Dietary mediation of maternal age effects on offspring performance in a seed beetle (Coleoptera: Bruchidae)

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Summary

1. In many animals, egg size and offspring performance (e.g. development time, body size and survivorship) are observed to decrease with increasing maternal age. This observed maternal age effect is generally attributed to a depletion of the female's resources.

2. We first quantify the influence of maternal age on offspring performance of the seed beetle, *Callosobruchus maculatus*. We then manipulate a female's nutritional status by providing either unlimited access to yeast and sugar–water, or by completely preventing access to yeast and sugar–water, and examine whether adult feeding reduces the magnitude of maternal age effects on egg size and offspring performance.

3. Offspring egg-to-adult survivorship decreased, while offspring development time increased, with increasing maternal age. There was at best a very weak effect of maternal age on offspring body size and no detectable effect on the proportion of eggs which hatched.

4. Adult feeding on yeast and sugar–water resulted in reduced development time and increased survivorship of offspring produced by old mothers, but had no detectable effect on offspring body size.

Key-words: *Callosobruchus maculatus*, egg size, larval performance, life history, nutrient stress

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Introduction

Maternal age influences offspring quality in many species of insects (Parsons 1964; Mousseau & Dingle 1991). Much of this influence may be mediated through maternal age effects on egg size (Mousseau & Dingle 1991): young mothers frequently lay larger eggs than old mothers (Leonard 1970; Harvey 1977; Jones, Hart & Bull 1982; Murphy, Launer & Ehrlich 1983; Wiklund & Persson 1983; Yuma 1984; Karlsson & Wiklund 1984, 1985; Wasserman & Asami 1985; Boggs 1986; Svard & Wiklund 1988; but see Moore & Singer 1987), and large eggs generally hatch earlier (Rossiter 1991; Wallin *et al.* 1992), have higher hatching success (Richards & Myers 1980; Simmons 1988), and produce larvae which have 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 & Monk 1987),

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and/or have higher starvation tolerance (Solbreck *et al.* 1989; Carlberg 1991; Tauber, Tauber & Tauber 1991; but see Lamb & Smith 1980) or desiccation tolerance (Sota & Mogi 1992).

This observed effect of maternal age on egg size, and thus offspring performance, is generally attributed to a depletion of the female's resources (Richards & Myers 1980; Wiklund & Karlsson 1984; Begon & Parker 1986). Although female insects frequently emerge as adults with numerous eggs already matured and ready to oviposit (Wilson & Hill 1989), in many species females subsequently mature more eggs, which are either oviposited or later resorbed (Engelmann 1970; Wilson & Hill 1989). Due to the gradual exhaustion of the female's resources, eggs that are matured post-emergence may be smaller and of poorer quality than eggs matured pre-emergence, particularly when the females are nutrient stressed. Maternal feeding has been reported to increase egg size in many insects (Harvey 1983; Murphy *et al.* 1983; Steinwascher 1984; Wallin *et al.* 1992), supporting this hypothesis of resource depletion.

In the bruchid beetle, *Callosobruchus maculatus*, older females lay smaller eggs than younger females
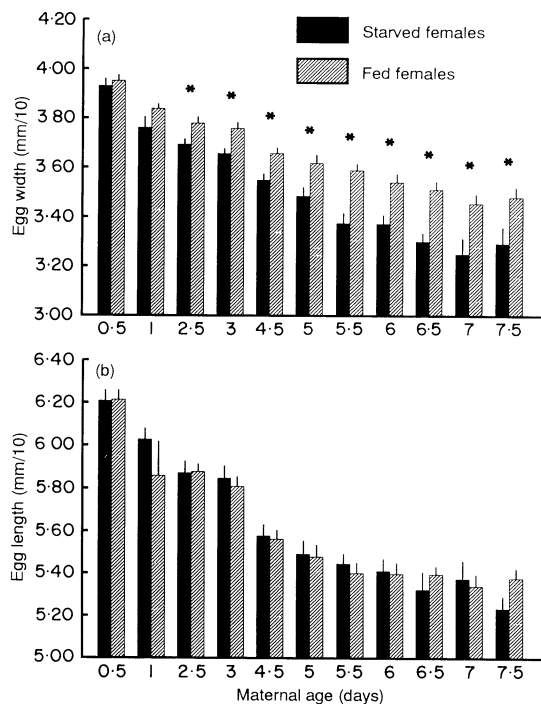
Fig. 1. The influence of maternal age and nutritional status on (a) egg width and (b) egg length for *Callosobruchus maculatus*. Eggs laid by younger mothers were significantly larger than eggs laid by the same mothers when they were older (Wilcoxon signed-rank tests, $P < 0.05$). *Significant treatment differences within an age class (Mann–Whitney U-test, $P < 0.05$). See Fox (1993a) for details.

