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Direct effects of larval competition on development time and fecundity in seed beetles

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ABSTRACT

Question: Does larval intraspecific competition result in reduced mass-corrected fecundity independent of any effects on adult body mass?

Methods: We measured egg-to-adult developmental period, body mass, number of eggs laid, and longevity of female *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) reared alone or with another larva on cowpeas in climate-controlled growth chambers.

Results: Although the presence of a competitor did not affect mean mass of females at emergence, females reared with another larva laid significantly fewer eggs for a given body mass than those reared alone. Females that were reared in competition with another larva had longer developmental periods on average than those that were reared alone, whereas there was no evidence for an effect of competition on longevity.

Conclusions: Intraspecific competition can have direct negative effects on fecundity of females, and increase the length of the developmental period, without affecting body mass.

Keywords: *Callosobruchus*, development time, fecundity, intraspecific competition, longevity.

INTRODUCTION

Individuals typically suffer reduced lifetime fitness when exposed to competition for limiting resources during development (Ullyett, 1950; Lewontin, 1955; Simmons, 1987). These effects are expected not only because individuals may obtain fewer resources as densities of conspecifics increase, but also because increased search costs or contests with other individuals may decrease energy and nutrients available for allocation to reproductive structures. In insects, there is a substantial body of evidence that intraspecific competition experienced during development can produce effects that persist throughout their lifetime (Mueller, 1988; Hess *et al.*, 1996; Bédhomme *et al.*, 2003; Vamosi, 2005). A number of fitness-related traits may be impacted, including length of developmental period (Mercer, 1999; Tammaru *et al.*, 2000; Gibbs *et al.*, 2004), body mass (Colegrave, 1993; Lane and Mills, 2003; Vamosi, 2005), longevity (Parrella, 1983; Hawley, 1985; Hess *et al.*, 1996), and fecundity (Colegrave, 1993; Vamosi, 2005). Furthermore, competition can result in trade-offs among various traits that influence fitness (Joshi and Mueller, 1996; Bédhomme *et al.*,

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2003; Marden *et al.*, 2003). In the presence of potential competitors, individuals with access to limited resources may, for example, maintain a constant body mass at emergence at the expense of a prolonged developmental period (Bédhomme *et al.*, 2003).

Although it is widely recognized that intraspecific competition affects fitness in female insects, these effects are typically assumed to be an indirect consequence of reduced body mass (Colegrave, 1993; Ellers *et al.*, 1998). That is, competition affects body size directly because of reduced per capita resource availability as larval densities increase. Because of positive correlations between body mass and fecundity (Ellers *et al.*, 1998; Rivero and West, 2002; Vamosi, 2005; reviewed by Honěk, 1993), smaller individuals are then expected to lay fewer eggs over their lifetime and/or experience reduced longevity. Experimental designs that do not explicitly test for direct effects of larval competition on fitness, independent of effects on body mass, may lead us to systematically underestimate such effects. Because of the lack of studies that have explicitly tested for direct effects of larval competition on adult fitness, it is not possible at present to make general statements about their incidence and/or magnitude.

Bruchid beetles have long been recognized as ideal species for studying the effects of intraspecific competition on life-history traits and resulting population dynamics (e.g. Utida, 1953; Bellows, 1982; Shimada and Tuda, 1996). Much of this effort has been focused on members of the genus *Callosobruchus*. As internally feeding granivores, these species are unable to migrate between hosts (Mitchell, 1975). Therefore, if more than one egg is laid on a bean, this sets the stage for competition for limited resources, which is expected to intensify with higher larval densities and/or smaller beans (Mitchell, 1975; Toquenaga and Fujii, 1990, 1991; Horng, 1997; Vamosi, 2005). Eggs laid on beans are easy to identify and, more importantly, excess eggs can easily be removed without affecting the development of other individuals. The progress and outcome of larval competition can be analysed by cutting open the beans and examining larval tunnels under a microscope. Finally, bruchids typically feed only during the larval stage, and therefore adult beetles have a finite set of resources to allocate to reproductive versus somatic tissues (Colgoni and Vamosi, 2006). As a consequence, the reserves built up by females during development become the limiting factor for how many eggs they can lay (Mitchell, 1975).

