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Abstract. 1. Maternal effects can modify progeny phenotypes to improve survival under variable conditions and may also interact with environment.

2. Four cohorts of *C. maculata* larvae were reared from four different points in their mothers' reproductive lives (1st, 12th, 24th and 36th oviposition days) and divided into two treatments for rearing; 30 min daily access to eggs of *Ephestia kuehniella* or ad libitum.

3. Progeny survival was lower on restricted food but increased over the first 12 oviposition days in both treatments, suggesting mothers did not conform to the theoretical norm, i.e., produce their 'best' progeny first.

4. Larval development was delayed on the restricted diet, but there was no effect of oviposition day on total developmental time, although pupation was faster in the final cohort than in the first.

5. The restricted diet amplified a developmental polymorphism evident in both treatments, increasing the percentage of larvae that added or subtracted an instar. The results suggest that mothers employ a mixed strategy and produce subsets of progeny that alternatively adopt an 'optimistic' or 'pessimistic' strategy when facing food limitation; undergo an additional instar to take advantage of any late improvement in the food supply, or forgo an instar and pupate at a small size.

6. A larger percentage of later cohorts pupated after only three instars in both treatments, suggesting that more later hatching progeny are maternally programmed for pessimism, as would be adaptive for larvae exploiting aphid populations in decline.

Key words. developmental polymorphism, egg size, fecundity, food limitation, reproduction

Introduction

Mothers sometimes use epigenetic mechanisms to manipulate the phenotype of their progeny in ways that improve their fitness under prevailing or anticipated environmental conditions (Fox and Mousseau 1998). It is now generally accepted that such 'maternal effects' are transgenerational signals subject to selection that serve to canalize the development of phenotypic plasticity, with potentially life-long impacts on progeny life histories (Mousseau et al. 2009). Maternal modification of progeny phenotype is most often adaptive when the optimal phenotype varies either spatially or temporally within the reproductive lifespan of the mother (Mousseau and Dingle 1991). Consequently, empirical studies of maternal effects have examined the influence of various aspects of the maternal environment such as food availability (Bashey 2006), food quality (Takakura 2004; Gonzalez-Teuber et al. 2008), availability of oviposition sites (Gottlieb et al. 2011), intensity of intraspecific competition (Marshall et al. 2006), and temperature (Huestis and Marshall 2006; Scharf et al. 2010). These comprise 'detection-based' maternal effects (*sensu* Shea et al. 2011). In contrast, 'selection-based' maternal effects – those that occur independent of the maternal environment, such as changes in progeny phenotype as a function of maternal age or birth order – have received far less empirical attention. For example, immature fresh water rotifers, *Brachionus calyciflorus* Pallas, develop longer defensive spines when their mothers are exposed to predation risk, but this phenotype is also expressed in offspring born late in the mother's life, regardless of maternal environment (Schröder and Gilbert 2009). Later born progeny of the waterflea *Daphnia galeata* Sars develop faster and become larger adults, illustrating a fixed birth order effect on offspring size (Sawinksa 2004).

Many aphidophagous coccinellid species depend on sporadic and ephemeral aphid outbreaks to supply the resources critical for both reproduction and subsequent offspring development. The larvae of such species face a challenging, but largely

predictable, trajectory of food availability. Aphid populations typically begin with low numbers (the initiation stage) and follow a trajectory of rapidly accelerating abundance (the exponential growth stage) followed inevitably by a precipitous decline in numbers (the collapse stage; Smith 1966, Michaud and Harwood 2012). The optimium time for coccinellid reproduction, the 'oviposition window', is early in the exponential growth phase, as both intra- and inter-specific competition intensifies for dwindling resources during the collapse phase (Kindlmann and Dixon 1993, 2010). It follows that progeny produced sequentially over this period do not experience equivalent conditions; those produced later face increasingly difficult conditions as the aphid bloom matures, such that selection-based maternal effects could evolve to improve maternal fitness via adaptive adjustments to offspring phenotype.

Variation in egg size has the potential to affect both developmental rate and final offspring size in many animals; in general, progeny hatching from larger eggs have higher survival, faster development and achieve larger adult size than those hatching from smaller eggs (Bernardo 1996; Fox 1994; Fox and Mousseau 1998). Although most arthropods tend to decrease egg size with advancing maternal age (Fox and Czesak 2000), periods of increase in egg size have been reported in *Coleomegilla maculata* De Geer and *Hippodamia convergens* Guerin-Meneville (Vargas et al. 2012, 2013a), and interpreted as a maternal effect that may enhance offspring fitness over the course of the female's reproductive cycle. However, egg size is only one measure of offspring quality and other, more cryptic, maternal signals may also influence progeny fitness (Bernardo 1996). For example, offspring of the soil mite *Sancassania berlesei* (Michael) produced by older mothers mature to larger body sizes, better enabling them to compete for limiting resources with earlier born siblings that are developmentally advanced (Benton et al. 2008). Cryptic maternal effects have also been reported in birds (Groothuis et al. 2005) and mammals (Dloniak et al. 2006). Recently, Vargas et al. (2013b), demonstrated age-specific maternal effects in *H. convergens* that appeared unrelated to changes in egg mass, but affected progeny developmental rate, the relative duration of particular developmental stages (fourth instar and pupa) and final adult size.

