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Factors affecting egg maturation in the bean weevil *Callosobruchus maculatus*

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ABSTRACT. This paper concerns the effects of mate and seed availability on the rate of egg maturation in the bean weevil *Callosobruchus maculatus* (F.). Egg maturation starts before emergence from the seed and, provided that both oviposition sites and mates are available, eggs are laid at a rate determined by the number of oviposition sites, and mature at a similar rate. If seeds or mates are absent then a small number of eggs are laid, but oocytes continue to mature until the oviduct-capacity is approached. The number of eggs that a female can store is dependent on her body weight and does not correlate with the number of ovarioles. If, after a period in which oocyte development has been halted, conditions for egg-laying become suitable, then egg maturation can be re-started, but only after the oviducts have been emptied of eggs. The rate of egg maturation is then similar to that for females of the same age which have been maturing eggs since emergence.

Key words. *Callosobruchus*, bean weevil, egg maturation, oviducts, oviposition.

Introduction

Although the bean weevil *Callosobruchus maculatus* (Coleoptera: Bruchidae) (F.) infests pulse crops in the field, its main impact is in seed stores where it is a serious economic pest (Southgate, 1978, 1979; Jackai & Daoust, 1986). For this reason research has focused on many aspects of the biology of this bruchid, but one aspect that has been neglected is the role of egg maturation in determining egg output. This paper reports an investigation into the effects of some external factors on the rate of egg maturation and oviposition in *C. maculatus*.

The egg output of insects is influenced by a variety of factors (Engelmann, 1970), including nutrition, temperature, light, humidity, interactions with other animals including mates, and food or host availability. Recent studies have demonstrated that both the type and amount of food consumed as a larva may affect the number of eggs laid by female bruchids (Wasserman, 1981; Credland *et al.*, 1986; K. Wilson, unpublished data); that females lay more eggs at 30°C than at 20°C, and at 90% r.h. than at lower relative humidities (Schoof, 1941; Giga & Smith, 1983, 1987); that the number of oviposition sites and the roughness of the seed coat may also influence the rate of egg laying and total egg production (Nwanze & Horber, 1976; Credland, 1986; Giga & Smith, 1987); and that whilst mating stimulates egg-laying, the presence of other females has an inhibitory effect on oviposition (Bellows, 1982a).

Engelmann (1970) has pointed out that

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measurements of daily or total egg output may be misleading as indicators of reproductive potential, because eggs may be matured within the female but then retained in the ovaries and later resorbed. Oviposition and maturation rates are therefore different measures of egg production and may be influenced independently by different factors. For example, in many dipteran and lepidopteran species mating stimulates egg laying but only indirectly affects egg maturation (Engelmann, 1970). In other insects, such as *Schistocerca gregaria*, mating accelerates egg maturation *per se* (Norris, 1954). The availability of oviposition sites can also have a direct effect on oogenesis. In the hymenopteran *Diadromus pulchellus* olfactory perception of host seeds is sufficient to stimulate egg maturation (Labeyrie, 1964).

The potential to exploit favourable conditions will be selected for in animals living in changing environments. In the field and in seed stores, *Callosobruchus* is likely to encounter local shortages of mates and oviposition sites and possibly fluctuations in temperature, humidity and light levels. The studies mentioned above illustrate that oviposition behaviour is sensitive to this variability, but only by understanding how these factors affect egg maturation, and hence a female's reservoir of mature eggs, can the efficiency of the response be assessed.

This paper describes a series of experiments to address the following questions about egg maturation in *C.maculatus*:

(a) When is egg maturation initiated, and what proportion of the total egg output is at the mature egg stage when the female emerges?

(b) What effect does the availability of males and/or suitable oviposition sites have on the rate at which eggs are matured?

(c) Do these factors exert their effect on the rate of egg maturation, the rate of egg laying, or on both?

(d) Once egg maturation has been halted can it be restarted, and if so at what rate?

(e) Since the oviposition rate is dependent on the number of suitable oviposition sites, can the rate of egg maturation be varied also, or is it an all-or-nothing response?

Materials and Methods

Culture methods. Stock cultures of *C.maculatus* were maintained on cowpeas, *Vigna unguiculata*, in a constant temperature room at 30°C and 75% r.h. with a LD 16:8 h cycle. These beetles are of Brazilian origin (R. H. Smith, personal communication) and have been in culture (at various locations) for a minimum of 150 generations. They are derived from the population maintained at Imperial College at Silwood Park, Berkshire (see Bellows, 1982a, b).

To obtain virgin females of known age, seeds containing adults ready to emerge were removed from the stock boxes and placed in individual cells of a divided Petri dish. Each hour, for a maximum of 4 h, females which had emerged in cells not containing males were removed. These newly emerged females were weighed using a Cahn 29 automatic electrobalance. Depending on the nature of the experiment, some females were given access to a mate of similar age and/or seeds. Only 'normal' phase, flightless beetles were used in the experiments (see Utida, 1972).