Here, we extend previous work on the direct effects of intraspecific larval competition on fecundity of adult female bruchid seed beetles (Colegrave, 1993; Vamosi, 2005). Geographically distinct populations, or those reared in different environments, can typically be categorized as displaying either contest (i.e. lethal combat, one to a few survivors) or scramble (i.e. avoidance of direct interactions, with a premium on obtaining resources before others) larval competition strategies (Toquenaga and Fujii, 1990). Previous investigations have focused on scramble competition strains of *C. maculatus* (F.) (Colegrave, 1993; Vamosi, 2005) and *C. chinensis* (L.) (Vamosi, 2005). Contest competition strains are more difficult to work with for such investigations, because the outcome of direct interactions among larvae often results in only a single adult emerging from smaller resource patches, such as mung (*Vigna radiata* (L.) Wilczek) or adzuki (*V. angularis* (Willd.) Ohwi & Ohashi) beans. However, the emergence rates of two adults from cowpeas (*V. unguiculata* (L.)) in the strain used in the current study are sufficiently high to allow for tests of competition treatment effects (S. Vamosi, personal observation). In addition to mass at emergence and fecundity, we also monitored two life-history traits, length of egg-to-adult development period and longevity, which may respond to competition (e.g. Messina. 1991a, 1991b, 2004) but were not considered in previous studies examining the direct effects of competition. Therefore, we ask: (1) Does intraspecific competition result in decreased mean body mass of females? (2) For a given body mass, do females that were reared with another larva lay fewer eggs than those that were reared alone? (3) Does the presence of another larva result in prolonged developmental periods and/or reduced longevity in females? (4) Is there an association between developmental periods and/or longevity and mass-corrected number of eggs laid?

MATERIALS AND METHODS

The experiment was conducted with the 'iQ' strain of *C. maculatus*. This strain was established from mung bean and black gram (*V. mungo* (L.) Hepper) in Tirunelveli, India in 1979 (Thanthianga and Mitchell, 1987) and has been reared continuously on mung beans. We obtained the culture from M. Tuda in 2002. The main stock culture and individuals used for the experiment were reared in growth chambers at 28 ± 1°C and 48 ± 3% relative humidity in 24-h darkness.

Larval competition experiments

To obtain females for the two treatment groups (i.e. reared with or without the opportunity for larval competition), several hundred individuals from the main stock culture were allowed to mate and lay eggs on approximately 250 cowpeas evenly spread across the bottom of a large mason jar sealed with a mesh covering. After 48 h had elapsed, beans were haphazardly assigned to one of the two competition treatments. To minimize the effects of poor-quality beans, we discarded any beans with less than two eggs (see Vamosi, 2005). Beans were examined under a lighted magnifying glass and, using scalpels, we scraped off all but one egg for the no-competition treatment, or all but two eggs for the competition treatment. Ninety and 148 cowpeas were thus prepared, respectively. Individual beans were subsequently weighed and placed in marked 1.5-ml microcentrifuge tubes with a small hole punched in the top to facilitate gas exchange. Microcentrifuge tubes were then returned to the growth chamber.

Beans were examined once daily beginning 21 days after eggs were laid. After we detected the initial emergences, beans were examined two to four times daily and time of emergence was recorded for individuals. Beans with two eggs were returned to the growth chamber to determine whether females had had an opportunity to interact with another larva. We recorded time of emergence (i.e. length of developmental period) for all females. For subsequent analyses and plots, we present corrected emergence time values for females – that is, the emergence time of the first female to emerge was scored as zero, and subsequent values were the amount of time elapsed after the first emergence. Values closer to zero, therefore, represent shorter developmental periods. Females were weighed and typically paired with the males from the same treatment. For less than 10% of the females, we mated them with virgin males isolated from the main stock culture if experimental males were unavailable. Because beans in the main stock culture have two or more eggs almost without exception (Colgoni and Vamosi, 2006; S. Vamosi, personal observation), we anticipated that using these males would introduce only a conservative bias to our results (e.g. some experimental females that did not experience larval competition were mated with stock males that had). Male–female pairs were placed into small Petri dishes with 100 adzuki beans and returned to the growth chamber. Females were allowed to lay eggs until they died. Time of death was recorded to the half day for each female and the number of eggs laid on all the beans was counted after dead adults were removed. Mass-corrected fecundity was calculated as the residuals from the relationship between body mass at emergence and number of eggs laid for the two competition treatments. In total, we obtained 47 and 39 females that survived, mated, and laid eggs after having been reared in cowpeas with and without the opportunity for larval competition, respectively.