Although *C. maculata* is an exceptionally polyphagous ladybeetle (Hodek 1996), North American populations commonly rely on aphid resources for reproduction (Wright

and Laing 1980; Michaud and Jyoti 2007). Coccinellids that exploit cereal aphids on the High Plains of the USA normally produce two generations per year, one in fall and the other in spring, with the potential for additional generations if summer weather is cool enough to permit additional aphid outbreaks (Michaud and Qureshi 2006). Since summer is normally passed in reproductive diapause due to food shortage, and winter in hibernation, cohorts of beetles normally complete development in one aphid season and reproduce in the next, with most females partitioning their reproductive effort over a single aphid population cycle.

In the present study, a series of four larval cohorts of *C. maculata*, obtained from the same mothers at four different points in their reproductive cycle, were reared to test for age-specific maternal effects and their interaction with larval environment. To test for an interaction between maternal effects and the progeny's environment (e.g. Harvey 1977; Ng 1988), each clutch was split into two feeding treatments, one receiving unlimited access and the other a highly restricted food supply. We hypothesized that (1) age-specific maternal effects would result in progeny phenotype alterations consistent with optimization of maternal fitness on a 'boom and bust' cycle of prey availability; and 2) certain age-specific maternal effects that might improve progeny survival under harsh conditions would be evident only in progeny developing under conditions of food deprivation.

Materials and Methods

Insect colony

A colony of *C. maculata* was established from adult beetles collected from sorghum plants in Hays, KS, USA, in August, 2010. Insects were held in a growth chamber with L16:D8 day length at a temperature of 24 ± 1°C. Adult females were isolated in plastic Petri dishes (5.5 cm diam.) and were fed a diet of frozen eggs of the flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), with water provided on a small cube of sponge, both refreshed daily. Eggs were laid on the inner surfaces of the Petri dishes and were collected daily by transferring the beetles to new dishes. Larvae of the

first laboratory generation were reared on frozen eggs of *E. kuehniella* and the offspring of these adults were used in the experiment.

Experimental protocol

Eggs were separated from clusters and isolated until eclosion to prevent any egg cannibalism which has significant effects on development (Michaud and Grant 2004). Upon hatching, 117 neonate larvae obtained from 30 different mothers were isolated in Petri dishes and reared under the same physical conditions as the stock colony. Larvae were fed frozen eggs of *E. kuehniella* ad libitum. Eggs of *E. kuehniella* are a highly suitable food for *C. maculata* that support both normal development and successful reproduction (Michaud and Jyoti 2008) and are more convenient than aphids to supply in a long term experiment.

Upon emergence, adults were weighed on an analytical balance and then isolated in a Petri dish with frozen *E. kuehniella* eggs provided *ad libitum* and refreshed daily. Mating pairs were established seven days after emergence, taking care not to pair siblings, and held together during the first four weeks of reproduction, whereupon males were removed to prevent egg cannibalism. For each female, daily observations were made on the number of eggs laid, the size of the eggs, and percentage of eggs hatching for a total of 36 oviposition days. We measured the length and width (to the nearest 0.02 mm) of a sample of 5 eggs from each female's daily oviposition using a stage micrometer under a stereomicroscope at 50x magnification. Assuming that eggs are ellipsoidal in shape, we used these measurements to estimate egg volume using the following formula for an ellipsoid (Takakura 2004):

$$Volume = Length*Width^2\pi/6 \tag{1}$$

A reference series of 115 eggs were collected, measured as above, and then weighed on a high resolution analytical microbalance to the nearest 10 µg. We then used linear regression to establish the relationship between egg volume and fresh mass as described by the following equation:

$$\text{Mass} = 0.8126*\text{Volume} + 0.0226, \ (F_{1,114} = 994.84; \ R^2 = 0.89; \ P < 0.0001) \ (2)$$

Since the weighing of individual eggs is exceedingly time-consuming, we measured eggs under the microscope, calculated volumes, and converted those values to egg mass using the equation above.