(Wasserman & Asami 1985; Fox 1993a). Larvae hatching from eggs laid by older females also develop more slowly and have lower survivorship than offspring from eggs of younger females (Wasserman & Asami 1985; Fox 1993a). In the experiments reported here, we examine the influence of a female's nutritional status on offspring performance in the seed beetle, *C. maculatus* (Coleoptera: Bruchidae) by manipulating female access to food and water. Fox (1993a) found that maternal diet had a large effect on the size of eggs produced by old females (Fig. 1). Here, we extend the results of Fox (1993a) by quantifying the influence of maternal diet on egg hatchability, offspring survivorship, offspring development time and offspring body size in *C. maculatus*.

Materials and methods

NATURAL HISTORY

Callosobruchus maculatus (Fabricius) is a cosmopolitan pest of stored legumes (Fabaceae), particularly beans of the genus *Vigna*. Females cement their eggs to the surface of host seeds (Messina 1991; Fox 1993b). Approximately 4–5 days 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.

Populations of *C. maculatus* are most commonly detected in stores of dried legumes. These beetles have likely been associated with dried legumes for thousands of years (Mitchell 1983; Messina 1991), and their life cycle appears well adapted for reproduction in a storage environment. Reproduction without access to food and water is typical for adults in storage conditions. Although adults will readily feed on yeast and sugar–water in the laboratory, which increase both survivorship and egg production of adult females (Møller, Smith & Sibly 1989; Fox 1993c), emerging adults require neither food nor water to reproduce. This beetle's short generation time and ease of laboratory rearing in semi-natural storage environment make *C. maculatus* an excellent animal for life-history studies.

All beetles used in these experiments were collected from stored azuki seeds [*V. angularis* (L.) Willd.] near San Francisco, California (Fox 1993b). The laboratory population was established with more than 1000 eggs and maintained on azuki seeds, at 27 ± 1 °C, 24 h light. The experiment presented here was performed at 26 ± 0.5 °C, 24 h light. Beetles from approximately the 20th laboratory generation were used in this experiment.

MATERNAL AGE AND NUTRITIONAL STATUS INFLUENCES ON EGG SIZE AND OFFSPRING

Performance

To produce full-sib families for an analysis of the influence of maternal age and maternal nutritional status on offspring performance, virgin females, collected within 12 h of adult emergence from isolated seeds, were presented with a single virgin male in a 30 mm Petri dish and allowed to copulate. Following a single copulation, females were transferred to 60 mm Petri dishes containing approximately 3·5 g dry azuki seeds (*V. angularis*) and allowed to oviposit. These were then divided into two treatment groups of 45 females each: (1) nutrient-stressed females, which were maintained without access to food or water; and (2) fed females, provided with baker's yeast (Red Star active dry yeast) *ad libitum* and a 5% sucrose solution (supplied in 0·5 dram shell vials stoppered with cotton). Every 12 h (until death) each female in each treatment was transferred to a new dish containing 3·5 g dry azuki seeds.

All offspring were reared to adult at densities of one beetle per azuki seed. Emerging adults were collected and weighed individually within 12 h of adult emergence. Beetles from age classes 1·5, 2, 3·5, and 4 days, however, were not reared to adult, and beetles from age classes 1 and 3 were not weighed as adults.