Two aspects of our experimental design warrant further elaboration. First, we included females in the analyses of the effects of competition only if they emerged from beans from which two adults emerged. This ensured that none of the 39 females inadvertently developed without the opportunity for competition. Second, there were two groups of focal females in our competition treatment: those that emerged from a bean in which a male had also developed (33 beans), and those that had developed with another female (3 beans). Thus, 33 males and 39 females emerged in the competition treatment, which is not significantly different from a 1:1 sex ratio ($\chi^2_1 = 0.25$, $P = 0.62$). Because preliminary data exploration revealed that the main effect of the competition treatment was significant whether we included only the first emerging female ($n = 36$; $P = 0.021$), only the second emerging female ($n = 36$; $P = 0.003$), or all females ($n = 39$; $P = 0.030$), subsequent analyses included all females. Although emergence order did not affect mass-corrected fecundity in the three beans with two females ($t_2 = 2.04$, $P = 0.18$), it is worth noting that females that emerged second had lower mass-corrected fecundity than the first female to emerge from the same bean in all three cases. Effects of emergence order on body mass and fecundity in 'all female' beans, therefore, may warrant additional investigation. However, the increased variation observed in the competition treatment (see Fig. 1) is not due to the inclusion of females from these three beans.

Statistical analyses

Effects of bean mass and competition treatment on female mass at emergence were analysed with an analysis of covariance (ANCOVA; covariate: bean mass). We also verified that bean mass did not differ between competition treatments with a one-way analysis of variance (ANOVA).

To examine the effects of body mass and competition treatment on number of eggs laid, we conducted an ANCOVA (covariate: body mass). Because the response variable (i.e. number of eggs laid) is a count, we applied a generalized linear model with a log link and Poisson errors (Crawley, 2005; see also Vamosi *et al.*, 2007). Exploratory analyses indicated that the data were significantly overdispersed (i.e. residual deviance was greater than residual degrees of freedom). Therefore, we applied quasi-Poisson errors, which account for overdispersion, in the analyses presented (Crawley, 2005).

Longevity of females in the two competition treatments was compared with survival analyses without censoring (i.e. individual females were monitored until death). For these analyses, we used the Cox proportional hazards model. The assumption of proportional hazards for the Cox regression model fit was not rejected ($P = 0.42$). Although a variety of models can be applied for analysing survivorship curves, the chi-squared and P values obtained for the analysis of baseline survival closely matched those obtained with a simple non-parametric ANOVA on the survival values for the two treatments (S. Vamosi, personal observation). We therefore believe our conclusions regarding longevity are robust to choice of model.

Finally, we tested for associations between mass-corrected number of eggs and the two life-history traits considered (i.e. length of developmental period, longevity) in the competition treatments with two ANCOVAs. Analyses of female mass at emergence, variation