A sample of 10 eggs was taken from each female on her 1st, 12th, 24th and 36th day of oviposition and divided into two groups of five for rearing. In cases where fewer than 10 eggs were laid, those available were divided equally between the two feeding treatments. Immediately after each egg was measured, it was isolated in a plastic Petri dish and assigned to one of two feeding treatments; either a continuous *ad libitum* diet of *E. kuehniella* eggs, refreshed daily, or a 30 min period of food access daily. All larvae were examined daily and all molts were recorded until pupation. Within 1-2 h of emergence, adults were placed singly into 5 dram glass vials and dried in an oven for 72 hours at 50 °C, after which they were weighed individually on an analytical balance.

Statistical analysis

Polynomial regression was used to describe trajectories of change in daily fecundity, egg mass, and fertility using PROC REG (SAS Institute 2008). The polynomials of best fit were obtained by adding terms for the independent variable (days) with successively higher exponents until doing so failed to increase the *F* value.

Treatment and oviposition day effects were compared by repeated measures ANOVA using PROC GLMMIX (SAS Institute 2012) followed by an LSM test to separate means. Subject (female) effects were considered random and females were treated as a block containing the two treatments (ad libitum and 30 minutes). The response variable was calculated as a sum of terms for overall mean, subject effect, treatment effect, oviposition day effect, and treatment x oviposition day interaction. The variance-covariance of the random variable of the repeated measurements was estimated using the first order autoregressive correlation model AR(1). Response distributions for fertility, survival, proportion of individuals pupating after the third, fourth, and fifth larval

instar and sex were considered binomial with link function Logit, whereas response distributions for the durations of larval development, pupal stage and total development were considered Poisson with link function Log. Distributions of egg mass and adult mass were considered normal with identity function as a link function. The Kenward-Roger method was used to estimate the denominator degrees of freedom (ddfm).

Results

A total of 53 pairs of beetles were established at the beginning of the experiment, but only 43 females completed the total of 36 oviposition days and were included in the analysis. Changes in daily fecundity and fertility as a function of female age were both described with high levels of significance by second order regressions (F = 136.62; df = 2,33; P < 0.001, R^2 = 0.89 and F = 52.15 P < 0.001, R^2 = 0.76, respectively) (Fig. 1A, B). Changes in egg mass best fit a third order regression (F = 295.05; df = 3,32; P < 0.001, R^2 = 0.96) (Fig. 1C). Females increased egg number and egg mass up to around 30th oviposition day (by 10 and 35%, respectively), whereas fertility peaked around day 18.

A larger proportion of larvae receiving ad libitum food survived compared to those receiving 30 min access daily (F = 103.95; df = 1,171.3; P < 0.001). There was also a significant main effect of oviposition day on larval survival (F = 3.94; df = 3,156.7; P = 0.009), but the interaction between oviposition day and treatment was not significant (F = 0.47; df = 3,244.8; P = 0.360) (Fig. 2). In both treatments, larvae derived from the 1st day of oviposition had lower survival than those derived from later oviposition days (LSM test, α = 0.05), although survival of those derived from the 36th oviposition day of 30 min females were intermediate and not significantly different from other oviposition days in this treatment. Sex ratios were not significantly different from 1:1, and were not affected by feeding regime (F = 2.08; df = 1,118.3; P = 0.151) or oviposition day (F = 1.79; df = 3,232.1; P = 0.149).

All viable eggs hatched in three days, regardless of cohort. There was a significant main effect of treatment on the total duration of larval development (F = 2,849.01; df = 1,295; P > 0.001), but the main effect of oviposition day was not

significant ($F = 0.54$; df = 3,552.2; $P = 0.652$), and there was no significant interaction between treatment and oviposition day ($F = 0.65$; df = 3,514.3; $P = 0.582$). The ad libitum treatment generated faster larval development (mean ± SE = 15.2 ± 0.03 d) than the 30 min feeding treatment (26.0 ± 0.02 d). The main effect of treatment was not significant for pupation time ($F = 0.47$; df = 1,480.2; $P = 0.494$), whereas the main effect for oviposition day was ($F = 6.78$; df = 3,664; $P < 0.001$), and the interaction between these independent variables was not significant ($F = 0.69$; df = 3,636.9; $P = 0.559$). Regardless of feeding treatment, progeny produced on the 36th oviposition day spent less time in the pupal stage than those produced on either the first or 12th oviposition day.

