

Triangular fecundity function and ageing in ladybird beetles

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Abstract. 1. In insects, the age schedules of fecundity tend to be triangular and this has been attributed more to temporal patterns of mortality than to fecundity. The objective of the work reported here was to test the assumption that senescence shapes the fecundity function in ladybird beetles, and in particular that the production function declines with age.

2. The results of a laboratory study on three species of predatory ladybird beetle indicated that the efficiency with which these insects acquire and process food declined with age. Although supplied with the same amount of food each day, after the onset of reproduction, these beetles ate less and less with increasing age. Egg production mirrored the decline in aphid consumption. Associated with this was a decline in fertility, assimilation, and speed of locomotion with age.

3. This study indicates that production declined with age and that this shaped the fecundity schedules in these ladybird beetles. In addition, the results indicated that ladybirds are income breeders and, as predicted, the reproductive effort of the small species was greater than that of the large species used in this study.

Key words. Ageing, fecundity functions, income breeders, insects, ladybirds, life-history traits, production function, reproductive effort, senescence.

Introduction

Studies on reproduction in insects have tended to assume that the fecundity schedule is shaped mainly by survivorship and that fecundity is dependent on adult size (Ziolko & Kozłowski, 1983; Kozłowski & Wiegert, 1986; Roff, 1992; Stearns, 1992). The latter is well supported by empirical data. If adult size is constant throughout adulthood, the prediction that fecundity is dependent on adult size means that fecundity per unit time of the survivors is also constant throughout adult life; however fewer individuals survive to reproduce in the second half of life than in the first. Thus selection would be expected to favour individuals that invest more in early reproduction even if this had an adverse effect on their potential longevity (Williams, 1974). In insects, the age schedules of fecundity tend to be triangular, however this is thought to be due more to temporal patterns of mortality than of fecundity (e.g. Lewontin, 1965; Meats, 1971).

Adult aphidophagous ladybird beetles need aphid prey to mature their gonads and lay eggs (e.g. Kawachi, 1981; Evans & Dixon, 1986), and the more aphids they are able to catch and process, the more eggs they can lay per unit time (Dixon & Guo, 1993). That is, the resource determining their fecundity is the availability of aphid prey in adult life. The implication of this is that they are income breeders (Sibly & Calow, 1986). Therefore, any deterioration with age in the efficiency with which they harvest and process prey should affect their reproduction. This deterioration in the effectiveness of an organism to maintain its well-being is senescence (Williams, 1996). Kindlmann *et al.* (2001) published an energy-partitioning model that predicts a triangular fecundity function in insects shaped by senescence rather than by mortality. An important assumption in this model is that if somatic size remains constant in adult life, production will decline with age. Expressed in terms of energy partitioning, somatic growth ceases on becoming adult and most energy is then switched to gonadal growth, i.e. in adult life, production is equated with gonadal growth. As in other insects (Partridge & Farquhar, 1981; Roitberg, 1989; Tartar *et al.*, 1993; Dixon & Kundu, 1997), both male and female ladybird beetles that reproduce have shorter adult lives than virgin beetles (Dixon, 2000). This indicates

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that reproduction is costly for both sexes. This being the case, they would be expected to show signs of ageing. Reproductive senescence has been reported in parasitoids (Fernando & Walter, 1999), Lepidoptera (Dunlap-Pianka *et al.*, 1977; Boggs, 1986, 1997), and ladybirds (Blackman, 1967). These observations imply a decline in production and/or exhaustion of reserves during adult life.

The objective of this laboratory study was to test the assumption made by Kindlmann *et al.* (2001) that if size remains constant, production declines with age in adult insects, and that this decline in production is associated closely with changes in the fecundity schedule. This was tested using ladybird beetles as model species.

Materials and methods

Stock culture of Menochilus sexmaculatus and Coccinella transversalis

Adults of *Menochilus sexmaculatus* and *Coccinella transversalis* were collected from a bean field in a suburb of Agartala, north-east India and used to establish stock cultures of the two species, which were kept at $25 \pm 2^\circ\text{C}$, LD 16:8 h photoperiod. Groups of 30 adult beetles (sex ratio 1:1) were kept in Perspex[®] containers (6 × 17.5 × 11.6 cm) containing damp tissue paper and a piece of corrugated filter paper (10 × 15 cm) for the adults to oviposit on. The beetles were fed daily an *ad libitum* supply of bean aphids *Aphis craccivora* Koch. Eight such containers were maintained for each of the species. The eggs were collected daily and the larvae were reared following Agarwala and Dixon (1992).