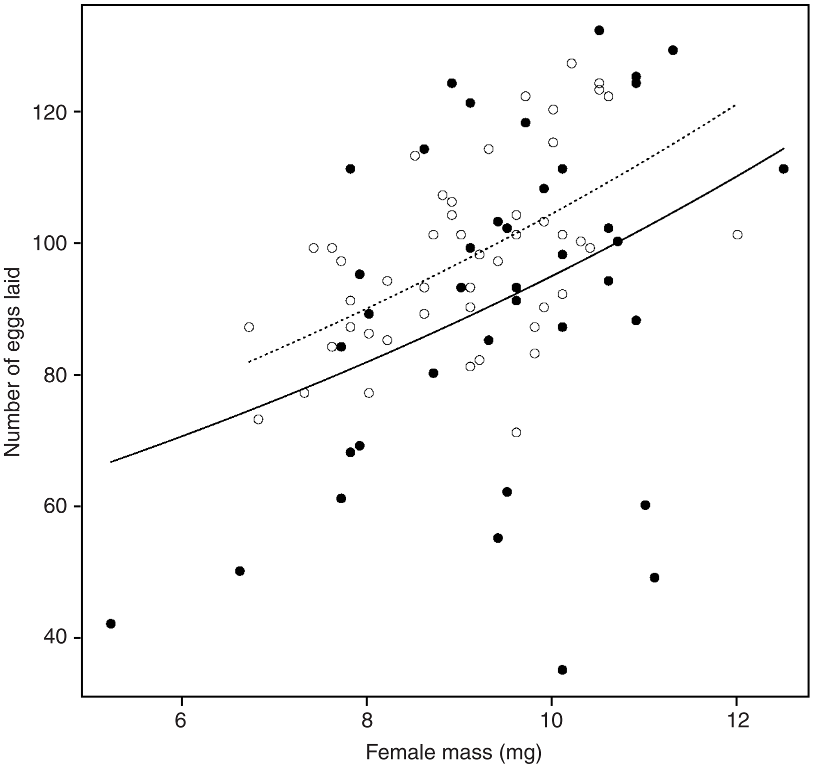

Fig. 1. Relationship between female mass at emergence (mg) and number of eggs laid for female *C. maculatus* reared on cowpeas alone (○, dotted line; i.e. larval density treatment of one egg per bean) or with another larva (●, solid line; i.e. larval density treatment of two eggs per bean).

in mass-corrected fecundity and emergence time were conducted using JMP 5.1.2 (SAS Institute, Inc.). All other analyses were conducted using R 2.1.1 (www.r-project.org).

RESULTS

Body mass and fecundity

Female mass at emergence was not affected by bean mass ($F_{1,83} = 0.004$, $P = 0.95$) or by larval competition treatment ($F_{1,83} = 0.005$, $P = 0.94$). Furthermore, there was no significant interaction between treatment and bean mass (ANCOVA: $F_{1,82} = 1.11$, $P = 0.30$). There was also no difference in the mass of beans assigned to the larval competition treatments ($F_{1,84} = 0.005$, $P = 0.94$). These results suggest that any direct effects of competition on emergence time and fecundity of focal females are not simply the result of resource limitation but, rather, physiological and/or behavioural responses during development due to the presence of other larvae. A *post hoc* examination of the relationship between female mass at emergence and length of developmental period (Fig. 2) suggests a potential explanation: females exposed to larval competition required longer developmental periods to attain the same body mass as females reared in the absence of competition (see also next sub-section, 'Emergence time, longevity, and fecundity').

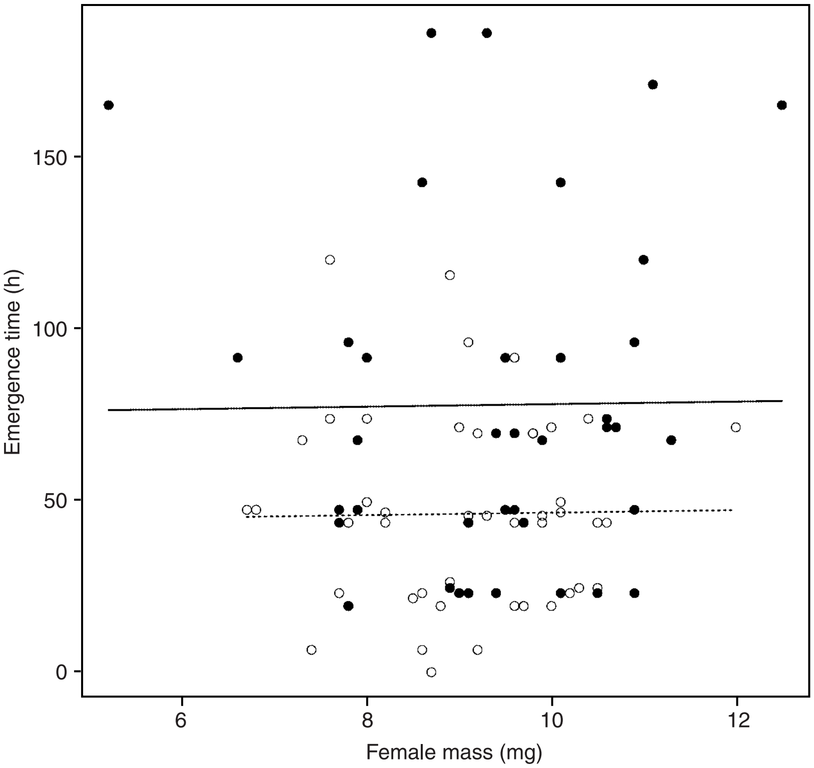

Fig. 2. Relationship between female mass at emergence (mg) and emergence time (i.e. length of egg-to-adult developmental period minus the value of the female with the shortest developmental period) for female *C. maculatus* reared alone (○; dotted line) or with another larva (●; solid line).