Both feeding treatment and oviposition day affected the number of larval stadia. A majority of individuals pupated after four larval instars in both feeding treatments (Fig. 3), but the percentage was greater in the ad libitum feeding treatment than in the 30 min treatment ($F = 74.11$; df = 1,148.6; $P < 0.001$). Oviposition day affected the percentage of individuals pupating after four instars ($F = 2.91$; df = 3, 283; $P = 0.033$); the percentage was higher on the two early days than on the two later days in the ad libitum feeding treatment, whereas it was higher on the first oviposition day compared to the 24th day in the 30 min feeding treatment (LSM test, $\alpha = 0.05$). There was no significant interaction between treatment and oviposition day for the percentage of individuals pupating after four instars ($F = 1.93$; df = 3,246.8; $P = 0.125$). A larger percentage of individuals pupated after only three instars in the 30 min feeding treatment than in the ad libitum treatment ($F = 56.35$; df = 1,152.5; $P < 0.001$) and there was a significant effect of oviposition day in both treatments ($F = 5.04$; df = 3,239.1; $P = 0.002$). In both feeding treatments, the percentage of third instar pupations was higher on later oviposition days than on earlier ones (LSM test, $\alpha = 0.05$) and the interaction between treatment and oviposition day was not significant ($F = 1.07$; df = 3,247.7; $P = 0.361$). A small fraction of individuals underwent a supernumary fifth larval instar and the percentage doing so was higher in the 30 min feeding treatment than in the ad libitum treatment ($F = 9.54$; df = 1,111.4; $P = 0.002$) but the effect of oviposition day was not significant ($F = 0.76$; df = 3,198; $P = 0.515$) and nor was the 2-way interaction term ($F = 1.59$; df = 3,232.2; $P = 0.191$).

A three way model considering 'treatment', 'oviposition day' and 'gender' as independent variables was significant overall for adult weight with significant main effects of treatment and gender, but not oviposition day, and with significant treatment*gender interaction (Table 1), so data were pooled across oviposition days for further analysis. Both males and females were almost three times as heavy when reared on the ad libitum diet as when restricted to 30 min daily food access (males: 3.03 ± 0.02 vs. 1.12 ± 0.01 mg; females: 3.36 ± 0.03 vs. 1.23 ± 0.01; P < 0.001 in both cases).

The number of larval stadia did not affect the final adult body weight of either males or females in either feeding treatment (30 min males: $F_{2,277}$ = 1.57, P = 0.209; 30 min females: $F_{2,322}$ = 0.35, P = 0.707; ad libitum males: $F_{2,391}$ = 2.26, P = 0.106; ad libitum females: $F_{2,381}$ = 0.14, P = 0.868). However, total larval development time was significantly longer for larvae that pupated after five larval instars compared to either three or four (mean ± SE = 32.2 ± 0.9 vs 28.8 ± 0.4 and 29.4 ± 0.2, respectively; $F_{2,602}$ = 5.14, P = 0.005), whereas the number of stadia did not affect developmental time for beetles fed ad libitum ($F_{2,777}$ = 2.56, P = 0.078).

Discussion

Both initial hypotheses were supported; age-specific maternal effects were evident in progeny development and some effects interacted with larval feeding treatment. Consistent with previous observations on this species (Vargas et al. 2012), there was a maternal effect on *C. maculata* egg size, the fresh mass of eggs increasing over the course of the first 20 days of female oviposition (Fig. 1). The declining trajectory of egg fertility late in the experiment is likely a function of normal aging, although the removal of males on day 28 and a lack of male seminal contributions thereafter may have contributed.

Larval survival was reduced by the restricted food supply (Fig. 2), but not so greatly considering the extreme food deprivation imposed in this treatment. More importantly, larvae from the first cohort had lower survival than later cohorts, independent of treatment. In general, egg size tends to decline with female age in

insects (Fox and Czesack 2000) and females are normally expected to produce their 'best' progeny early in life, if only because the risk of mortality discounts the value of future reproductive effort compared to present (e.g. Mousseau and Dingle 1991; Tschinkel 1993). Indeed, Singh and Omkar (2009) found that parental age was positively correlated with developmental time in *Cheilomenes sexmaculata* (F.) and negatively correlated with survival and adult body weight. However, there are ecological reasons why female *C. maculata* may benefit by increasing egg size (and offspring quality) as a function of oviposition sequence. Species that exploit aphid outbreaks begin reproduction on an abundant food supply which permits the survival of small, low quality offspring, but increasingly adverse conditions develop as the outbreak matures, favoring the production of larger, more competitive ones (Vargas et al. 2012; 2013a). Although the food deprivation treatment extended larval development, there was no main effect of oviposition day on total larval development time. In contrast, *H. convergens* larvae from later cohorts develop faster than those from earlier ones, largely due to faster egg hatching and shorter pupation times (Vargas et al. 2013b). Notably, the final cohort of *C. maculata* in this study did have shorter pupation times than earlier ones, independent of feeding treatment. The pupal stage is especially vulnerable to cannibalism and intraguild predation, so a reduction in pupation time is advantageous for later cohorts if mothers produce them as environmental conditions are deteriorating and these hazards are increasing.