Changes in adult weight, food consumption, and egg production. The adults used in the experiments were reared individually from egg hatch to adult emergence in 5-cm Petri dishes. The larvae were fed daily an *ad libitum* supply of bean aphids. On emergence from the pupae, the adults were weighed then 10 male–female pairs of each species were transferred individually to 9-cm Petri dishes and fed an *ad libitum* supply of bean aphids. Each dish contained a piece of corrugated filter paper for egg laying and the base was lined with filter paper. The filter paper was changed every day; the Petri dish was changed every third day. As soon as a female started ovipositing, it was weighed and its mate was removed. Subsequently these females were weighed daily at the time the food was changed. Every third day, after the dishes had been cleaned and prior to feeding, a male, not necessarily the original mate, was placed in the dish with the female for 1 h for mating. Eggs were collected daily and the number and cluster size were recorded. The *C. transversalis* and *M. sexmaculatus* female beetles were fed 60 and 40 adult bean aphids respectively each day. An earlier functional response study showed that young beetles of these two species were satiated at these feeding rates. The number of aphids eaten was recorded daily.

Faecal production. At the time of the food change, the faeces of four of the females of *C. transversalis* were collected and weighed. This was done during the first 12 days

and days 22–34 of their reproductive life. The faeces were not dried prior to weighing because of technical difficulties.

Hatching success. The hatching success of the eggs produced by five of the *M. sexmaculatus* females was monitored over the first 12 days and days 32–42 of reproductive life. To record this, the eggs were placed in 5-cm Petri dishes lined with dampened filter paper.

All the experiments were carried out at $25 \pm 2^\circ\text{C}$ and a LD 16:8 h photoperiod.

Stock culture of Harmonia axyridis

For the experiments on *Harmonia axyridis* (Pallas), 6-day-old pupae were collected from the stock cultures of these beetles maintained at Yamagata University, Japan.

Gonadal development. Even when supplied with aphids *ad libitum*, *C. transversalis* and *M. sexmaculatus* did not start reproducing for 5 and 6 days respectively. If this reflects the time it takes to ovulate and mature eggs, there should be no eggs in the gonads of ladybirds on emerging from pupae. In addition, the time it takes for a ladybird to start ovipositing once fed aphids should be the same whether it is fed aphids *ad libitum* on emerging from a pupa or after feeding only on honey for a few days, a diet that does not result in oviposition.

Eleven of the *H. axyridis* pupae were dissected under a zoom stereo-microscope and the gonads of the five that were female were removed carefully and placed individually in 0.1 ml of insect ringer on glass slides. A drop of 1% eosin was added to each gonad to stain the tissues and make them more obvious. Using fine needles, the ovarioles and oviducts of each gonad were examined for developing and mature eggs. On the day of emergence from pupae, eight female *H. axyridis* were anaesthetised with carbon dioxide, dissected, and their gonads similarly removed, stained, and examined for mature and developing eggs.

Other freshly emerged females of *H. axyridis* were divided into two groups. The individuals in one group ($n = 12$) were each placed in a 9-cm Petri dish lined with filter paper and fed daily an excess of pea aphids *Acyrtosiphon pisum* Harris from day 1. Individuals in the other group ($n = 10$) were similarly placed individually in Petri dishes but for the first 5 days were supplied daily with drops of undiluted honey on filter paper, plus cotton wool dampened with water. Other ladybirds are known not to lay eggs when fed only sugar solution (Evans *et al.*, 1999; Evans, 2000). On day 6, their diet was changed and they were fed an excess of pea aphids daily. Similar-aged males were placed in each Petri dish for 2 h on day 1 then every other day, when the food was being changed and just prior to them being fed. Any eggs laid were removed and the number and day on which they were laid were recorded.

Faecal production. Twelve females of *H. axyridis* were kept individually in 9-cm Petri dishes from emergence and fed daily a fixed number of aphids of a particular size. As above, these females were mated at regular intervals. Each day, the number of aphids eaten was determined and

the aphids were replaced. The weight of aphids eaten was obtained by multiplying the number eaten by the average weight of the aphids. In addition, when the food was changed the faeces were collected and weighed. This information was used to determine whether the weight of faeces produced per unit weight of aphids consumed differed on the first and the 31st day of reproduction.

Egg size. In order to determine whether egg size changed with age, the eggs laid by each beetle on the first day of reproduction, and on the 11th, 21st, and 31st day of their reproductive lives, were weighed.

Speed of locomotion. The speed of walking of these females was also determined daily. The beetles were placed individually at the base of a vertical wooden rod, 8 mm in diameter, 50 cm long. The rod was hand held and inverted when the beetle reached the top. All beetles moved directly upwards and the distance they had travelled was noted after 1 min.

