The influence of egg size on offspring performance in the seed beetle, Callosobruchus maculatus

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Variation in egg size among female insects is often correlated with the performance of their offspring. In the seed beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae), egg size varies both within and among females. Here I test the hypothesis that *C. maculatus* offspring developing from larger eggs perform better than offspring from smaller eggs. I find that offspring from large eggs develop faster, and emerge as larger adults, than offspring from small eggs. There was at best a weak effect of egg size on larval survivorship (significant in one of three analyses).

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Egg size often varies among females within insect populations, and this variation is often correlated with offspring performance: progeny from larger eggs generally survive better, develop faster, and emerge larger than progeny from smaller eggs (reviewed in Fox 1993). Thus, selection for large egg size, counterbalanced by an egg size/egg number trade-off, may be responsible for maintaining egg size variation within populations (but see Rossiter et al. 1988). However, numerous studies have failed to detect an effect of egg size on offspring performance (Richards and Myers 1980, Wiklund and Persson 1983, Steinwascher 1984, Karlsson and Wiklund 1984, 1985, Wiklund and Karlsson 1984, Fox 1993). These latter studies have raised questions about the evolution of egg size in natural populations of these insects.

In the seed beetle, *Callosobruchus maculatus* F. (Coleoptera: Bruchidae), egg size varies substantially among females (Fox 1993). Much of this variation can be explained by variation in female size (Fox 1993) and age (Wasserman and Asami 1985, Fox 1993). Older female *C. maculatus* lay smaller eggs than younger females, corresponding to a maternal age effect on offspring life history: larval development time increases, and survivor-ship decreases, with increasing maternal age (Wasserman and Asami 1985, Fox 1993, Fox and Dingle 1994). These results suggest that egg size directly affects larval development rate and survivorship. However, Fox (1993) was unable to detect an effect of variation in egg size on progeny performance when female age was controlled for. In this paper, I examine whether among-female variation in egg size influences among-family variation in larval life-history, independent of female age. I discover that offspring developing from larger eggs develop faster and become larger adults than offspring developing from smaller eggs.

Methods

Natural history

Callosobruchus maculatus (Fabricius) (Coleoptera: Bruchidae) is a cosmopolitan pest of stored legumes (Fabaceae). These beetles have likely been associated with dried legumes for thousands of years (Mitchell 1983, Messina 1991), and their life cycle appears well adapted
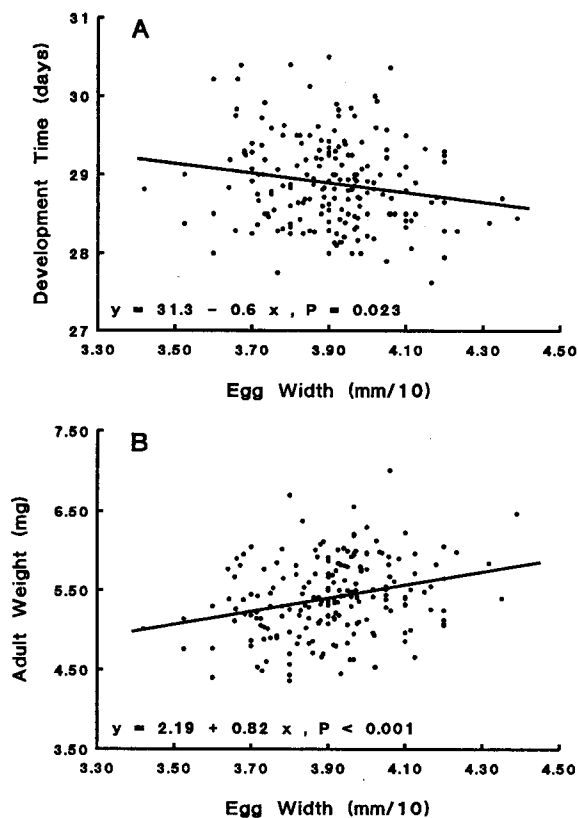
Fig. 1. The influence of egg width on (A) development time and (B) adult weight at emergence for female offspring of *Calloso-bruchus maculatus*. Analyses are based on family means (195 families). Data for male offspring are qualitatively the same (dev. time: $y = 31.9 - 0.8x$, $P = 0.004$; adult wt: $y = 2.17 + 0.53x$, $P < 0.001$).

for reproduction in a storage environment. Following mating, females cement their eggs to the surface of host seeds (Southgate 1979). Approximately 4–5 d later (at 26–28°C), the eggs hatch and the first instar larvae burrow through the seed coat and into the seed. Larval development and pupation are completed entirely within a single seed, without access to an external source of food or water. This beetle's short generation time and ease of laboratory rearing in a semi-natural storage environment make *C. maculatus* an excellent animal for life-history studies.