The variation observed in number of larval stadia is relatively unusual in this group, although not in other insects (reviewed by Esperk et al. 2007a). Coccinellids almost invariably have four instars and this has been assumed to represent a phylogenetic constraint, as fewer instars would presumably afford faster development on ephemeral resources (Dixon 2000; Nedved and Honek 2012). Supernumary fifth instars have been reported in *Callicaria superba* (Mulsant) (Iwata 1932), *Chilocorus nigritus* (F.) (Chazeau 1981), *Harmonia axyridis* Pallas (Labrie et al. (2006) and *C. maculata* (Warren and Tadic 1967), but most cases involve only a small fraction of individuals. Reports of coccinellid pupation after only three instars are even fewer, but examples include *Hyperaspis campestris* (Herbst) (McKenzie 1932) and *Coccinella undecimnotata* L. (Iablokoff-Khnzorian 1982). In *Nephaspis oculatus* (Blatchley), a

significant fraction of individuals can be induced to pupate after the third instar by subjecting them to high temperature stress (≥ 29 ºC) (Ren et al. 2002). In the present study, food deprivation decreased the percentage of individuals undergoing 'normal' development with four stadia and increased the percentage undergoing either three or five stadia, most notably the former. Alterations in number of stadia in response to both food and temperature stress are well known in the Lepidoptera. A nitrogen-deficient diet will induce the soybean looper, *Pseudoplusia includens* (Walker), to extend development and for some larvae to undergo supernumary stadia (Wier and Boethel 1995). An increased number of stadia can be induced in some larvae of *Spodoptera exigua* (Hubner) by extremes of temperature and by feeding on a low quality food plant, *Gossypium hirsutum* L. (Ali and Gaylor 1992). Similarly, development on low quality food plant results in supernumary instars in the tortricid *Acleris minuta* (Robinson) (Weatherby and Hart 1986).

In the context of life history theory, it is often assumed there exists a tradeoff between developmental time and size at maturity (Roff 1992; Stearns 1992); attainment of a large body size permits higher fecundity (Honěk 1993) but requires a longer period of growth to achieve, thus incurring a cost in terms of delayed development. For example, in the tiger moth *Eilema depressum* (Esper), directly developing larvae pupate at smaller sizes after fewer instars compared to larvae that overwinter (Poykko and Hyvarinen 2012). However, other species of Lepidoptera pupate upon reaching a critical weight, regardless of instar, such that adult size is unaffected by number of stadia (Davidowitz et al. 2003; Kingsolver 2007). It has been argued that the optimal number of instars is that which maximizes food acquisition while minimizing the costs of molting (Hutchinson et al. 1997). In general, the addition of stadia is a strategy for attaining greater (or critical) body size, whereas the subtraction of stadia is a means of speeding development. In some cases, individual eclosing from smaller eggs are more likely to undergo additional instars (Leonard 1970, Frago et al. 2009). In insects sexually dimorphic for instar number, females tend to have more instars than males (e.g. Berthiaume et al. 2007), and sexual size dimorphism is often pronounced in these species (Esperk and Tammaru 2006; Esperk et al. 2007b). For example, females of the grasshopper *Heteracris littoralis* (Rambur) (Acrididae) require a longer developmental

period and pass through six-seven instars, as opposed to only five for males, in order to achieve a significantly larger body size at maturity (Singh and Chaudhary 1999). Etile and Despland (2008) argued that variation in instar number provides insects flexibility to compensate for poor growing conditions. We interpret the present results (Fig. 3) as representing two divergent larval strategies for dealing with food deprivation that might be characterized as optimistic and pessimistic, respectively. The addition of a fifth instar would presumably pay off if food conditions improved toward the end of development and greater body size could be achieved by the additional feeding time, rendering it an optimistic strategy. For example, Chen and Ruberson (2008) showed that two days of starvation for beet armyworm larvae in the first instar caused a greater proportion to undergo a supernumary sixth instar and that such larvae ultimately achieved comparable pupal weights, albeit after a longer developmental time. In contrast, if food conditions do not improve (as in the case of this experiment), there is little to be gained by extending development and larvae pupating after only three instars may save energy and risk associated with additional molts. Clearly, pessimists outnumbered optimists in this experiment and were rewarded in the food deprivation treatment; whereas optimists paid a time cost for adding an instar, pessimists that subtracted an instar did not pay a cost in reduced body size.