Data used in all statistical tests are the average larval survivorship, development time, or body size of
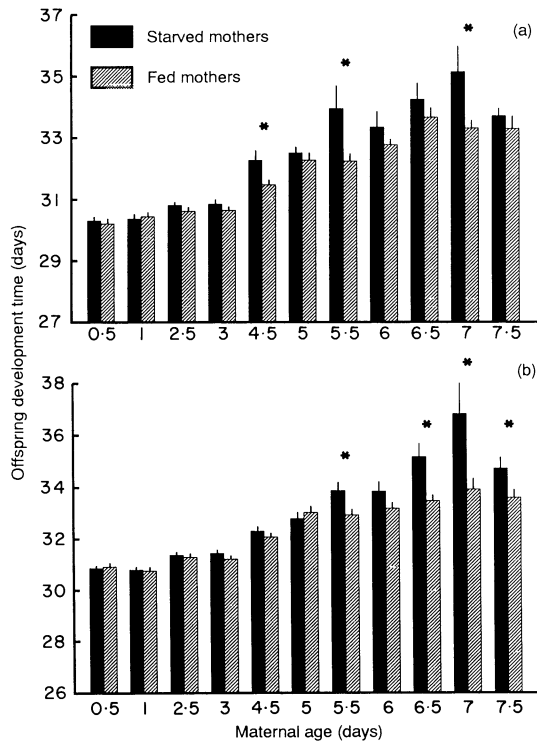
Fig. 2. The influence of maternal age and nutritional status on development time of (a) male and (b) female offspring for *Callosobruchus maculatus*. Offspring reared from eggs laid by young mothers developed significantly faster than offspring reared from eggs laid by the same mothers when they were older (Wilcoxon signed-rank tests, $P<0.05$). *Significant treatment differences within an age class (Mann–Whitney U-test, $P<0.05$).

Results

In total, 2302 offspring from 45 families were reared in the nutrient-stressed treatment, and 3617 offspring from 45 families in the treatment supplemented with yeast and sugar–water. The difference in number of offspring reared per treatment is due largely to the increased egg production by older females when they have access to yeast and sugar–water [see Fox (1993c) for discussion].

All statistical comparisons presented below are corrected for multiple comparisons using the sequential bonferroni procedure as described by Rice (1989).

MATERNAL AGE AND OFFSPRING PERFORMANCE

For both treatments and sexes, offspring of older mothers took significantly longer to develop than offspring of younger mothers: development time of offspring reared from eggs laid in age class 0·5 was shorter than development time of offspring reared from eggs laid in all other age classes, except age class 1·0 (Wilcoxon signed-rank tests, $P<0.05$) (Fig. 2). Although they developed more slowly, offspring of older mothers were only sometimes slightly smaller than offspring of younger mothers: in 13 of 32 comparisons, offspring of older age classes were smaller than beetles reared from eggs laid in age class 0·5 (Wilcoxon signed-rank tests, $P<0.05$) (Fig. 3).

offspring produced by each mother during each 12 h period post-emergence (age class). For example, the estimate of development time for offspring of female 1 in age class 6 is the average development time of all her offspring developing from eggs laid between 5·5 and 6 days post-emergence. Most analyses involve non-parametric methods (discussed below), and are corrected for multiple comparisons following the sequential bonferroni procedure of Rice (1989). Analyses of covariance are inappropriate to assess the effects of age for most comparisons because the covariate (age) is not a normally distributed continuous variable. Repeated-measures analyses of variance are likewise inappropriate because most major statistical packages (e.g. SYSTAT; Wilkinson 1990) are extremely sensitive to missing cells: any female that fails to lay eggs in even one age class must be deleted from the analysis (performed automatically by most statistical packages). This is troublesome because most females miss laying eggs in at least one of the older age classes (age class > 5), and thus the number of remaining families (without any empty cells) rapidly approaches 0 as older age classes are added to the analysis. Non-parametric statistical approaches avoid these concerns.
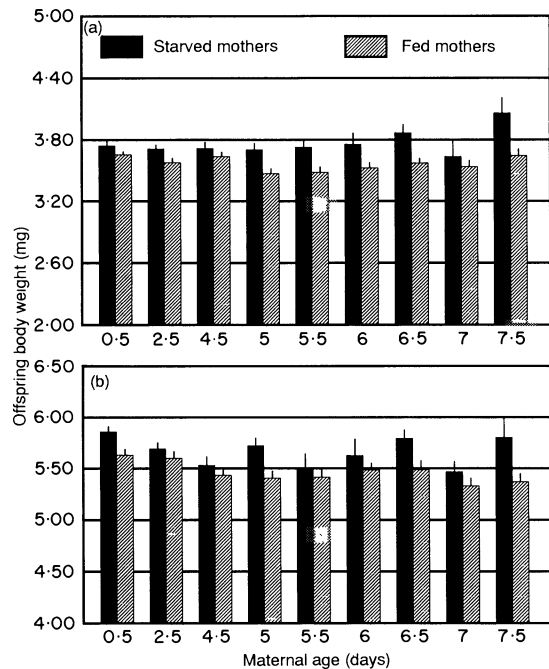