Despite the lack of an effect of competition on mean mass at emergence, mass ($t_{1,83} = 4.34$, $P < 0.0001$) and competition treatment ($t_{1,83} = 2.22$, $P = 0.030$) had significant effects on fecundity (Fig. 1). There was no significant interaction between mass and treatment ($t_{1,82} = 0.40$, $P = 0.69$). Females that emerged from beans that had two eggs per bean laid significantly fewer eggs on average (least-squares mean ± standard error: 90.0 ± 2.9) than females from beans with one egg (98.7 ± 2.7). The other noticeable pattern is the significantly greater variation in mass-corrected fecundity among females that emerged from beans with two eggs (coefficient of variation = 36.0%) than for those reared alone (coefficient of variation = 16.3%). This pattern, confirmed with a Levene test ($F_{1,84} = 11.70$, $P = 0.0010$), is consistent with results obtained with *C. chinensis*, and with a scramble competition strain of *C. maculatus*, in mung beans (Vamosi, 2005).

Emergence time, longevity, and fecundity

Females reared in beans that had two eggs emerged significantly later (i.e. had longer developmental periods) than did those that were reared alone ($\chi^2_1 = 9.83$, $P = 0.0017$) (Fig. 3). The difference in median time of emergence between the two treatments was 26 h, which is approximately 17% of the median longevity. In addition to this overall treatment

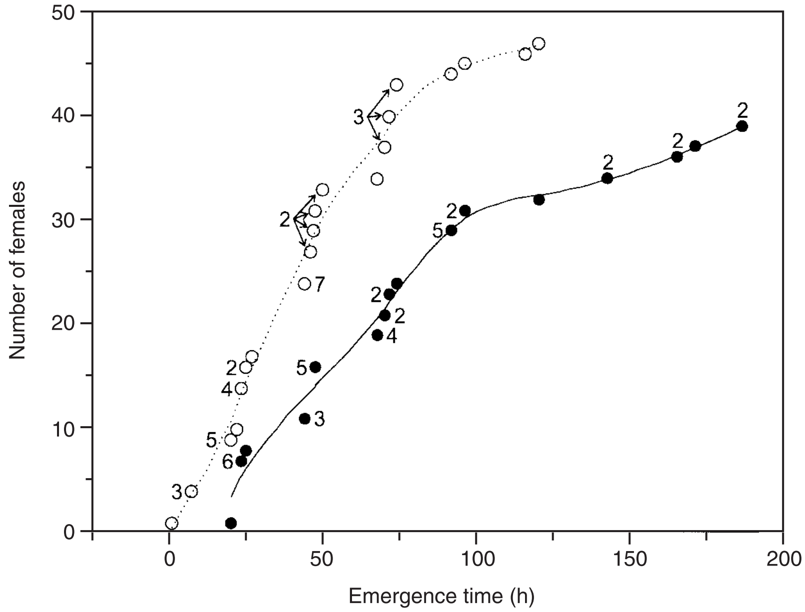

Fig. 3. Emergence time of females that were reared alone (○; dotted line) or with another larva (●; solid line). Note that emergence time is the length of egg-to-adult developmental period for each female minus the value of the female with the shortest developmental period. Number of females emerging at a given time indicated by appropriate points when $n > 1$. Lines were fitted by cubic spline interpolation, and are shown to guide the reader's eye.

effect, it is worth noting that only one of the first 10 females to emerge had been reared with another larva. This early emergence advantage persisted for approximately 2 days, with 31 of the first 47 (66.0%) females that emerged having been reared alone. In contrast to the patterns observed for emergence time, competition treatment did not have a significant effect on longevity (i.e. baseline survival) of females ($\chi^2_1 = 1.10$, $P = 0.30$) (Fig. 4). Analysis of covariance revealed only a marginally significant positive effect of body mass on longevity in females reared with another larva ($Z_1 = 1.90$, $P = 0.057$). Overall, there was a significant, albeit weak, negative correlation between emergence time and longevity ($r = -0.26$, $n = 86$, $P = 0.016$).