Dissections. Females were killed by immersion in 70% alcohol and dissected soon afterwards. The reproductive system was exposed by pulling the abdomen away from the thorax and teasing the body plates apart. Mature eggs in the oviducts were dissected free and counted. For some females the number of immature eggs in the ovarioles and the number of ovarioles were also determined. In the text that follows, the term dissection refers to the procedure outlined above.

Statistics. All means are given with their standard errors and sample sizes (n). Parametric tests have been used (e.g. Pearson's correlation test; analysis of variance; analysis of covariance; and t-tests) only on normally distributed data or on data that has been transformed to make it so. Non-parametric tests have been used when appropriate. If an experiment was repeated on different dates to provide adequate sample sizes, the validity of combining the data sets was checked statistically. There were no significant differences between the emergent weights of females between treatments in any of the experiments.

Results

Experiment 1a. Effect of seed and mate availability on egg maturation rate

Four experimental treatments were set up

using newly emerged virgin females. Group 1 females were given access to a male and two cowpeas; group 2 females were allowed a mate but no seeds; group 3 were given two seeds but no males; and group 4 were denied access to both males and suitable oviposition sites. Eggs on seeds and 'dumped' eggs (see later) were counted each day. The number of females belonging to each group which were dissected each day ranged between five and fifteen.

Forty-five females were dissected within 30 min of emerging from the seed, and the number of mature eggs contained in their oviducts counted.

(i) *Newly emerged females.* Females held 8.02±0.75 eggs at emergence. Elytra length correlates well with weight at emergence (r=0.935, d.f.=28, P<0.001), therefore weight, which is easier to determine, was used as a measure of body size. The number of mature eggs at emergence was not correlated with emergence weight (r=0.120, d.f.=22, NS), but the total number of visible oocytes in the ovarioles (together with the mature eggs in the oviducts) was (r=0.557, d.f.=16, P<0.05).

(ii) *Number of mature eggs in the oviducts.* Both experimental treatment and female age affected the number of mature eggs held by a female (two-factor ANOVA: treatment $F_{3,164}$ =66.95, P<0.001, female age $F_{4,164}$= 3.64, P<0.01) (see Fig. 1), but there was no interaction between age and experimental group ($F_{12,164}$=1.55, NS). There was no difference between groups 2, 3 and 4 in the number of mature eggs carried (Tukey's comparison of means (HSD) test, see SAS Institute Inc., 1985). However, group 1 females (those given access to both males and oviposition sites) had fewer eggs in their oviducts than females from the other three groups (P<0.05).

Females had between eight and thirteen ovarioles (median eleven), but this variation was not correlated with weight at emergence (r=0.006, d.f.=161, NS). The number of mature eggs held by females denied a mate and/or seeds remained relatively constant after day 2, and there was a significant correlation between emergence weight and the number of mature eggs in the oviducts of females belonging to groups 2, 3 and 4, dissected on days 2–5 (r=0.415, d.f.=92, P<0.001; Fig. 2). The correlation for day 1 alone was not significant (r=0.041, d.f.=36, NS).

Some females 'dumped' eggs on the sides of containers (or on seeds) which could not produce viable progeny, either because the eggs were infertile (groups 3 and 4) or were laid on unsuitable substrates (groups 2 and 4). When these 'dumpers' were excluded from the above analysis the correlation between emergence weight and number of eggs in the oviducts after day 1 disappeared (r=0.172, d.f.=42, NS). The

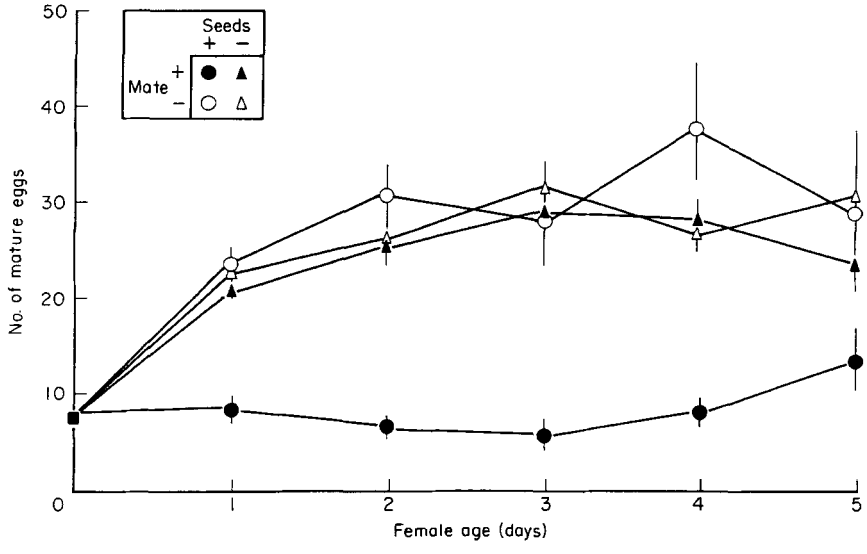

FIG. 1. The mean number of mature eggs in the oviducts on days 1–5. Vertical bars represent standard errors. Each mean was calculated from five to fifteen different females.