Fig. 3. The influence of maternal age on body size of (a) male and (b) female offspring. *Callosobruchus maculatus* offspring reared from eggs laid by young mothers developed to be approximately the same size (on average) as offspring reared from eggs laid by the same mother when she was older (Wilcoxon signed-rank tests, $P>0.05$). There were no significant treatment differences.
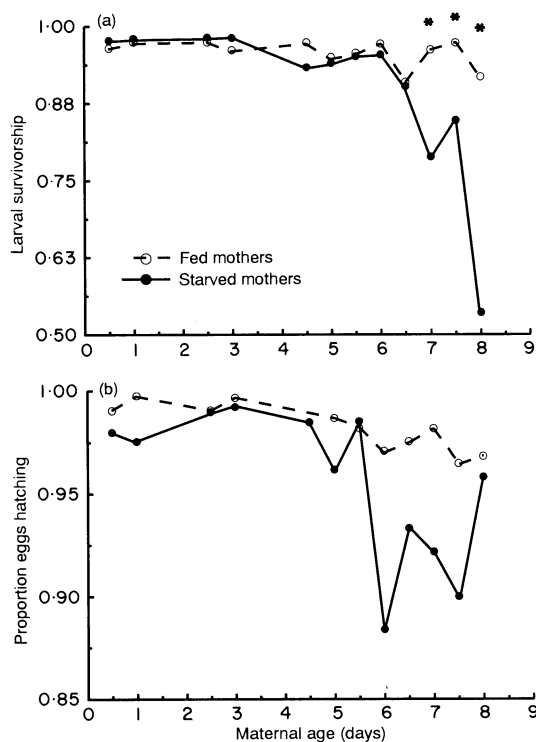
Fig. 4. The influence of maternal age on (a) larval survivorship and (b) egg hatchability of *Callosobruchus maculatus*. *Significant treatment differences within an age class (Mann–Whitney U-test, $P < 0.05$). There was no significant effect of age or treatment of egg hatchability.

Survivorship of offspring also decreased with increasing maternal age: larval survivorship of offspring laid in age classes 7 and 8 in the starved female treatment, and in age class 6·5 for the fed female treatment, differed significantly from survivorship of offspring laid in age class 0·5 (Wilcoxon signed-rank tests; $P < 0.05$) (Fig. 4a). Although there was a trend towards reduced egg hatchability as females aged, there was no significant effect of maternal age on the proportion of eggs which hatched (Wilcoxon signed-rank tests; $P > 0.05$) (Fig. 4b).

MATERNAL NUTRITIONAL STATUS AND OFFSPRING PERFORMANCE

Maternal feeding treatment (starved *vs* fed yeast and sugar–water) influenced development time (Fig. 2) and larval survivorship (Fig. 4a) of offspring from older mothers. Offspring from older mothers that had access to yeast and sugar–water developed faster than offspring from older mothers that were starved (Fig. 2; Mann–Whitney U-tests, $P < 0.05$). Similarly, offspring of older mothers that had been fed survived from egg hatch to adult better than offspring of starved mothers (Fig. 4a; Mann–Whitney U-tests, $P < 0.05$). There was no detectable effect of treatment, however, on the pro-

portion of eggs hatching (Mann–Whitney U-tests; $P > 0.05$) (Fig. 4b).