All these experiments were carried out at $22 \pm 1^\circ\text{C}$ with a LD 16:8 h photoperiod.

Production

During the course of adult life, the weight of female ladybirds first increases then declines back to about the starting weight. As there are no eggs in the gonads of freshly emerged females, it seems reasonable to assume that the changes in adult weight reflect mainly the growth of their gonads. In addition, they produce eggs, which weigh on average 0.135 and 0.114 mg in *C. transversalis* and *M. sexmaculatus* respectively. Production can then be calculated by correcting the daily biomass production of eggs by either adding the gain in weight of the gonads over the same period or by subtracting if there is a loss in weight. The estimates of production were determined from the onset of reproduction, as prior to that the system was apparently affected by the delay in the time it took to ovulate and develop eggs to a stage at which the gonads could operate at maximum efficiency.

The trend in production with age so obtained was compared with the trend predicted by the function used by Kindlmann *et al.* (2001) to define the changes in production (Mg) with age in insects:

$$g' = \exp(-dt^2) \cdot as^\alpha - Mg$$

$$g(0) = 0$$

where g is gonadal size at time t , t is time, s is adult somatic size, a , α , and d are constants, M is a constant describing the conversion rate from gonads to offspring.

Results

Adult size

In both *C. transversalis* and *M. sexmaculatus*, body weight first increased then decreased during the course of

adult life (Figs 1a and 2a). Their maximum weight was 140 and 124% respectively of their initial weight and the first deaths were recorded on days 44 and 36 respectively. The weight just prior to the first death in each species was similar to the initial weight. That is, in both species, weight did not remain constant throughout adulthood, but first showed a marked increase, then a decrease, with the beetles dying at a weight similar to that at emergence from the puparia.

Aphid consumption

Although the beetles were supplied daily with the same number of aphids, consumption during adult life was not constant but showed a similar trend to adult weight. There was an initial slight increase in consumption then a marked decline as the beetles aged (Figs 1b and 2b).

Reproductive schedule

Number of eggs. Both species showed a reproductive delay, which was 5 ± 0.4 days in *C. transversalis* and 6 ± 0.4 days in *M. sexmaculatus*. Immediately following the reproductive delay, the number of eggs laid per day started high then declined gradually and reached a low level just prior to the first deaths in both species (Figs 1c and 2c). The peak in egg production in both species coincided with the peak in aphid consumption. The decline in the number of eggs laid per day by each species showed the same form and timing as the decline in aphid consumption (cf. Figs 1b and 2b). The relationships between the logarithm of the number of eggs laid (E) and the logarithm of the number of aphids consumed (A) per day over this period took the form: $\log E = -0.65 + 1.35 \log A$ ($n = 18$, $r = 0.99$, $b > 1$, $t = 6.25$, $P < 0.001$) for *C. transversalis*; $\log E = -0.91 + 1.54 \log A$ ($n = 15$, $r = 0.99$, $b > 1$, $t = 12.86$, $P < 0.001$) for *M. sexmaculatus*. In both cases, the slopes of the relationships were significantly greater than one, indicating that the decline in the consumption of aphids was less than the decline in the number of eggs laid per day.

Accompanying the decrease in reproduction over time, there was also a decrease in body weight. Therefore, it is possible that these ladybirds also sustain egg production by utilising body tissues and that the contribution from this source increases with age. This was tested by correlating the proportion of the wet weight of the eggs laid over a 2-day period that could have come from the decrease in body weight over the same period (Y) against age (X), throughout reproductive life. In both species, there was a significant increase in the proportion of the wet weight of the eggs that could have come from body tissues with age: *C. transversalis*: $Y = 5.2 + 0.27 X$ ($r = 0.41$, $n = 18$, $P < 0.05$); *M. sexmaculatus*: $Y = -3.5 + 0.41 X$ ($r = 0.81$, $n = 15$, $P < 0.001$).

Thus, with increasing age, and in both species, proportionally more of the resources for egg production may have come from their body tissues.