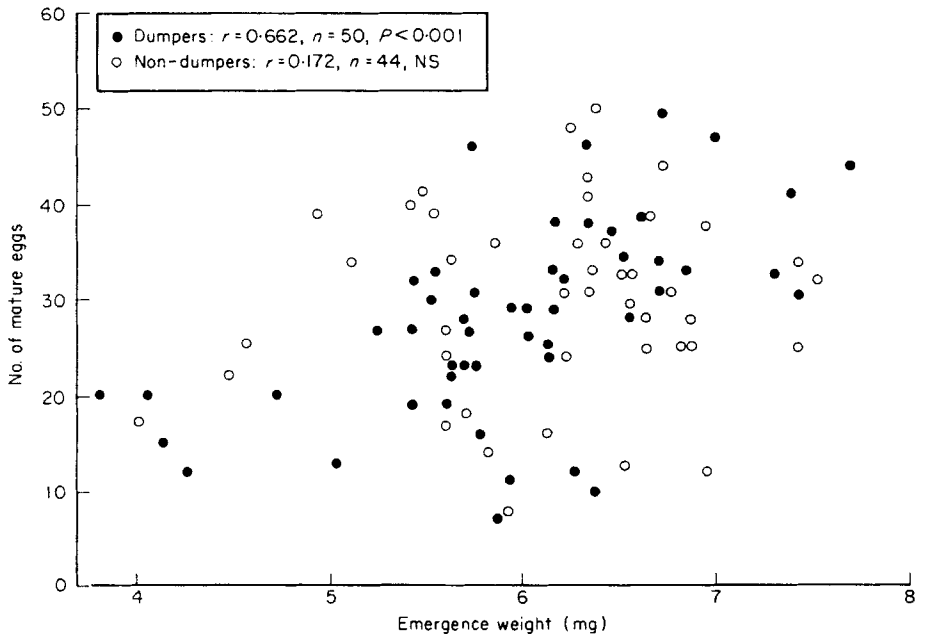

FIG. 2. The relationship between number of mature eggs in the oviducts on days 2–5 and emergence weight for females denied access to a mate and/or seeds (groups 2–4). 'Dumpers' and 'non-dumpers' are defined in the text. Overall correlation: $r=0.415$, $n=94$, $P<0.001$.

correlation for dumpers alone was significant ($r=0.662$, d.f.$=48$, $P<0.001$). Those females which laid eggs (dumpers) were significantly lighter than those which did not ($t=2.12$, d.f.$=92$, $P<0.05$), and dumpers held slightly fewer eggs (27.05 ± 1.4, $n=44$) than non-dumpers (30.0 ± 1.5, $n=50$), but this difference was not significant ($t=1.42$, d.f.$=92$, $P<0.16$).

(iii) *Number of eggs laid.* Only females belonging to groups 1 and 3 were given seeds on

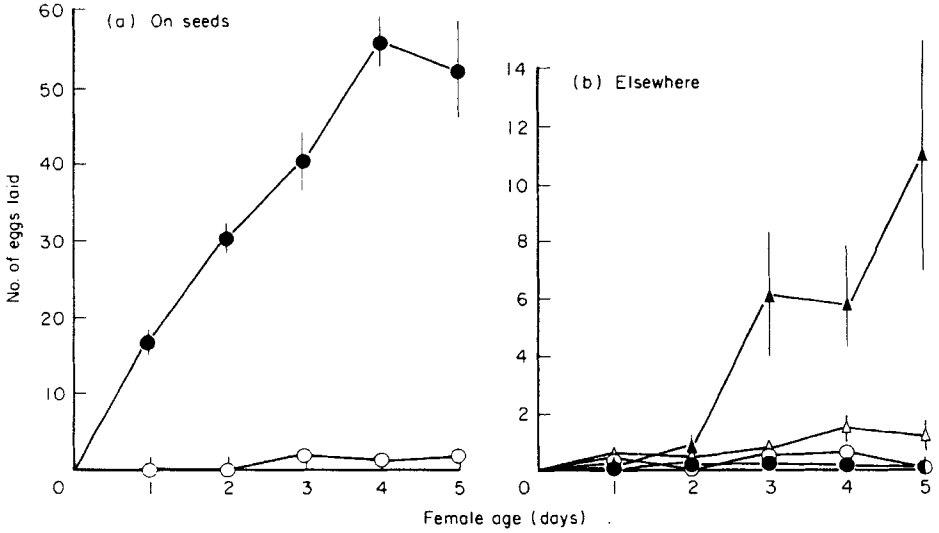

FIG. 3. The mean (±SE) cumulative number of eggs laid on seeds and elsewhere (e.g. sides of container) during the first 5 days of life. Symbols are as for Fig. 1. Each mean was calculated from five to fifteen different females.

which to lay. Group 1 females were also allowed to mate, and laid approximately fifteen eggs per day for the first 4 days, after which time the oviposition rate decreased (see Fig. 3 and Giga & Smith, 1983, for similar constant egg-laying rate over this period). Group 3 females were virgins and laid a negligible number of eggs on seeds.