Analyses of treatment effects on body size were complicated in this experiment because body size of offspring in the two treatments differed in age class 0·5, for both male and female offspring (Fig. 3). This effect, however, cannot be accounted for as a treatment effect for two reasons: first, eggs laid in the first half-day are almost entirely matured before mothers eclose as adults (Wilson & Hill 1989) and thus are not influenced by adult feeding, and second, females in the fed treatment did not begin feeding on the yeast and sugar–water until well after the first half-day. This difference in body size among treatments thus appears to be due to either genetic or random differences in body size between beetles in the two treatments. To control for this difference, estimates of body weight for all age classes greater than day 0·5 were corrected by dividing each individual's body weight by the average body weight of that individual's siblings reared from eggs laid in age class 0·5. Following this standardization, there was no detectable effect of maternal feeding treatment on body size of her offspring (Fig. 3; Mann–Whitney U-tests, $P > 0.05$).

Discussion

For *C. maculatus*, egg size decreases with increasing maternal age (Fox 1993a; Fig. 1) and this corresponds with reduced offspring performance (Figs 2 and 4). Maternal feeding on yeast and sugar–water modulates the influence of maternal age on egg size (Fig. 1), offspring development time (Fig. 2) and larval survivorship (Fig. 4). The body size of offspring was generally unaffected by increasing maternal age and was not influenced by maternal feeding treatment (Fig. 3).

An initial inspection of Fig. 3 suggests that nutrient-stressed females produce larger offspring than fed females, suggesting a negative maternal effect. Negative maternal effects, in which smaller, less fecund females produce larger offspring, or in which late-maturing mothers produce offspring which mature earlier, have been reported for both insects (Janssen et al. 1988; Rossiter 1991) and vertebrates (e.g. Falconer 1965). However, it is unlikely the differences observed for *C. maculatus* represent negative maternal effects because (1) eggs laid in the first half-day are almost entirely matured before mothers eclose as adults (Wilson & Hill 1989), and thus are not influenced by adult feeding, and (2) females in the fed treatment did not begin feeding on the yeast and sugar–water until after the first half-day, such that the two treatments are effectively the same until after the first half-day. We thus believe these differences are the result of either genetic differences among the females in the two treatments, or to some other sampling error, and in our analyses of treatment effects on

offspring body size we have corrected our data for a difference in offspring body size during the first half-day. Following these corrections, there is no detectable effect of treatment on body size.

In this study, we were able to detect at best a very weak influence of maternal age on the body size of offspring. Similarly, Wasserman & Asami (1985) could not detect any influence of maternal age on offspring lifetime fecundity (which is positively correlated with body size; Credland, Dick & Wright 1986; Fox 1993c). These results imply that offspring can compensate for smaller size at hatch (because of smaller eggs) by extending the period of larval feeding. If offspring are capable of compensating for small egg size, we must wonder why females do not lay more small eggs rather than fewer large eggs? It may be that there is no trade-off between fecundity and egg weight for females with access to a food source, as is observed in insects such as the gypsy moth, *Lymantria dispar* (Rossiter, Schultz & Baldwin 1988). However, another explanation may be that our larvae were reared at low density on a uniformly high-quality resource. It is often found that variation in egg size may be of significance only when offspring are reared under adverse conditions, such as low quality or quantity of a resource (Solbreck *et al.* 1989; Carlberg 1991; Tauber *et al.* 1991; Sota & Mogi 1992; but see Lamb & Smith 1980). Thus, we may see many more dramatic effects of egg size on offspring survivorship, or in a larva's ability to compensate for small eggs, as host quality decreases. Also, in many populations of *C. maculatus*, multiple females may lay eggs on a single seed, and thus larvae may be forced to compete for resources (Mitchell 1975; Messina 1991). Under these conditions, offspring from large eggs may develop more rapidly (as suggested by Fig. 2), and thus have an advantage over offspring from small eggs, although this has yet to be explored experimentally.

Alternatively, variation in egg size may have little effect on offspring body size and survivorship above some minimum egg size, while there may be a minimum egg size below which survivorship dramatically decreases (Karlsson & Wiklund 1984). For example, there may be a minimum head capsule size below which a *Callosobruchus* larva cannot successfully penetrate the coat of an azuki seed, as has been suggested by Murphy *et al.* (1983) for *Euphydryas editha*. Our data would be consistent with this hypothesis because, at a maternal age of approximately 7 days, survivorship dramatically drops in the nutrient-stressed treatment (Fig. 4a). At about this age, females may begin producing eggs which are below this minimum size threshold.

