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SHORT COMMUNICATION

Size-independent effects of larval host on adult fitness in *Callosobruchus maculatus*

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Introduction

The conditions that organisms experience during development can have profound effects on adult fitness and behaviour. One way for this to happen is through nutritional effects, and the impact of juvenile feeding on subsequent fitness has been studied widely. One group of insects in which the effects of developmental conditions on adult traits have been studied particularly well is bruchid beetles, such as those in the genus *Callosobruchus* (Coleoptera: Bruchidae). These beetles develop as larvae within various cultivated legumes, such as black-eyed beans (*Vigna unguiculata*) and mung beans (*V. radiata*) (Southgate, 1979), and are restricted to the host chosen by their mother for the whole of their development (Mitchell, 1975). As these beetles do not feed as adults, their reproductive potential, longevity, and growth are determined entirely by resources accumulated during development. Hence, differences in bean quality are likely to be especially important. Indeed, previous studies on *Callosobruchus maculatus* (Fab.) have shown that host size (Credland *et al*., 1986), host species (Wasserman, 1986), and larval competition (Bellows, 1982; Wilson, 1989) can all affect larval survival and development time, and also the fecundity of emerging adults.

In most of these studies, the effects of developmental conditions on female lifetime fecundity have not been measured directly. Instead, the emergence size of females has been used as a surrogate measure (e.g. Smith & Lessells, 1985; Colegrave, 1995), because there is a strong relationship between female fecundity and emergence size (Credland *et al*., 1986). This assumes, however, that the only effects of developmental conditions on fecundity are via effects on size, and that there are no direct effects on fecundity. In other words, the relationship between fecundity and elytral length is the same for beetles that develop under different conditions.

Although Colegrave (1993) has shown that this is so for *C. maculatus* larvae raised with or without competition in a single host species, it might not apply to situations where the bean species differ. This paper reports an investigation into a potential effect of larval host on adult fitness in *C. maculatus*. The effects of larval host type on female fecundity, independent of any effect on emergence size, were examined. Beetles were raised in two hosts (black-eyed bean and mung bean), and their lifetime fecundity and elytral length were measured. The relationship between fecundity and size for beetles raised in each host type was compared.

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Materials and methods

The Campinas strain of Mitchell (1975), Credland *et al*. (1986), and Colegrave (1993) was used. It is derived from a stock cultured at Royal Holloway and Bedford New College, University of London, which was originally collected in Brazil in 1975, and has been cultured on black-eyed beans since then. All the experiments were performed on beetles from a single subculture, and were carried out at 30 °C, the optimum temperature for development (Giga & Smith, 1983).

To obtain adults from different host types, ≈ 250 adult female *C. maculatus* beetles were placed in a container with an excess of males and 300 black-eyed beans or mung beans, and allowed to oviposit overnight (19 h). This was sufficient time to allow at least one egg to be laid on each bean. The beans were then examined, and egg load was reduced to one per bean by removing excess eggs with a scalpel. This removes any confounding effects of larval competition. Beans were incubated at 30 °C in individual cells in a partitioned Petri dish to ensure that emerging beetles could not mate, and females could not begin to lay eggs. After 3 weeks, the beans were examined daily and any newly-emerged adults were removed and sexed using elytral patterns (Southgate *et al*., 1957). Thus, all beetles used in the experiments were virgins and had emerged within the previous 24 h.

To measure female lifetime fecundity, twenty-one pairs of males and females from each type of host bean were each given 100 black-eyed beans for females to oviposit on. They were put in a container that allowed the beans to cover the bottom in a single layer (≈ 8 cm diameter) so that all beans were equally accessible. After the females died (≈ 6 days), the total number of eggs laid on all the beans was counted to measure their lifetime fecundity. The female's left elytron was removed and measured (to the nearest 0.02 mm) using a binocular microscope and micrometer eyepiece; this has been shown previously to be an accurate measure of body size in this species (Wilson, 1989).

Results and discussion

Larval host did not affect female emergence size, but did affect female lifetime fecundity (Fig. 1). Females raised in black-eyed beans did not differ in size from those raised in mung beans ($t = 0.79$, d.f. $= 40$, $P =$ NS), but they laid fewer eggs ($t = 2.95$, d.f. $= 40$, $P < 0.01$).