Emergence time was negatively correlated with mass-corrected number of eggs laid ($F_{1,83} = 3.30$, $P = 0.0014$), although a larval competition effect was not detected ($t_{1,83} = 1.25$, $P = 0.22$). Early emerging females (i.e. those with relatively shorter developmental periods) tended to lay more eggs than predicted for their body mass than those that emerged late (Fig. 5a). There was no evidence for a significant interaction between treatment and emergence time (ANCOVA: $t_{1,82} = 0.14$, $P = 0.89$). Longevity also had a significant effect on mass-corrected number of eggs laid ($t_{1,83} = 3.07$, $P = 0.0029$), and a larval competition effect was again not detected ($t_{1,83} = 0.45$, $P = 0.65$). Females that lived relatively long typically laid more eggs than predicted for their body mass than those with short life spans (Fig. 5b). Although we did not monitor egg-laying rates at set intervals in this experiment, females tend to lay most of their eggs early in life. For example, a sample ($n = 86$) of scramble strain *C. maculatus* females laid 61.3 ± 1.9% of their eggs within the first 48 h after emergence

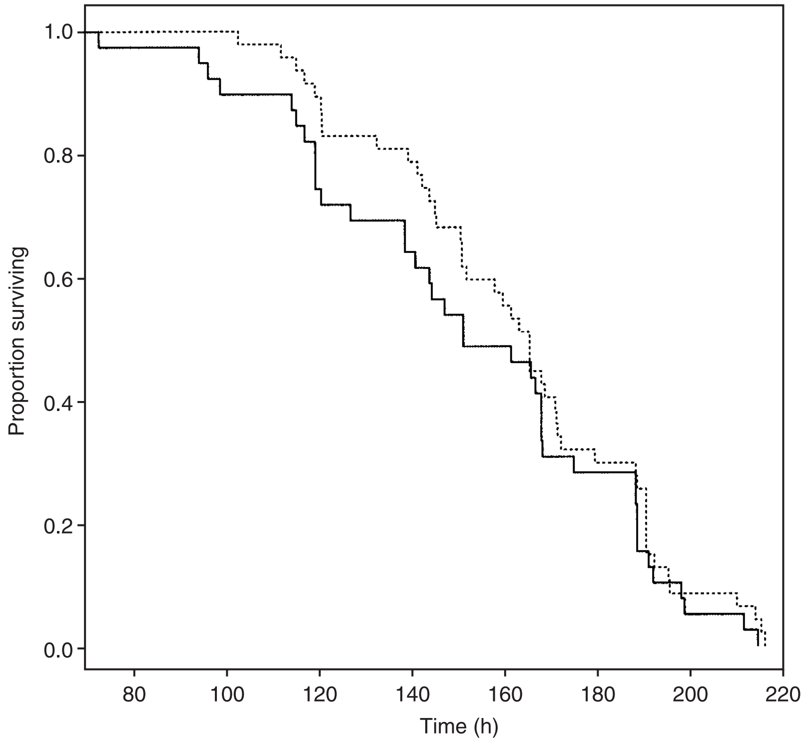

Fig. 4. Survivorship curves for females that were reared alone (dotted line) or with another larva (solid line). Relationships derived by applying a Cox proportional hazards model.

(D. Schade and S. Vamosi, unpublished data). Therefore, we expect that higher egg-laying rates early in life may have had a greater effect on the difference than the fact that long-lived females simply had more time to lay eggs. Finally, there was no evidence for an interaction between treatment and longevity (ANCOVA: $t_{1,82} = 0.88$, $P = 0.38$).