The maternal effect of oviposition sequence on number of stadia was similar in both treatments; offpsring produced later in the life of their mother were more likely to be pessimistic and subtract an instar, but laying sequence did not affect the tendency to add one and is consistent with a scenario of increasing pessimism for female coccinellids ovipositing in aphid outbreaks. On the High Plains, females of aphidophagaous species normally encounter only a single reproductive opportunity (aphid outbreak) in either spring or fall (Michaud and Qureshi 2006) and do not oviposit in the outbreak that supports their development. Previously (Vargas et al. 2012, 2013a), we argued that a fixed schedule of increasing offspring quality (and/or developmental rate) as a function of oviposition sequence would maximize maternal fitness when the progeny develop on aphids, the abundance of which shifts from exponentially increasing to precipitously declining within a period as short as 2-3 weeks. In *H. convergens*, females accomplish this by shortening progeny developmental time in

later clutches, in particular by reducing the duration of the most vulnerable stages, egg and pupa (Vargas et al. 2013b). In *C. maculata*, the maternal effect appears to be a developmental polymorphism in which mothers increase the tendency of later progeny to truncate their life history and pupate after only three instars. To our knowledge, this is the first demonstration of a maternal effect on developmental polymorphism in a holometabolous insect. Although larvae forgoing a fourth instar did not achieve faster development, the normal pattern of change in food supply (abundant to scarce) was not reflected in either feeding treatment. Thus it remains conceivable that the three instar phenotype might yield fitness benefits when development begins on abundant food and ends in deficit. It is also notable that a combination of all three phenotypes was produced in all cohorts (there were even five cases of larvae with six instars, excluded from analysis), suggesting females employ a baseline strategy of producing multiple developmental phenotypes in their progeny, but modify the relative proportions of each over the course of their reproductive lives.

Acknowledgements

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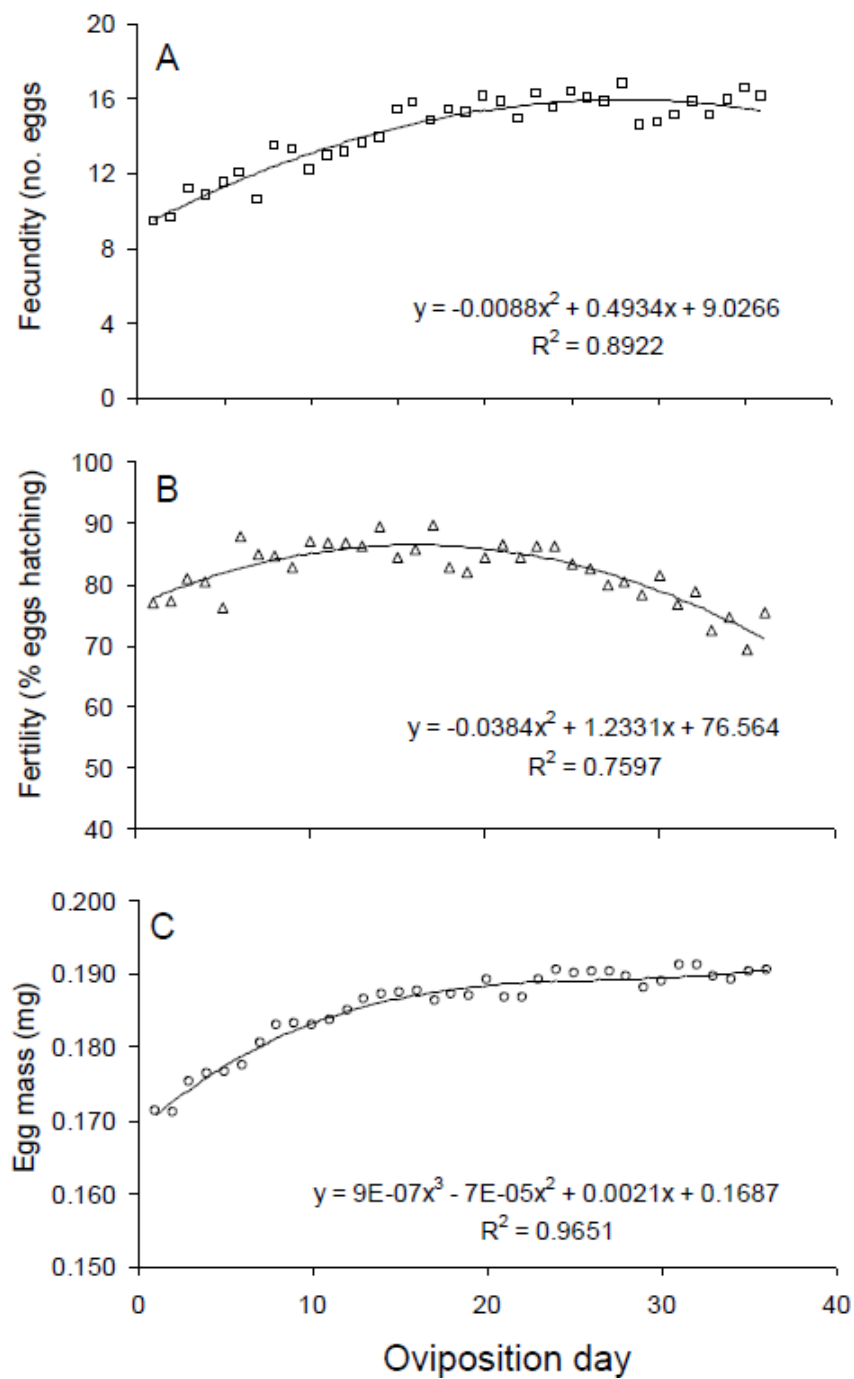
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Figures

Fig. 1. Changes in mean daily fecundity (A), egg fertility (B), and egg mass (C) of 43 C. maculata females over the course of 36 oviposition days. Females were fed eggs of E. kuehniella ad libitum during both development and reproduction.