Overall, there was a relationship between lifetime fecundity and adult female elytron length (Fig. 2), with bigger females laying more eggs. When larval host was fitted as a factor in an ANCOVA (Sokal & Rohlf, 1981), with elytral length as a covariate, the interaction between host and elytral length did not explain a significant amount of the variance in fecundity ($F_{1,38} = 0.50$, $P =$ NS), indicating that there was no significant difference in the slope of the relationship between fecundity and size for the two treatments. This means that any direct effect of host type on fecundity can be determined by omitting the interaction term from the analysis, and when this was done, larval host explained a significant amount of the remaining variance ($F_{1,39} = 9.43$, $P < 0.01$). The larval host type does affect fecundity directly, independently of any effect on adult size, and a beetle raised in a mung bean lays, on average, 7.5 (≈ 8%) more eggs than a beetle of the same size raised in a black-eyed bean.

The relationship between fecundity and size has been demonstrated previously in *Callosobruchus* beetles (Smith & Lessells, 1985; Credland *et al.*, 1986; Messina, 1991), and many other insect species (Varley *et al.*, 1973; Waage & Ng, 1984; Charnov & Skinner, 1985). However, so far as the author is aware, a difference in the relationship for larvae raised in different larval hosts has not been reported previously. Data on another strain of *C. maculatus* appear to show a similar pattern (see Fig. 1 in Kawecki, 1997): females raised in mung or red beans had different fecundities but apparently similar weights, although the relationship between fecundity and size on the two hosts was not examined explicitly.

One way for larvae developing in black-eyed beans to compensate for their lower fitness to body size ratio might be to spend longer developing, and thus emerge at a larger size; there seems to be more than enough resource left for further development. The fact that the beetles in this experiment did not differ in size suggests that this does not occur. Perhaps the fact that they are stored-product pests (Southgate, 1979) can account for this. Stored-product pests usually occur in rapidly expanding populations. Under these conditions, there should be strong selection for rapid development, so that females can begin egg laying as quickly as possible before the resources are exhausted. Under these circumstances, delaying maturation to maximize the number of eggs laid may not be the main target of selection.

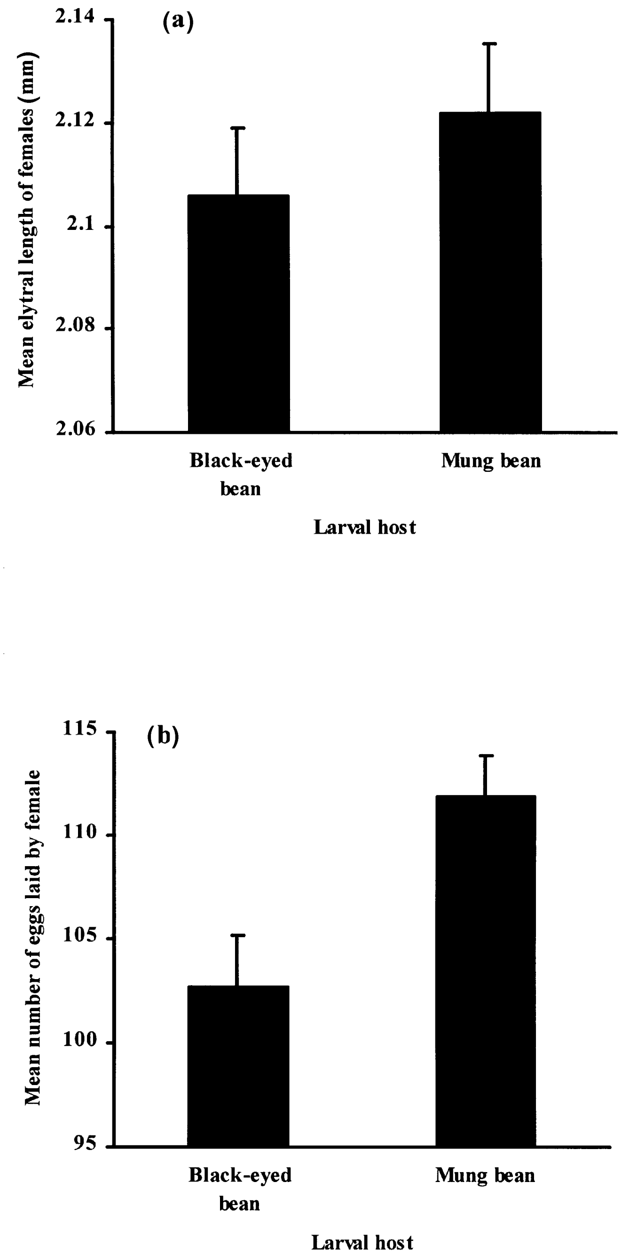

Fig. 1. The effect of larval host (black-eyed bean or mung bean) on (a) mean elytral length and (b) mean lifetime fecundity of female *Callosobruchus maculatus*. Error bars represent one standard error.