The other two groups were not allowed seeds, but some females laid eggs on the sides of the containers. Of the four groups, the only one to dump an average of more than two eggs over the 5 days of the experiment was group 2. These beetles were mated but denied access to suitable oviposition sites. Despite this, they dumped approximately three eggs per day after the first couple of days, and one female dumped thirty-seven eggs over 5 days, a behaviour which requires explanation because none of these eggs will produce young.

(iv) *Total egg production*. The sum of the number of eggs laid and the number remaining in the female's oviducts is a measure of the rate of egg maturation. There was no difference in the rate of maturation by females belonging to groups 2, 3 and 4 (analysis of covariance for days 1–5: test for homogeneity of slopes, $F_{2,126}=1.06$, NS; test for homogeneity of intercepts, $F_{2,128}=0.84$, NS) (see Fig. 4). These groups were therefore combined in an analysis to compare the regression line for females given access to males and seeds with that for females denied either or both of these factors. The slopes of both regression lines were significantly different from zero (group 1: $F_{1,50}=151.5$, $P<0.001$; groups 2–4 combined: $F_{1,130}=23.6$, $P<0.001$), but also differed from each other (ANCOVA: test of slope, $F_{1,180}=74.5$, $P<0.001$; test of intercept is therefore inappropriate). In other words, all females continued to mature eggs after day 1, but the rate of maturation was significantly higher for females belonging to group 1 than for the other three groups. There were no significant differences in the numbers of eggs matured by females from the four groups on day 1 (ANOVA: $F_{3,49}=0.86$, NS), but on day 2 and subsequent days the differences between the groups in the cumulative number of eggs matured became apparent (ANOVA: $F_{3,23}\geq 3.63$, $P<0.05$), suggesting that it is only after day 1 that egg maturation is restrained by females belonging to groups 2–4.

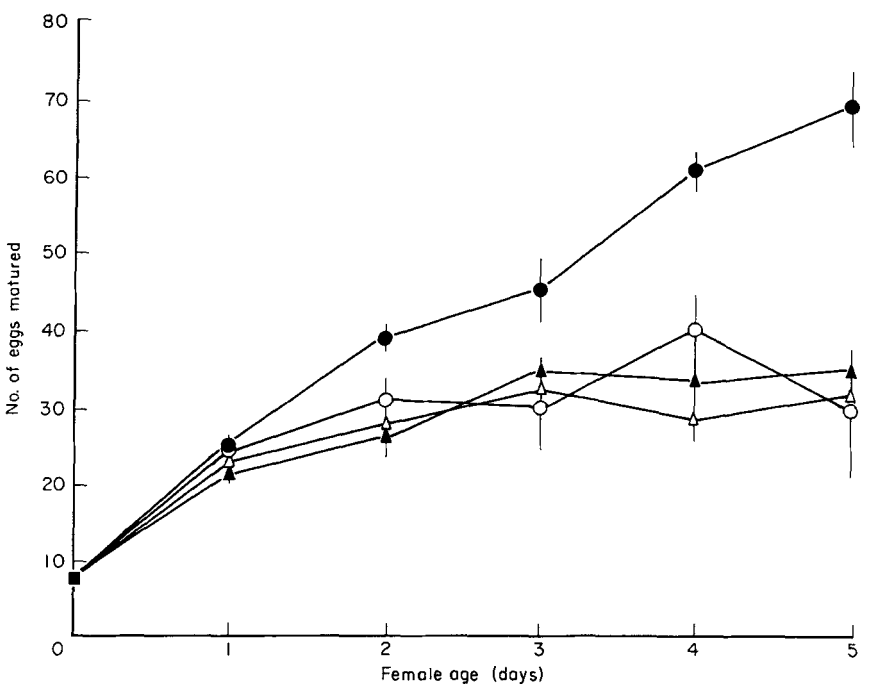

FIG. 4. The mean (±SE) cumulative number of eggs matured (number in oviducts plus number laid) during the first 5 days of life. Symbols are as for Fig. 1. Each mean was calculated from five to fifteen different females.

Experiment 1b. When are mature eggs fertilized?

This experiment was designed to determine when fertilization of mature eggs occurs, but investigated also the effect of delaying oviposition on the viability of stored eggs.

At emergence females were weighed and then given a mate. 24 h later, on day 1, all of the males were removed and half of the females provided with four cowpeas each (group A). The other half were denied access to seeds (group B). On day 2 the seeds of group A females were removed and isolated in a divided Petri dish, to be replaced by four new seeds. On day 3 both groups were given four fresh seeds. On all subsequent days until their deaths, females from both groups were given fresh seeds to replace those that had been oviposited on during the previous 24 h. Thus, the first eggs laid by group A females (on day 1) could have been fertilized a maximum of 24 h previously, whereas group B females' first eggs (laid on day 3) could have been fertilized up to 48 h sooner. Seeds were inspected daily to determine the length of the pre-hatch period. This was defined as the time taken for the dark head of the first instar larva to appear.