All beetles used in these experiments were collected from infested pods of cowpea (*Vigna unguiculata*) in Niamey, Niger, at the Univ. of Niamey Experiment Station. Beetles were maintained in laboratory growth chambers for approximately 37 generations at large population sizes (more than 1000 individuals per generation) before this experiment. The experiments reported here were performed at constant light, 26°C.

Experimental design

Virgin females, collected from isolated seeds within 12 h of adult emergence, were each presented with a single virgin male in a 30-mm petri dish and allowed to copulate. Following a single copulation, each female was transferred to a 60-mm petri dish containing approximately 25 dried cowpea seeds (*V. unguiculata*), estimated by volume, and allowed to oviposit for 12 h. Females were then transferred to another 60-mm petri dish, also containing approximately 25 cowpea seeds, and allowed to oviposit for another 12 h.

Length and width of all eggs laid during the first 12 h post-mating were measured using an optical micrometer on a 50× dissecting scope. Because eggs are glued directly to host seeds, the eggs cannot be removed and weighed without damaging them. Although I cannot report a correlation between egg dimensions and either egg mass or egg volume, following many hours of visually inspecting eggs, and after considering the results of previous experiments (Fox 1993), I am confident that these two morphological characters are sufficient to quantify
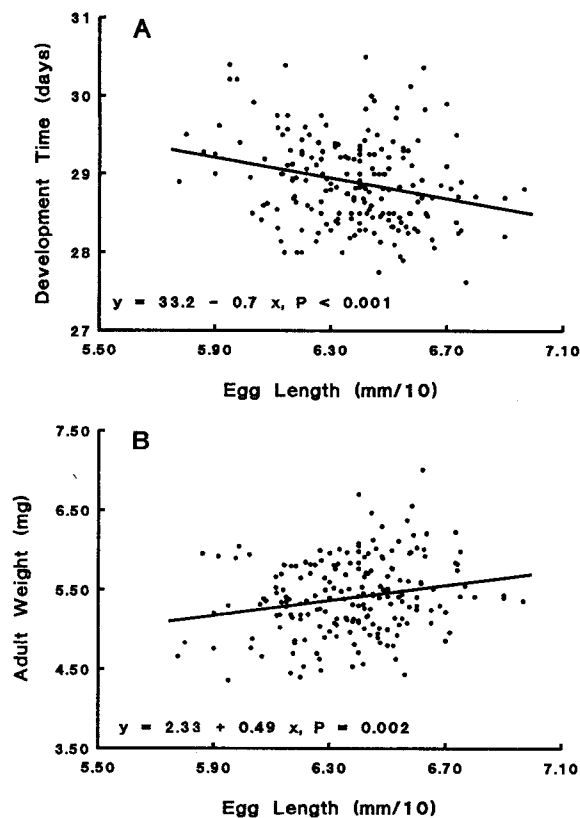

Fig. 2. The influence of egg length on (A) development time and (B) adult weight at emergence for female offspring of *Calloso-bruchus maculatus*. Analyses are based on family means (195 families). Data for male offspring are qualitatively the same (dev. time: $y = 32.3 - 0.6x$, $P = 0.007$; adult wt: $y = 2.02 + 0.35x$, $P = 0.004$).
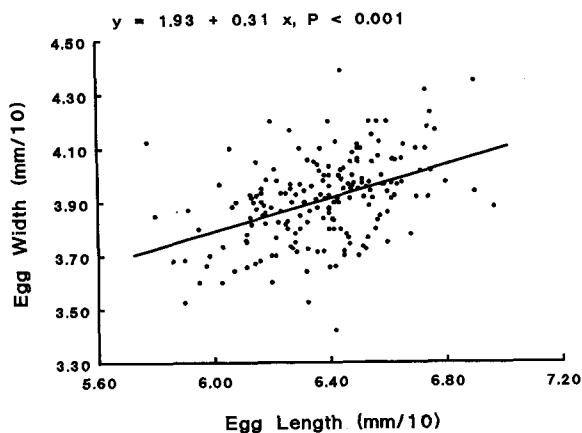
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y = 1.93 + 0.31 x, P < 0.001

Fig. 3. The relationship between egg width and egg length for *Callosobruchus maculatus* (n = 195 females).

egg size. The results presented below confirm this observation.

All eggs laid during the first 24 h were reared to adult at densities of one beetle per seed, 26°C, constant light. Development time was estimated as the time between egg-laying and adult emergence, and thus includes embryonic, larval, and pupal development time. Emerging adults were collected and weighed individually on an electronic balance within 16 h of adult emergence. Larval survivorship was also recorded.

To determine the influence of egg size on offspring performance, 3206 offspring from 195 families were reared to adult. Family means of each performance estimate were regressed against their mother's mean egg width and egg length using the MGLH procedure of Systat (Wilkinson 1990). Distributions of development time, body weight, and both measures of egg size (length and width) were consistent with the assumptions of the linear models applied here, and thus no transformations were necessary.

