergence were analysed with one-way ANOVA. I determined which competition treatments were different for the case of Adzuki Beans using Dunnett's comparison with control method (with a larval density of one egg per bean designated the control). *Post hoc* tests were not needed to interpret differences observed in Mung Beans, which had only two larval density treatments. To examine the effects of competition treatment and mass on fecundity, I first conducted an ANCOVA to determine whether there was a significant interaction between the effects of competition treatment and mass. The interaction term was not significant in any of the four cases (see Results), indicating that the slope of the relationship between fecundity and mass did not differ between competition treatments for each beetle species reared on a particular bean. Thus, I subsequently analysed the effects of competition treatment and mass using two-way ANOVA. The variable of primary interest in this analysis is competition treatment, with a significant effect indicating a difference in the intercept (i.e. the fecundity of a female of a given mass depends on the larval density of the bean that it was reared in) because the null hypothesis of equal of slopes was not rejected by ANCOVA.

Results

BODY MASS AT EMERGENCE

There was a marginal effect of competition treatment on mass for *C. maculatus* females reared on Adzuki Beans ($F_{2,69} = 2.75$, $P = 0.07$; Table 1). Females from beans with a load of three eggs were significantly smaller than those reared alone (Dunnett's comparison with control). For females reared on Mung Beans, in contrast, there was a highly significant effect of treatment ($F_{1,46} = 17.62$, $P = 0.0001$). Females from beans with a load of two eggs were significantly smaller than those

Table 1. Effects of competition treatments on female mass at emergence. Values shown for mass are least square means \pm pooled estimate of error variance calculated with one-way ANOVA. Significant differences are shown in bold. $N = 24$ for each treatment combination (i.e. species \times bean \times larval density)

Species	Bean	Larval density	Mass (mg)	<i>P</i>
<i>C. maculatus</i>	Adzuki	1	5.84 \pm 0.15	0.07
		2	5.67 \pm 0.15	
		3	5.35 \pm 0.15	
	Mung	1	6.02 \pm 0.12	0.0001
		2	5.30 \pm 0.12	
<i>C. chinensis</i>	Adzuki	1	5.34 \pm 0.13	0.73
		2	5.46 \pm 0.13	
		3	5.34 \pm 0.13	
	Mung	1	5.51 \pm 0.11	0.31
		2	5.34 \pm 0.11	

reared alone, which can be appreciated by comparing the range of x -values spanned by the regression lines for the two treatments in Fig. 1(b).

The competition treatments did not have a significant effect on mass for *C. chinensis* females reared in either resource type (Adzuki: $F_{2,69} = 0.32$, $P = 0.73$; Mung: $F_{1,46} = 1.06$, $P = 0.31$). These results contrast strongly with those observed for *C. maculatus* females, especially those reared in Mung Beans (Table 1).

FECUNDITY

Mass ($F_{1,68} = 62.70$, $P < 0.0001$) and competition treatment ($F_{2,68} = 10.57$, $P = 0.0001$) had highly significant effects on fecundity for *C. maculatus* females reared in Adzuki Beans (Fig. 1a). Females from Adzuki Beans with a larval density of three eggs per bean laid fewer eggs than those from beans with a larval density of either one or two eggs, with no difference between the latter two groups (Tukey's HSD test). Mass ($F_{1,45} = 6.08$, $P = 0.02$) had a significant effect, and competition treatment had a marginally significant effect, on fecundity for females reared on Mung Beans (Fig. 1b). There was no significant interaction between the effects of competition treatment and mass on fecundity for females reared on either resource type (ANCOVA; Adzuki: $F_{2,66} = 1.03$, $P = 0.36$; Mung: $F_{1,44} = 0.08$, $P = 0.78$). The effects of resource type and competition treatments on fecundity of *C. maculatus* females are summarized in Table 2.

Mass had a highly significant effect ($F_{1,68} = 85.20$, $P < 0.0001$), whereas competition treatment had no effect ($F_{2,68} = 0.82$, $P = 0.45$), on fecundity of *C. chinensis* females reared in Adzuki Beans (Fig. 2a). In contrast, mass ($F_{1,45} = 25.13$, $P < 0.0001$) and treatment ($F_{1,45} = 7.21$, $P = 0.01$) had significant effects on fecundity of females reared in Mung Beans. Females reared in Mung Beans with a larval density of two eggs per bean laid significantly fewer eggs than those from beans with a larval density of one egg per bean (Fig. 2b). There was no significant interaction between the effects of competition

Table 2. Effects of resource type and competition on number of eggs laid by females. Values shown for fecundity are (least square means \pm standard error) calculated with two-way ANOVA (factors: mass, larval density). Significant differences indicated by different letters. $N = 24$ for each treatment combination (i.e. species \times bean \times larval density)

Species	Bean	Larval density	Fecundity	<i>P</i>
<i>C. maculatus</i>	Adzuki	1	67.0 \pm 1.8 ^a	0.0001
		2	66.7 \pm 1.8 ^a	
		3	56.3 \pm 1.9 ^b	
<i>C. maculatus</i>	Mung	1	59.2 \pm 3.6	0.085
		2	49.6 \pm 3.6	
<i>C. chinensis</i>	Adzuki	1	56.7 \pm 1.4	0.45
		2	54.6 \pm 1.5	
		3	54.3 \pm 1.4	
	Mung	1	57.2 \pm 1.6 ^a	0.01
2		51.0 \pm 1.6 ^b		

treatment and mass on fecundity for females reared on either resource type (ANCOVA; Adzuki: $F_{2,66} = 1.08$, $P = 0.34$; Mung: $F_{1,44} = 0.20$, $P = 0.65$). The effects of resource type and competition treatments on fecundity of *C. chinensis* females are summarized in Table 2.