The first eggs laid by group A females (on day 1) started to hatch on day 5, those laid by females belonging to group B (on day 3) began hatching on day 7. As group B were not provided with seeds until 2 days after group A, the shortest hatching period for eggs laid by both groups of females was approximately the same. Therefore, assuming that embryogenesis begins at fertilization, this suggests that females belonging to group B had not fertilized their eggs any longer before oviposition than those of group A.

A more detailed analysis showed that the mean hatching period of the two groups was not constant for all eggs. Those laid late in the oviposition sequence took significantly longer to hatch than those laid early on (Fig. 5). When the duration of the hatch period was plotted against the number of days for which females had been allowed seeds on which to oviposit, the regression lines produced for the two groups did not coincide. The slopes of the lines were similar, but the line for group B was higher than that for group A (ANCOVA: test of slopes, $F_{1,72}=0.49$, NS; test of intercepts, $F_{1,73}=16.33$, $P<0.001$). This difference disappeared, however, when the duration of the hatch period was plotted instead against female age (ANCOVA: slopes, $F_{1,72}=0.49$, NS; intercepts, $F_{1,73}=0.03$, NS; note the fine dashed line in Fig. 5).

For both groups the hatching success was similar (mean percentage hatch: 82.0±9.8, $n=33$; t (arcsine transformed data)=0.35, d.f.=31, NS) and the decline with female age was not signifi-

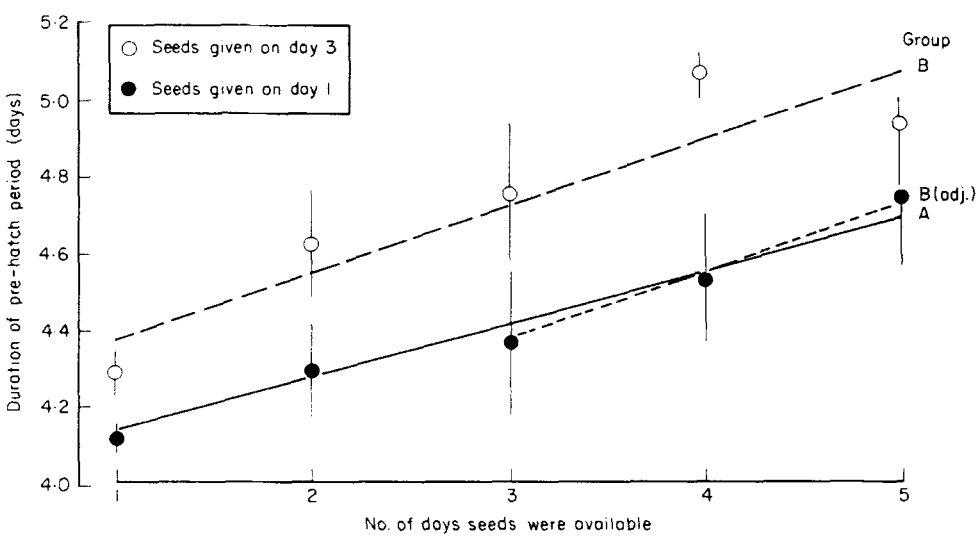

FIG. 5. The mean duration (±SE) of the pre-hatch period relative to the number of days since seeds were first introduced. Each mean was calculated from the means of four to fourteen females. The fine broken line is the regression line for group B when the abscissa is female age at oviposition. The line for group A is not altered by this change in the x-axis. Details of regression analysis are given in the text.

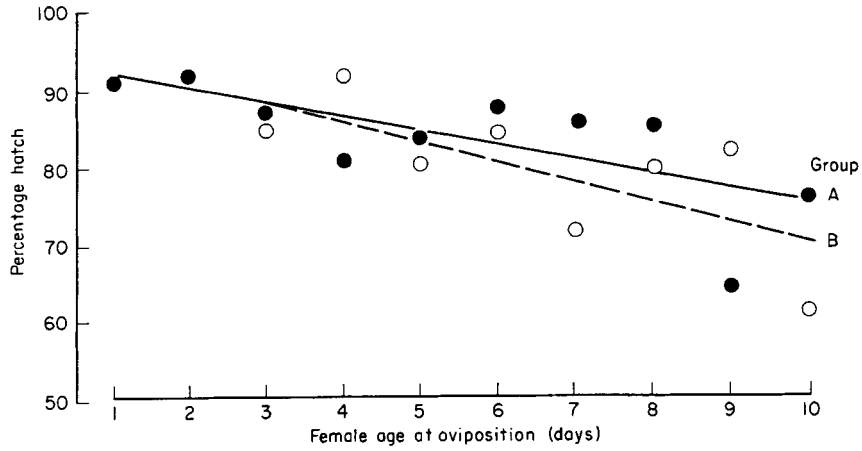

FIG. 6. The mean percentage of eggs to hatch relative to female age at oviposition. Symbols are as for Fig. 5. Each mean was calculated from the means of four to fourteen females. Regression analysis was performed on the arcsine-transformed data (details in the text).