Results and discussion

Among-female variation in egg width and egg length influenced both larval development time and body size of *C. maculatus*: offspring from wider eggs developed faster and emerged as larger adults (Fig. 1) than offspring from smaller eggs. The results for egg length are qualitatively identical (Fig. 2). This is not surprising because egg length and egg width were positively correlated (Fig. 3), such that large eggs tended to be both wide and long. Because body size is positively correlated with egg load and lifetime fecundity (Credland et al. 1986, Møller et al. 1989, Wilson and Hill 1989), these results suggest variation in lifetime fecundity is also correlated with the observed egg size variation in *C. maculatus*.

For most families, survivorship was 100%, such that

the statistical models used above cannot be applied to these survivorship data. Instead, survivorship data were analyzed in two different ways. First, families were divided into two classes: those with survivorship of 100%, and those with survivorship less than 100%. Egg size was compared between the two classes. In this analysis, there was evidence for a weak effect of egg width on survivorship (1-sided Mann-Whitney U-test, U = 3980, χ^2 = 2.73 with 1 df, P = 0.049), but no difference in egg length between the two survivorship classes (1-sided Mann-Whitney U-test, U = 3066, χ^2 = 0.281 with 1 df, P > 0.05). Second, the regression between egg size and survivorship was examined after all families with 100% survivorship were deleted from the data set. Here, there was no evidence for a relationship between egg size on offspring survivorship (y = survivorship, x = egg size; egg width: y = 1.21−0.08 x, P > 0.05; egg length; y = 0.75 + 0.02 x, P > 0.05)

These results are consistent with those of most experiments examining egg size − offspring performance relationships: offspring developing from larger eggs often hatch earlier (Rossiter 1991, Wallin et al. 1992), have higher hatching success (Richards and Myers 1980, Simmons 1988), higher larval survivorship (Wallin et al. 1992), develop faster (Steinwascher 1984, Yuma 1984, Rossiter 1991), develop into larger adults or pupae (Steinwascher 1984, Yuma 1984, Honek 1987, Rossiter 1991), breed earlier (Sibly and Monk 1987), and/or have higher starvation tolerance (Solbreck et al. 1989, Carlberg 1991, Tauber et al. 1991, but see Lamb and Smith 1980) or desiccation tolerance (Sota and Mogi 1992). However, some studies have failed to detect an effect of egg size on offspring performance (Richards and Myers 1980, Wiklund and Persson 1983; Steinwascher 1984, Karlsson and Wiklund 1984, 1985, Wiklund and Karlsson 1984). In these latter systems, it is likely that egg size variation may have implications for offspring performance only under adverse conditions, such as during larval competition, periods of starvation, desiccation, or when larvae feed on low quality hosts (Solbreck et al. 1989, Carlberg 1991, Tauber et al. 1991, Sota and Mogi 1992, but see Lamb and Smith 1980). Alternatively, Murphy et al. (1983) and Karlsson and Wiklund (1984) have suggested that, in some systems, variation in egg size may have little effect on offspring above some minimum egg size, while there may be a minimum egg size below which survivorship dramatically decreases.

In a previous experiment with another population of *C. maculatus* I was unable to detect an effect of egg size on development time, body size, or survivorship (Fox 1993). These earlier results were interpreted as a possible consequence of using a high quality host under low density conditions, which may obscure egg-size effects detectable only under adverse conditions (discussed above). However, the design of the experiment presented here was nearly identical to that of Fox (1993), likewise using a high quality host under low density conditions, and yet egg size effects were detected for two characters. Thus, it

is unclear whether the differences among experiments represent among-population differences, or are possibly due to the substantially smaller number of families examined in Fox (1993).

The observed egg size variation within this Niger population of C. maculatus may be maintained by balancing selection simultaneously favoring both large eggs and numerous eggs. Although females tend to avoid laying eggs on host seeds which are currently occupied by other conspecific eggs (Mitchell 1975, Messina and Renwick 1985a,b, Wilson 1988), high population densities generally result in multiple eggs being laid on a single seed, and thus competition among larvae for a limited resource (Messina 1991, Toquenaga 1993). Because larvae from large eggs can assimilate resources faster than larvae from small eggs (Figs 1 and 2), large egg size may provide an advantage in larval competition. This is consistent with the observations of Messina (1991), who notes that eggs of his S strain, in which larvae compete vigorously, are approximately 8% larger than eggs in his I strain, in which larvae are less competitive. However, if an egg size/egg number trade-off exists, such that females producing large eggs lay fewer eggs than females producing small eggs (e.g. Leather and Burnard 1987, Berrigan 1991), selection may also favor small eggs, particularly when population densities are low and larval competition is less intense. This egg size – egg number trade-off has not yet been documented for C. maculatus, but is particularly likely because females generally do not feed as adults, and thus have limited resources for egg laying.

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