DISCUSSION

Competition is typically assumed to affect fitness only indirectly through its effects on body size (e.g. Colegrave, 1993; Ellers *et al.*, 1998; Hirschberger, 1999). Here, we tested the direct effects of competition on fecundity after accounting for potential effects on body mass in female bruchid beetles. Additionally, to extend the results of earlier studies (Colegrave, 1993; Vamosi, 2005), we monitored the effects of competition on length of developmental period and longevity, to test the associations between these life-history traits and mass-corrected fecundity. Mean female mass was not affected by competition treatment, possibly because there may be complex strain × resource × initial larval density interactions (Mitchell and Thanthianga, 1990; Toquenaga and Fujii, 1990; Messina, 2004; Vamosi, 2005). A lack of an effect of larval competition on adult mass in contest – but not scramble – strains may be attributable to size-mediated survival in the study by Toquenaga and Fujii (1990). However, our analyses included only those females that emerged from beans that produced another adult. The comparable mass at emergence of females in the two treatment groups appears to be associated with an increased

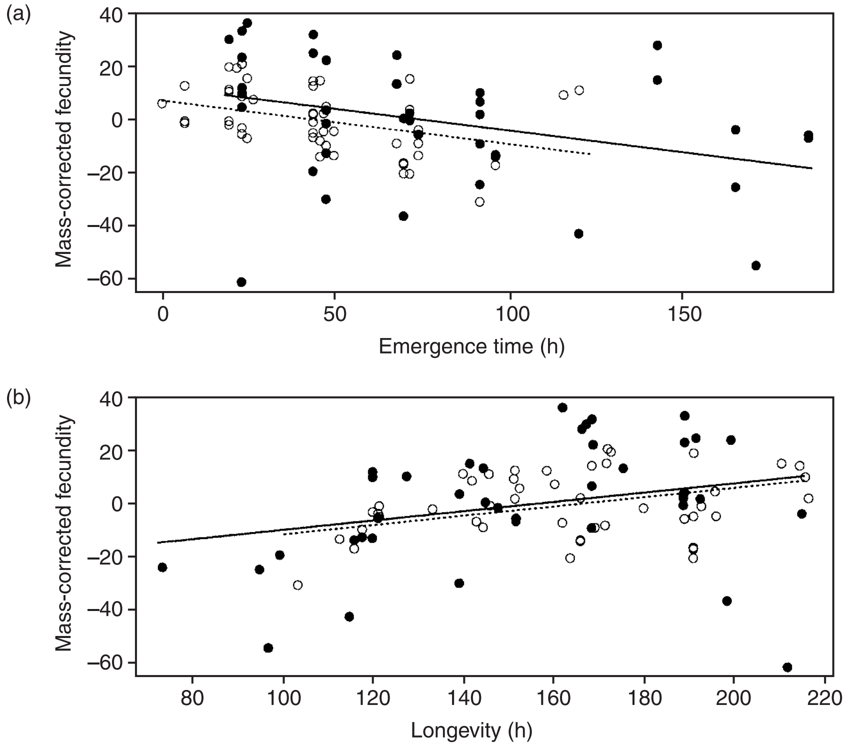

Fig. 5. Mass-corrected number of eggs laid as a function of emergence time (a) and longevity (b) for females that were reared alone (○; dotted line) or with another larva (●; solid line).

egg-to-adult developmental period in females reared with another larva. Although a willingness for females to accept a longer developmental period to maintain body mass in the face of competition has been observed in other studies (e.g. Bédhomme *et al.*, 2003), to our knowledge this is the first demonstration that it does not lead to a full recovery of mass-corrected fecundity.

Despite the lack of an effect of competition on mass, we detected a significant reduction in the number of eggs laid by females of a given mass in response to competition. One possible explanation for these findings, in addition to those considered earlier (Vamosi, 2005), is the limited supply of a micronutrient within beans essential for egg production but not growth (Colegrave, 1993). We also observed increased variation in mass-corrected fecundity in females that experienced the opportunity for competition. At present, we do not fully understand why some females show markedly greater responses to larval competition than others in terms of fecundity despite often achieving average to above-average body mass at emergence. Congruent patterns in scramble and contest competition strains suggest that direct interactions with other larvae are unlikely to be responsible. Further investigations into the proximate mechanism(s) resulting in reduced mass-corrected fecundity are warranted.