cantly different (ANCOVA: slopes, $F_{1,116}$ =0.08, NS) (Fig. 6). The percentage of eggs which hatched declined as a function of the number of days since the female had emerged (ANCOVA: intercept, $F_{1,117}$=0.43, NS) rather than the number of days that seeds had been available for oviposition (ANCOVA: intercept, $F_{1,117}$=4.79, P<0.05). In other words, both the time taken for eggs to hatch and the proportion of eggs which hatched, were correlated with the age of the female at oviposition rather than at egg maturation.

Experiment 2. Can egg maturation be restarted?

There were two main experimental treatments. Females belonging to the first (group I) were given a mate plus four seeds each day for the duration of the experiment, whilst the second (group II) were given neither seeds nor mates. A sub-set of group II females was given seeds plus a mate on day 3 and on subsequent days (set IIa), the remainder (set IIb) were not. In order to make the best use of the animals that were available, females were not dissected on every day of the experiment: females from group I were dissected on days 3, 4 and 5; half of set IIa was dissected on day 4 and the other half on day 5; and set IIb was dissected on days 3 and 5. Thus comparisons could be made between the rates of egg maturation of similar-aged females differing only in their egg-laying experience.

The patterns of egg maturation for females of groups I and IIb (see Fig. 7) were similar to those of females in equivalent groups in the first experiment (group 1 and group 4 respectively), but the mean number of eggs matured was slightly lower. There was no significant difference between total egg production by group IIb females dissected on days 3 and 5. Therefore, an

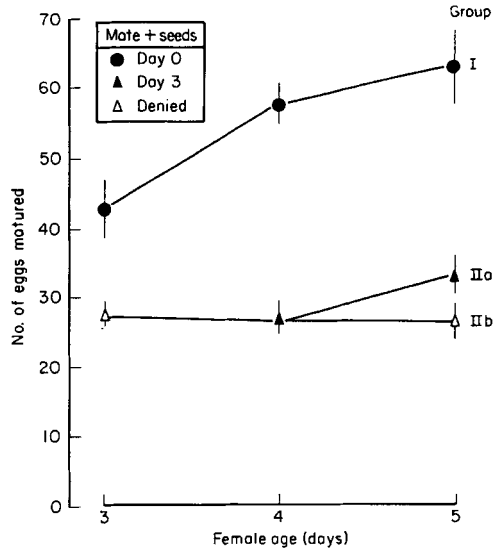

FIG. 7. The mean (±SE) cumulative number of eggs matured on days 3–5 following emergence. The means were calculated from sixteen to twenty-eight different females.

estimate of the mean number of eggs matured by group IIb females up to day 4 could be calculated by taking the mean of days 3 and 5 combined. This figure was then compared with the mean for group IIa females dissected on this day. There was no difference between the mean number of eggs matured up to day 4 by females given seeds and a mate on day 3 (group IIa) with those denied access to both of these (group IIb, $t=-0.02$, d.f.$=62$, NS). Group IIa females dissected on day 5 had matured significantly more eggs than similar-aged females belonging to group IIb ($t=2.18$, d.f.$=69$, $P<0.05$). Hence, it appears that egg maturation can be restarted if seeds and mates are provided, but that the response is not immediate.

The mean number of eggs matured between day 4 and 5 by females which were given seeds and a mate from day 0 (group 1) was 5.9 (see Fig. 7). Females given a mate and seeds on day 3 (group IIa) matured 6.3 eggs over this period. Thus, when egg maturation is restarted it does so at a rate comparable with that of females which have been laying eggs since day 0. Although similar numbers of eggs were matured by both sets of animals between days 4 and 5, group I females laid only about five eggs over this period compared with about twenty by group IIa females. This indicates that, under such circumstances, the egg maturation rate is not directly proportional to the oviposition rate.

Experiment 3. Effect of number of oviposition sites on egg maturation rate

To assess the effect of different numbers of oviposition sites on the rate of egg maturation, two groups of beetles were set up: group A females were given a mate plus one seed on day 0, and group B females a mate plus ten seeds. On each of the next two days the beetles were provided with one and ten fresh seeds respectively. On day 3, females belonging to both groups were dissected and the number of mature eggs in the oviducts counted. When added to the number of eggs that had been laid on seeds, the total number of eggs matured over the first 3 days could be determined.