It is unclear why bean type should affect fecundity without affecting emergence size. One possibility is that different hosts provide different qualities of resource (Janzen, 1977). A particular host species could boost fecundity by providing micronutrients or vitamins necessary for egg production, that are not essential for normal body growth. Alternatively, fecundity might be depressed by toxins, either from toxin accumulation, or mediated through costs of detoxification. A

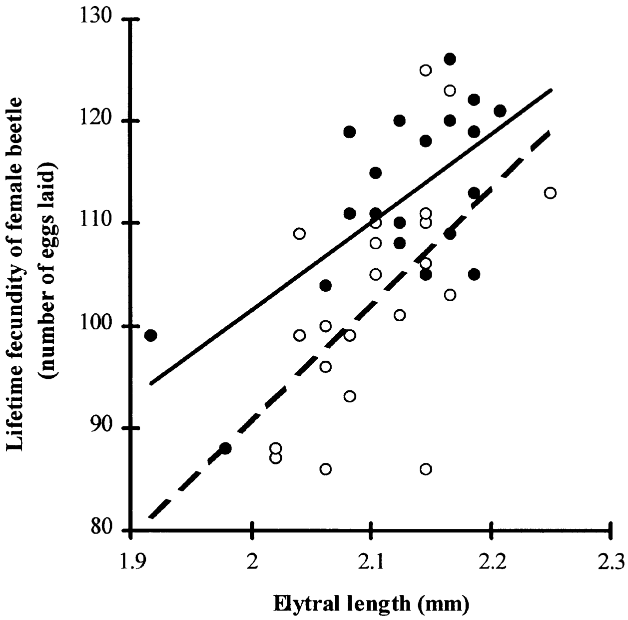

Fig. 2. The relationship between female lifetime fecundity and elytral length in black-eyed bean hosts (○, broken line: fecundity = 114 elytra – 137, $r^2 = 0.35$) and in mung bean hosts (●, solid line: fecundity = 86 elytra – 68, $r^2 = 0.46$).

further explanation is that females from different hosts may lay different sized eggs. Life-history theory predicts that, due to the finite amount of resources available for egg production, there will be a trade-off between the size and the number of eggs that a female can lay (Lessells, 1991; Roff, 1992). Whilst there is known to be variation in egg size in *C. maculatus*, this is due largely to egg size decreasing with maternal age (Fox, 1993). Although egg size was not measured in this study, it is not obvious why females raised in different bean species should alter the size of the egg that they lay.

Colegrave (1993) showed that the relationship between fecundity and emergence size did not differ for *C. maculatus* larvae raised with and without competition. It may be that differences in conditions are greater when larvae are raised in beans of different species. Competition reduces the amount of resource, whereas different species of bean affect the type of resource accessible to larvae.

It is interesting that mung bean appears to be the better host, considering that this strain was originally isolated from black-eyed beans, and has been cultured on this host for the last 21 years (P. Credland, pers. comm.). Although natural selection is expected to produce organisms that are well adapted to their normal environment, this does not mean that they will never have higher fitness when transferred to a novel environment. Indeed, many species of bruchid beetles that normally develop in wild legumes that have a high toxin content, have a much higher fitness if allowed to develop in cultivated legumes that have been selected for a low toxin content (Toquenaga & Fujii, 1990).

This study shows that larval host does affect fecundity directly, with beetles raised in mung beans having a higher fitness per unit body size.

Moreover, the lack of a difference between the sizes of beetles raised in the two host types suggests that beetles from mung beans have a higher absolute fitness, as well as a higher fitness per unit size. These findings suggest that body size might not always be a suitable surrogate for fitness in studies comparing individuals raised in different hosts.

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