Discussion

A common assumption in studies of intra- and inter-specific competition is that developmental conditions affect adult fitness only indirectly through their effects on body mass (e.g. Charnov & Skinner 1985; Godfray 1987; Wilson 1994; Ellers, Van Alphen & Sevenster 1998; Hirschberger 1999). Here, I explicitly tested the assumptions that the relationship between fecundity and body mass is invariant to larval rearing conditions and, further, that closely related species should respond in similar ways. The results obtained failed to uphold either assumption. In both species tested, I documented direct effects of competition and resource type on fecundity that were often independent of their effects on body mass. Furthermore, females of two congeneric species of seed beetles responded differentially to both competition and larval host type. Body mass and fecundity of female *C. maculatus* were marginally to highly significantly reduced in competition treatments, with body mass and fecundity reduced to the greatest degree in Adzuki and Mung beans, respectively. Conversely, fecundity of female *C. chinensis* was reduced

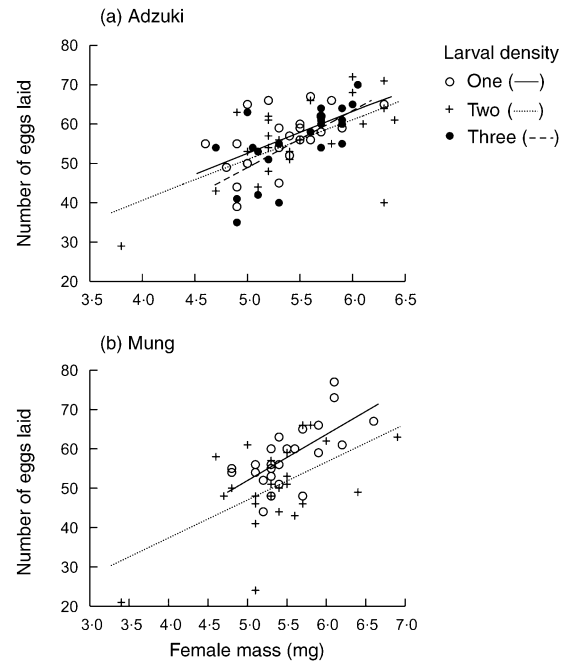


Fig. 2. Relationship between female mass at emergence (mg) and number of eggs laid for *C. chinensis* females reared on Adzuki (a) or Mung (b) Beans. Females reared on Adzuki Beans were reared alone (○ solid line; larval density of one egg per bean), with another larva (+ dotted line; larval density of two eggs per bean), or with two other larvae (● dashed line; larval density of three eggs per bean). Females reared on Mung Beans were reared alone or with another larva.

only in Mung Beans, in the absence of an effect of competition on mass at emergence. Differences between the two species in their responses to competition as a function of larval resource are summarized in Table 3.

The findings of previous studies using *Callosobruchus* beetles (e.g. Credland *et al.* 1986; Colegrave 1993; Timms 1998) can now be placed into a broader context. First, Colegrave (1993, p. 276) stated 'in *C. maculatus* at least, there is no effect of larval competition on adult fecundity independent of its effect on adult weight. This means that the work done by previous authors based on this assumption is safe.' The results of the present study strongly suggest that larval competition can have significant direct effects on adult fecundity independent of its effects of body mass. Furthermore, preliminary trials with the 'iQ' strain (contest larval competition strategy) of *C. maculatus* suggest that such direct effects may be common. The experimental design described earlier was followed, with the exception of eggs loads of one ($n = 12$) or two ($n = 8$) eggs per bean on Cowpeas alone. Although competition did not have a significant effect on female mass at emergence, fecundity was significantly reduced in response to competition. Second, in accordance with previous studies, fecundity of females increased with body mass at emergence. Over the range of body masses considered, an increase in 1.0 mg tended to be accompanied by the laying of an additional ten eggs. Finally, the relative magnitude of

Table 3. A summary of the effects of competition on mass at emergence and fecundity. Numbers refer to larval densities (i.e. one [1], two [2] or three [3] eggs per Adzuki Bean)

Species	Bean	Mass	Fecundity
<i>C. maculatus</i>	Adzuki	Marginal (1 > 3)	Highly significant (1 = 2 > 3)
	Mung	Highly significant	Marginal
<i>C. chinensis</i>	Adzuki	Not significant	Not significant
	Mung	Not significant	Significant

the effect of larval host appears to depend on both the host and seed parasite species. In the present study, fecundity was not affected by larval host type for *C. chinensis* females and was higher for *C. maculatus* females reared alone on Adzuki Beans than for those reared on Mung Beans (Table 2). In contrast, females of the 'Campinas' strain of *C. maculatus* reared on Mung Beans laid significantly more eggs than females of the same size reared on Cowpeas (Timms 1998). Similarly, beetles of the 'South India' and 'Burkina Faso' strains reared on Mung Beans lived longer than those reared on Cowpeas (Fox, Czesak & Wallin 2004).