The effects of competition on mass-corrected fecundity of females are revealing in light of two previous studies (Colegrave, 1993; Vamosi, 2005). Colegrave (1993) first tested the assumption that larval competition affects fecundity only indirectly, through its effects on body mass, in bruchid beetles. This investigation, which was limited to one strain of *C. maculatus* reared on a single resource type, found that the relationship between fecundity and body mass was not affected by competition treatment. Vamosi (2005) conducted a similar investigation, with increased replicates of species, resource type, and levels of competition. The results of that study revealed variation in the outcome of competition, with two of five contrasts with different species–resource type combinations revealing a significant reduction, and a third contrast providing marginally significant evidence for a reduction, in mass-corrected fecundity of female seed beetles. Although the results of Vamosi (2005) called into question the assumption that mass-corrected fecundity is invariant to larval rearing densities, the main experiment was limited to scramble strains. The results of the current study concur with, and extend upon, those of a limited pilot experiment with this strain, briefly discussed in Vamosi (2005) – that is, no effect of competition on mean body mass accompanied by a significant reduction in mass-corrected fecundity. A partial explanation for the apparent absence of evidence for direct effects on fecundity may simply be the lack of studies that explicitly set out to measure these phenomena (but see Timms, 1998).

Competition had an effect on length of developmental period, whereas it had no effect on longevity. A negative effect of intraspecific competition on egg-to-adult developmental periods has been demonstrated for several insect species (e.g. Averill and Prokopy, 1987; Mercer, 1999; Tammaru *et al.*, 2000; Gibbs *et al.*, 2004), including *C. maculatus* (e.g. Thanthianga and Mitchell, 1990; Messina, 2004). As with body mass, the effects of competition on developmental periods may be strain-specific (Messina, 1991a). Given the ecology of bruchid beetles attacking grain stores, we expect that an increased development time may be quite costly for contest competition strain females. There is considerable evidence to suggest that females prefer beans that have not been previously parasitized, although they will superparasitize egg-laden beans when beans are in limited supply (e.g. Messina and Renwick, 1985; Messina *et al.*, 1992; Horng, 1997; Cope and Fox, 2003). Eggs that are laid earlier will tend to hatch earlier, giving those larvae a size advantage in later contests with other larvae (Averill and Prokopy, 1987; Toquenaga and Fujii, 1990). Thus, females that escape competition as larvae may not only lay more eggs, but their offspring may experience higher survival rates because they tend to be laid earlier.

The lack of an effect of competition on longevity may be the result of several factors. One likely explanation is that longevity did not differ between competition treatments simply because mass at emergence did not differ between the competition treatments. Adult longevity in insects is positively correlated with pupal and/or adult mass (e.g. Parrella, 1983; Quiring and McNeil, 1984; Hess *et al.*, 1996; Sato *et al.*, 2004). Alternatively, the competition treatment may have elicited responses in fecundity and development time without constituting a sufficiently ‘stressful environment’ to affect the relationship between fecundity and longevity (Marden *et al.*, 2003). This possibility warrants further investigation with additional competition levels and resource types of varying quality.

In conclusion, we present results that demonstrate further that larval competition may directly affect adult fitness, even in the absence of reductions in mean body mass at emergence (see also Vamosi, 2005). Because intraspecific competition has the ability to regulate population dynamics of insect species, including economically significant pests (Ullyett, 1950; Beaver, 1974; Amezaga and Garbisu, 2000; Dukas *et al.*, 2001), we advocate further research into its direct effects on individual fitness. In addition to studies on other species with similar life histories, we advocate investigations into the behavioural and/or physiological bases of the observed reduction in mass-corrected fecundity and increase in developmental period. Depending on the ecological context, accumulation of frass and other chemical products may play a significant role (Jones *et al.*, 1990; Bédhomme *et al.*, 2005). Another promising avenue appears to be investigation of the potential sex-specific responses to larval densities (e.g. Bédhomme *et al.*, 2003; Gibbs *et al.*, 2004; Gibbs and Breuker, 2006). Bédhomme *et al.* (2003) monitored, among other traits, length of development period and adult mass of male and female mosquitoes (*Aedes aegypti* (Linnaeus)) reared alone or with a competitor, holding the amount of food per individual constant. Males maintained the length of their development period at the expense of adult mass, whereas the converse was true for females. Finally, we expect that significant advances in our understanding of the ecological and evolutionary consequences of intraspecific competition will result from the integration of disciplines that have traditionally been studied somewhat independently, such as investigations into the costs of multiple mating (Wilson *et al.*, 1999).

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