During the first day of oviposition, group B females laid significantly more eggs on ten seeds than group A females laid on a single seed ($t=5.45$, d.f.$=104$, $P<0.001$) (see Table 1). Although there was no difference between the groups in the oviposition rate on days 2 and 3, the total number of eggs laid over the first 3 days of egg-laying did differ between groups ($t=3.62$, d.f.$=104$, $P<0.001$). Females belonging to both groups held approximately six mature eggs in their oviducts at dissection. Therefore, the total number of eggs matured by females given ten seeds on which to lay (51.38 ± 1.53) was significantly higher than that by females given only one suitable oviposition site (45.45 ± 1.39) ($t=2.85$, d.f.$=104$, $P<0.002$). Thus, it appears that egg maturation is not an all-or-nothing response to suitable environmental cues, but is a graded response sensitive to the oviposition rate.

Discussion

The rate of egg maturation

Insects exhibit immense variation in the number of eggs that they have available for laying when they reach the adult stage. In some species, such as *Cimex lectularius* (Hemiptera), no eggs are matured unless mating first takes place (Davis, 1964), whilst in others, notably many noctuid moths, a full complement of eggs is available on the day of emergence (see Engelmann, 1970). The majority of insects, however, emerge with just a portion of their eggs

TABLE 1. Egg laying and maturation rates (mean ±SE) over 3 days for females given one or ten seeds each.

No. of eggs	One seed ($n=51$)	Ten seeds ($n=55$)	t	Significance
Laid on day 1	12.77 ± 0.78	19.36 ± 0.92	-5.45	$P<0.001$
Laid on day 2	15.14 ± 0.70	17.01 ± 0.84	-1.71	$P<0.1$
Laid on day 3	9.92 ± 0.63	9.15 ± 0.52	0.96	NS
Laid on day 1+2	27.90 ± 1.11	36.38 ± 1.24	-5.06	$P<0.001$
Laid on day 1+2+3	37.82 ± 1.53	45.53 ± 1.48	-3.62	$P<0.001$
In oviducts	7.63 ± 0.69	5.86 ± 0.44	2.21	$P<0.05$
Matured at day 3	45.45 ± 1.39	51.38 ± 1.53	-2.85	$P<0.01$

matured, and oocytes continue to develop for some time after emergence. Female *C. maculatus* carry approximately eight eggs in their oviducts when they emerge from seeds and maintain a similar number when laying. Extrapolation of the data in this study suggests that egg maturation begins during the day before emergence, approximately 1 day after the female ecloses (Bellows, 1982b). Under the conditions of experiment 1a, females mature an additional fifteen eggs over the next day, regardless of whether seeds or mates are present. However, only mated females given suitable oviposition sites (group 1) continue to mature eggs at such a high rate. Females denied seeds or mates cease egg maturation after a couple of days and, because very few eggs are laid, the oviducts become packed with eggs. It is likely that this in some way reduces the activity of the neuro-endocrine system, thus inhibiting further maturation of eggs. If seeds and mates become available, then the rate of oviposition increases. After an initial delay of approximately a day, oogenesis is stimulated once more and eggs are matured at a rate comparable with that of females that have been maturing eggs continuously since their emergence.

In an experiment similar to experiment 1a of the present study, Ouedraogo & Huignard (1981) also found that both seeds and a mate were necessary to maintain egg maturation after day 2. However, contrary to the present study, females denied seeds or mates matured fewer eggs up to day 2 than females given either of these for the two days. This suggests that, in some populations at least, the presence of mates or oviposition sites *may* independently stimulate oogenesis.

Credland (1986) showed that the oviposition rate of *C.maculatus* is sensitive to the number of potential oviposition sites available. However, it is not possible to infer from his results, whether the rate of egg maturation shows the same sensitivity. Under normal conditions, where mates and seeds are available, eggs are matured at the same rate as they are laid, and the rate of oviposition is proportional to the number of oviposition sites, hence the observed relationship between the number of seeds and the maturation rate. Experiment 3 indicates that egg maturation is not simply turned on and off, but that when seeds and mates are accessible the response is graded in accordance with the oviposition rates. The availability of mates and seeds therefore has an indirect effect on the maturation rate.

Egg-storing capacity

During their lifetime (of usually 7–10 days), females in this study laid eighty or more eggs (K. Wilson, unpublished data). However, they only retained about half this number in their oviducts at any one time. A female's capacity for storing eggs is correlated with her body weight but not with the number of ovarioles in her ovaries, as is the case for some flies (Bennettova & Fraenkel, 1981) and aphids (Wiktelius & Chiverton, 1985). In the absence of seeds or mates, egg maturation is inhibited as the beetle approaches her capacity for storing eggs, at about day 2. Some females (non-dumpers) turn off egg maturation before their egg-storing capacity is reached, whilst other (generally smaller) females fail to do so and 'dump' their excess eggs (see below).

Why do some beetles dump eggs?