We have assumed so far that the observed influence of maternal age and of maternal feeding treatment on offspring development time and survivorship are likely a direct result of the observed influence on egg size. However, these experiments do not directly manipulate egg size, and thus have not controlled for other maternal effects which may influence offspring performance, independent of egg size. For example, Rossiter (1991) suggests that maternal influences on egg quality (e.g. yolk content, lipid content, etc.) may be more important than those on egg size. We have not quantified egg quality in this experiment, but it seems likely that egg quality will differ for eggs laid by females in the two treatments.

A dramatic decline in egg size with increasing maternal age has also been detected in other insects (Leonard 1970; Harvey 1977; Jones *et al.* 1982; Murphy *et al.* 1983; Wiklund & Persson 1983; Yuma 1984; Karlsson & Wiklund 1984, 1985; Boggs 1986; Svard & Wiklund 1988; but see Kasule 1991). The two hypotheses proposed to account for this pattern both assume that larger eggs produce 'better' offspring than smaller eggs. The most common explanation is the 'resource depletion' hypothesis (reviewed in Begon & Parker 1986), which suggests that the amount of resource expended on each egg is an unchanging function of the current resources available for egg production. Thus, as a female ages and her resources available for egg production diminish, she is expected to produce smaller eggs, which perform more poorly. The results of the experiment presented here are consistent with this hypothesis: females which were less nutrient stressed laid larger eggs than females which were starved. Maternal feeding has also been reported to increase egg size in other insects (Harvey 1983; Murphy *et al.* 1983; Steinwascher 1984; Wallin *et al.* 1992), likewise consistent with this hypothesis.

Another hypothesis, proposed by Begon & Parker (1986), may also be consistent with the observed decrease in egg size with increasing maternal age. Begon & Parker (1986) suggest that, for species which amass resources before the onset of reproduction, if maternal mortality is age independent then optimal egg size will decrease with increasing maternal age. Further, the rate of this decline in egg size is dependent on the probability of survival between successive ovipositions, as well as a female's energy reserves. This adaptive hypothesis differs from the non-adaptive 'resource depletion' hypothesis in that the rate of decline of egg size is treated as an adaptation to external mortality sources interacting with diminishing reserves, rather than just as a result of physiological constraints on egg size. The Begon & Parker model is based on the assumption that larger eggs have higher fitness than smaller eggs. Although the effect is very small, it is clear that *C. maculatus* offspring from older eggs have lower survivorship. The predictions of Begon & Parker's model should be applicable to *C. maculatus* because populations of in stored legumes generally do not feed as adults. The experiment presented here, however, was not designed to test the Begon–Parker and resource depletion hypotheses.

In summary, both egg size and performance of off-spring decrease with increasing maternal age in *C. maculatus*. However, adult behaviour which influences a female's nutritional status, such as mating and feeding, can also influence the performance of her off-spring (Wasserman & Asami 1985; Fox 1993a), in addition to influencing the number of eggs she lays (Fox 1993c; Møller *et al.* 1989). These behavioural influences on offspring performance are likely important in natural populations of *C. maculatus*. For example, adult females mate frequently throughout their lifetime, although only one, or occasionally two, matings are required to fertilize a female's eggs. However, males contribute approximately 5% of their body mass to a female in their ejaculate, and thus multiple mating may be favoured as a strategy to improve a female's nutritional state (Fox 1993a,c). This ejaculate appears to be used for both female somatic maintenance and egg production (Fox 1993a,c): females which mate multiply live longer (Fox 1993c), lay more eggs (Fox 1993c), and lay larger eggs than females which mate only once (Fox 1993a), although this increase in egg size does not translate into increased offspring performance (but see Wasserman & Asami 1985). Similarly, although females do not have access to a food source in stored legumes, many bruchids feed on pollen, nectar and fungi outside a storage environment (e.g. Shinoda & Yoshida 1987). Maternal feeding results in improved survivorship and development time of offspring, and thus should be favoured in an environment where an adult food source is accessible. Both feeding and mating thus allow females to compensate partially for negative effects of maternal age.

Acknowledgements

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