A

$y = -0.0088x^2 + 0.4934x + 9.0266$
$R^2 = 0.8922$

B

$y = -0.0384x^2 + 1.2331x + 76.564$
$R^2 = 0.7597$

C

$y = 9E\text{-}07x^3 - 7E\text{-}05x^2 + 0.0021x + 0.1687$
$R^2 = 0.9651$

Fecundity (no. eggs)

Fertility (% eggs hatching)

Egg mass (mg)

Oviposition day

Fig. 2. Mean (± SE) survival of *C. maculata* progeny produced from the 1st, 12th, 24th and 36th oviposition days of their mothers and reared under two periods of daily access to food (eggs of *E. kuehniella*), 30 minutes vs ad libitum. Larvae fed ad libitum had higher survival ($P < 0.001$) than those reared with 30 min daily access; different letters denote significant differences (LSM, $\alpha = 0.05$) among oviposition days within treatments.
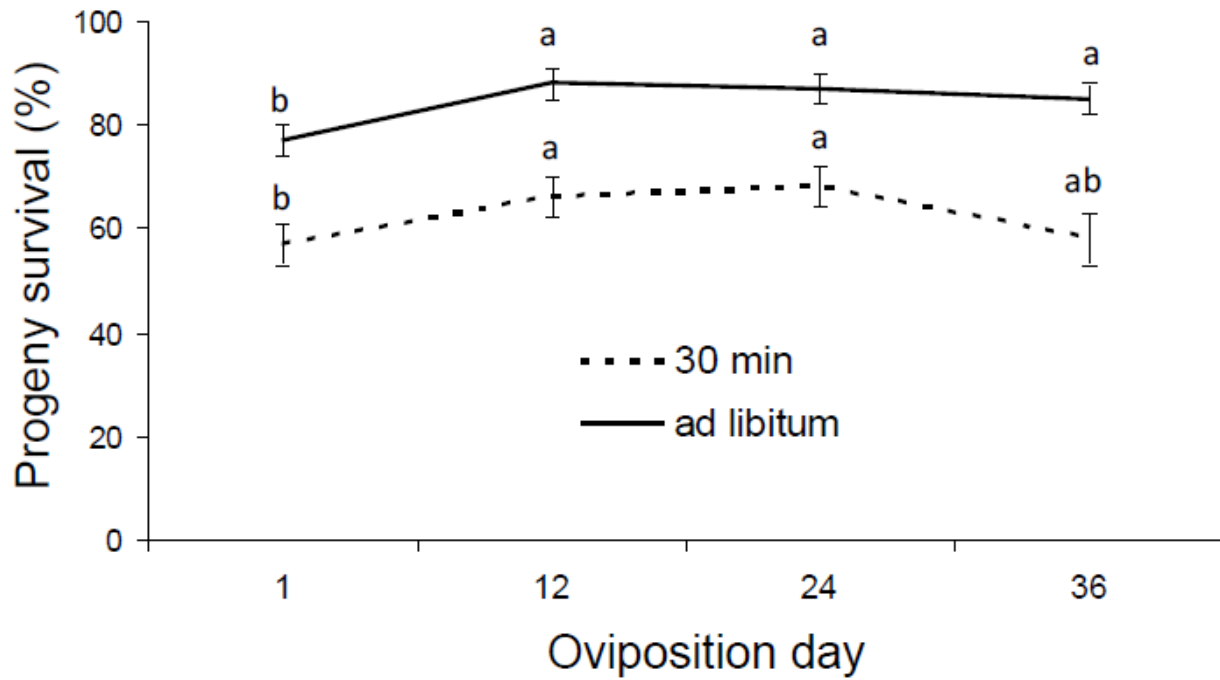
Fig. 3. Percentages of *C. maculata* larvae reared from four different maternal cohorts (oviposition days) that pupated after three (open segments), four (shaded segments), or five (solid segments) stadia when reared with access to food (eggs of *E. kuehniella*) for 30 min daily (A) or ad libitum (B). Treatment contrasts were the same across all oviposition days: three and five instars, A > B; four instars A < B. Within feeding treatments, column segments bearing different letters were significantly different among oviposition days (LSM, α = 0.05). The percentage of larvae pupating after five instars did not vary significantly among oviposition days in either treatment. Numbers indicate sample sizes for each stacked column.
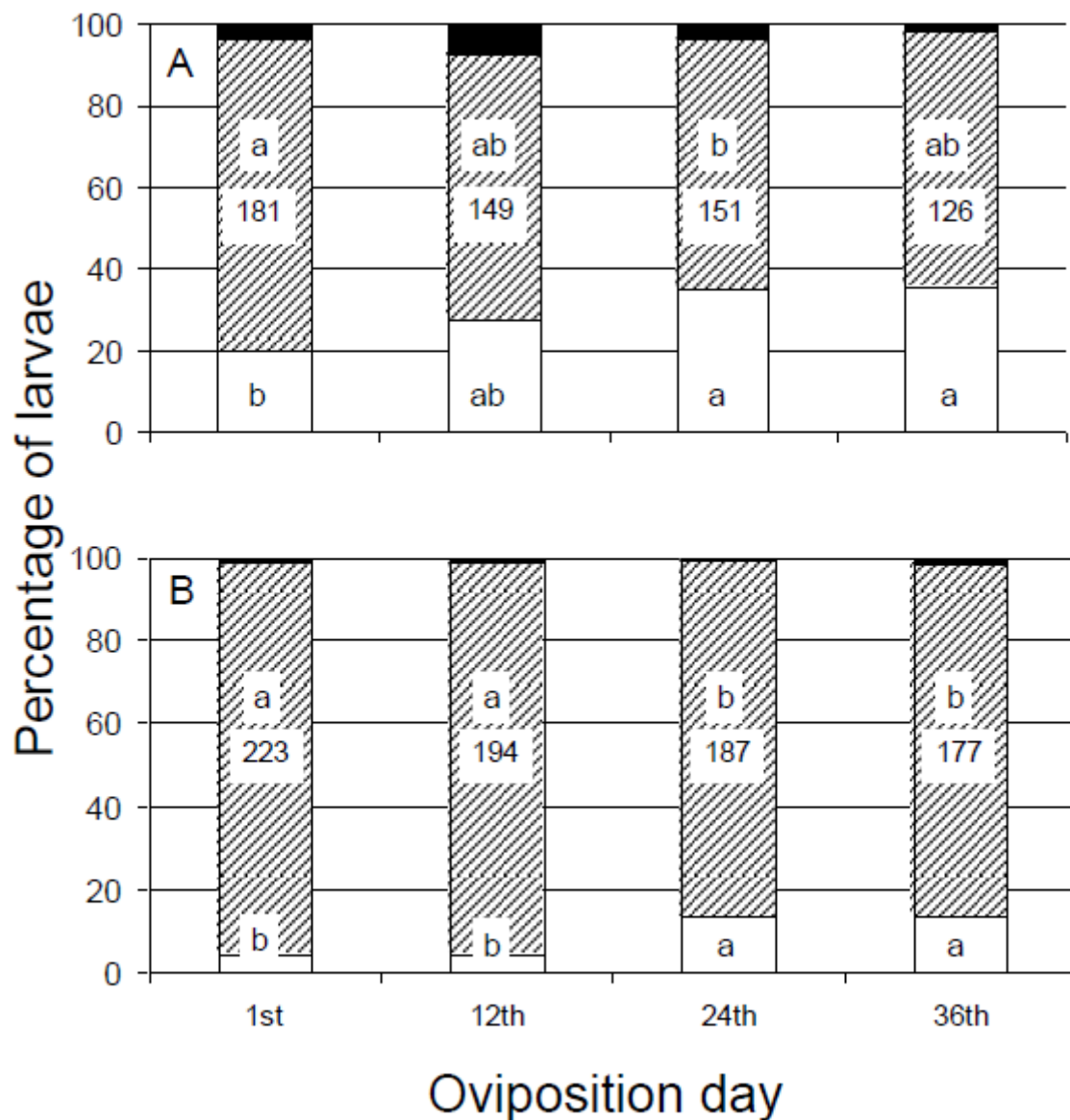
Table 1. Three-way ANOVA showing effects of larval feeding treatment (30 min daily access vs. ad libitum), maternal oviposition day (1st, 12th, 24th or 36th), and gender (male / female) on *C. maculata* adult dry mass at emergence.

Source of variation	F	df	P
Corrected model	683.23	15	< 0.001
Treatment	9915.66	1	< 0.001
Oviposition day	0.91	3	0.434
Gender	17.35	1	< 0.001
Treatment*oviposition day	0.19	3	0.249
Treatment*gender	29.29	1	< 0.001
Oviposition day*gender	0.61	3	0.612
Treatment*oviposition day*gender	0.35	3	0.792
Error		1380	
Total		1396	