The dumping of eggs, either by virgins or by mated females on unsuitable substrates, is common amongst many insects (see Engelmann, 1970). Results from this study suggest two explanations for its occurrence in *C.maculatus* and refute two others. One explanation is that dumping has evolved as a response to reduce the degree of egg-crowding in the oviducts below a level at which egg and/or female fitness is reduced. This hypothesis is supported by the following evidence: beetles from all three groups which were discouraged from egg-laying dumped some eggs. The correlation between emergence weight and the number of eggs in the oviducts only held true for dumpers, suggesting that non-dumpers were females that had turned off egg maturation before reaching their egg-storing capacity. If the stimulus to stop egg maturation is independent of body weight, as is the rate itself, then smaller individuals are more likely to reach their egg-storing capacity before halting egg maturation, and so are more likely to dump, than larger ones. This is reflected in the heavier weight of non-dumpers. Bruchids usually disperse their eggs uniformly over the seed population (Utida, 1943). Avidov *et al.* (1965) suggested that the aggregration of eggs by *C.chinensis* that occurs after 4 days of storing

viable eggs could be a response to relieve the internal pressure resulting from the accumulation of eggs.

A second hypothesis seeks to explain why mated females should be more likely to dump than virgins, a common occurrence in many insects. It is proposed that dumping occurs because of the females' inability to retain eggs that enter the posterior portion of her reproductive tract. It is envisaged that in preparation for oviposition eggs move slowly down the oviducts into an area unsuitable for their long-term storage, and that mating accelerates movement of eggs into this region. This hypothesis would account for why females given a mate but no seeds dumped more eggs than any other group of females. These two hypotheses are not mutually exclusive, and the true explanation may be a combination of the two.

A third hypothesis speculates that eggs are dumped because fertilization and embryogenesis are initiated at mating and the eggs would otherwise hatch within the female. Competition between larvae within a seed is age-dependent (Bellows, 1982b). If embryogenesis is triggered by fertilization, a female which fertilized her eggs earlier relative to oviposition than conspecifics, in anticipation of finding suitable oviposition sites, would be at a selective advantage because the pre-hatch period of her eggs would be relatively shorter. If this was correct, then females would have to dump these eggs within 4 days of mating because eggs start to hatch at 4 days old. Although this was the case, the results from experiment 1b do not support this hypothesis: eggs laid 2 days after maturation took just as long to hatch following oviposition as eggs laid soon after maturation, suggesting that embryogenesis was initiated at the same time by all groups of females, probably at oviposition (see Went, 1982).

The last hypothesis considered is that eggs are dumped because after prolonged storage they have a lower fitness than freshly matured eggs and that, by dumping, a female is making way for fitter eggs. However, this is not the case: egg fitness (as measured by the duration of the pre-hatch period and the percentage of eggs which hatched) decreased as a function of the age of the ovipositing female. The number of days that the eggs had been stored in the oviducts did not exert any additional effect. This does not necessarily mean that egg fitness is directly dependent on the age of the female; it may be a consequence of the age of the fertilizing sperm (see Wasserman & Asami, 1985).

The entomological literature contains many reports of the apparently maladaptive behaviour of dumping. However, as yet, nobody has drawn the evidence together to suggest why there is such variability between species in the level of dumping. The probability of finding a mate, the likelihood of locating suitable oviposition sites, the relative cost of each egg, and the potential fecundity and longevity of the insect may all influence the prevalence of dumping.

An evolutionary perspective

The beetles used in this study are probably adapted to life in seed stores (see Wilson, 1988). Within stores, oviposition sites may be locally in short supply and, because eggs are continually being laid, the suitability of these sites will decline with time. Consequently, natural selection is likely to favour those females that are quickest to exploit conditions when they are good and that are able to respond fastest to changes in the environment. Under this scenario it is predicted that females will begin maturing eggs prior to emergence. Although this is observed in *C.maculatus* it begs the question of why females do not mature their full complement of eggs prior to emerging, rather than just a fraction of them.

Just as turning egg maturation on prior to emergence is likely to be selected for, so is refraining from turning it off until the oviducts are full of mature eggs. When females are competing for oviposition sites, those females able to exploit conditions when they become suitable for egg-laying, such as when a patch of egg-free seeds is encountered, will tend to do best. As predicted, the beetles in this study halted egg maturation at about the same time as their egg-storing capacity was reached. The ability to restart maturing eggs will also be favoured; however, the response observed in *C.maculatus* is not immediate and may be constrained by adaptations to prevent dumping.

Callosobruchus beetles do not usually feed as adults and so must live off reserves accumulated during larval development. Therefore, energetic reserves and resources available for egg production are limited and natural selection should act

against beetles that waste expensive eggs. Virgin *C.maculatus* dumped an average of less than two eggs during the first 5 days as an adult. It is interesting to note that virgin *Drosophila melanogaster* (which feed as adults and produce large numbers of presumably inexpensive eggs) lay just as many eggs as mated females (Partridge *et al.*, 1986). *C.maculatus* dumped most eggs when mated but denied seeds. This may be because in the natural environment mates and oviposition sites are usually located together, and so selection to restrain egg-laying is not as strong as for virgins.

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