What could be driving the observed reductions in fecundity of adult female *C. chinensis* reared on Mung, *C. maculatus* (hQ strain) reared on Adzuki, and *C. maculatus* (iQ strain) reared on Cowpeas in response to the presence of other larvae? In females that exhibit a scramble larval strategy (i.e. the former two groups), some of the effect may have been due to avoidance of other larvae, which is accomplished by increased peripheral feeding (Toquenaga & Fujii 1990; Toquenaga 1993). Conversely, increased antagonistic encounters between larvae that exhibit a contest strategy may have contributed to the effect observed in the latter strain. In the iQ strain, larvae bite others in an attempt to kill them (Toquenaga 1993), which may be an energetically costly behaviour. Individual larvae, especially those that employ a contest strategy, may also encounter and ingest greater amounts of frass (i.e. assorted by-products of larval growth; Park 1938; Jones *et al.* 1990) at higher larval densities. Although growth can continue long after uncontaminated resources are consumed (e.g. Gordon *et al.* 1988), the reduced quality of frass may have significant effects on development. At present, it is not known whether increased frass can affect larvae if burrows do not intersect. One difficulty with all of the preceding explanations is that the direct effects of competition on reduced fecundity of focal females reported here have taken into account differences in mass at emergence. Increased peripheral feeding, for example, may reduce growth rates but it is not clear how it would depress fecundity in the absence of an effect on body mass. Finally, females may divert resources away from reproductive structures when reared at higher larval densities. Increased allocation to wing size or musculature would enable female bruchid beetles to disperse in response to the perceived reduced quality or quantity of the resources available for their offspring (Messina & Renwick 1985; Silim-Nahdy, Silim & Ellis 1999; Appleby & Credland 2001). I did not observe either a shift to dispersal morphs or a reduced larval duration in adults reared with two or more larvae. The potential for subtle yet important shifts, however, remains a possibility that deserves further investigation.

Variation in the response of females to competition, both within and between species, is likely the result of a number of factors. The reduced impacts of competition on female *C. chinensis* may be correlated with

differences in body size; in the absence of competition, mean body mass of female *C. chinensis* was 91.4% and 91.5% that of female *C. maculatus* in Adzuki and Mung, respectively. Female *C. chinensis*, thus, would be expected to have lower energy requirements than female *C. maculatus*. Development time and body mass were affected by larval competition in *Stator limbatus*, a species that tends to lay single eggs on small beans, but not *S. beali*, which tends to lay eggs on large seeds (Fox *et al.* 1996). Together, these observations suggest that responses to competition will often be affected by the ratio of resource size to adult size. Within species, body mass had a highly significant effect on fecundity, although body mass alone did not fully explain variation among females. Messina & Slade (1999), for example, have shown a positive correlation between longevity and fecundity in female *C. maculatus* when females were presented with many seeds. Another factor that may contribute to variation in the fecundity of females is the sex of the other larvae with which the focal female was reared. Given the larger size of females compared with males in both species, focal females that emerged from beans that supported one or two other females may have suffered greater reductions in their fecundity than those reared with males. Effects of longevity and sex of competitors warrant closer examination in future studies of the direct effects of competition on adult fitness.

An understanding of the effects of intra- and inter-specific competition, and implications for optimal clutch sizes and competition strategies, requires that the relationship between body size and fitness be well characterized (e.g. Charnov & Skinner 1984; Waage & Ng 1984; Godfray 1987; Allen & Hunt 2001; Rivero & West 2002). Most current models make the assumption that the effects of competition on reproductive success are manifested only through direct reductions in body size. Relationships used to connect body mass to fecundity, for example, are frequently derived in the absence of competition or in a single resource. The results presented here suggest that the effects of competition may be more context-dependent than currently accepted. Future investigations should examine the effects of competition in further species and document the physiological and life-history bases of reduced fitness that cannot be attributed to body mass differences.

Acknowledgements

I am indebted to M. den Hollander for invaluable assistance with maintenance of stock cultures and egg counting, M. Tuda for supplying initial stock cultures, P. Abrams and L. Rowe for laboratory space and logistic support, R. Bonduriansky and D. Punzalan for helpful advice, and C. Fox, F. Messina, and an anonymous reviewer for insightful comments on an earlier draft of the paper. This research was funded by the Natural Sciences and Engineering Research Council of Canada.

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Received 28 December 2004; revised 3 May 2005; accepted 5 May 2005