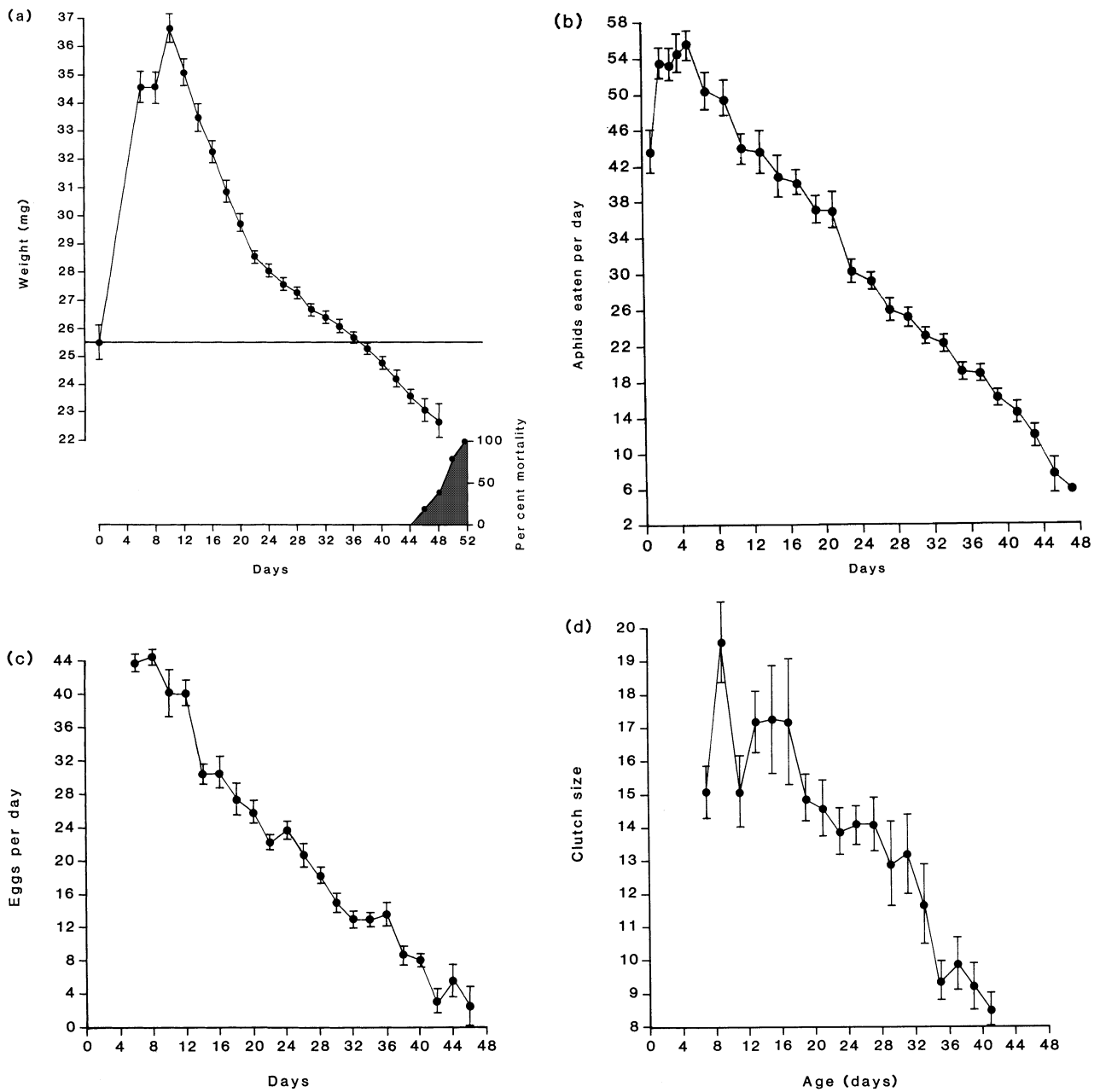


Fig. 1. Trends with age in (a) adult weight and mortality, (b) aphid consumption per day, (c) eggs laid per day, and (d) clutch size of *Coccinella transversalis* fed an abundance of aphids daily.

Reproduction can also be expressed in terms of age. In both species, there was a significant decline in the number of eggs laid per day with age: log number of eggs = $2.60 - 0.95 \log \text{age}$ ($n = 18$, $r = -0.94$) for *C. transversalis*; log number of eggs = $2.54 - 0.97 \log \text{age}$ ($n = 15$, $r = -0.86$) for *M. sexmaculatus*.

Clutch size. As with the number of eggs laid per day, there was a significant decline in clutch size with age in both species: *C. transversalis*: log clutch size = $1.62 - 0.37 \log \text{age}$ ($n = 18$, $r = -0.816$); *M. sexmaculatus*: log clutch

size = $1.75 - 0.57 \log \text{age}$ ($n = 15$, $r = -0.93$). Interestingly, clutch size declined less rapidly with age than the number of eggs, which might imply that clutch size was more constrained than the number of eggs.

In conclusion, when fed an abundance of aphids, both species of ladybird beetle, after a pre-reproductive delay of 5–6 days, start reproducing at a high rate then show a marked decline in daily egg production, clutch size, and number of aphids eaten with age.

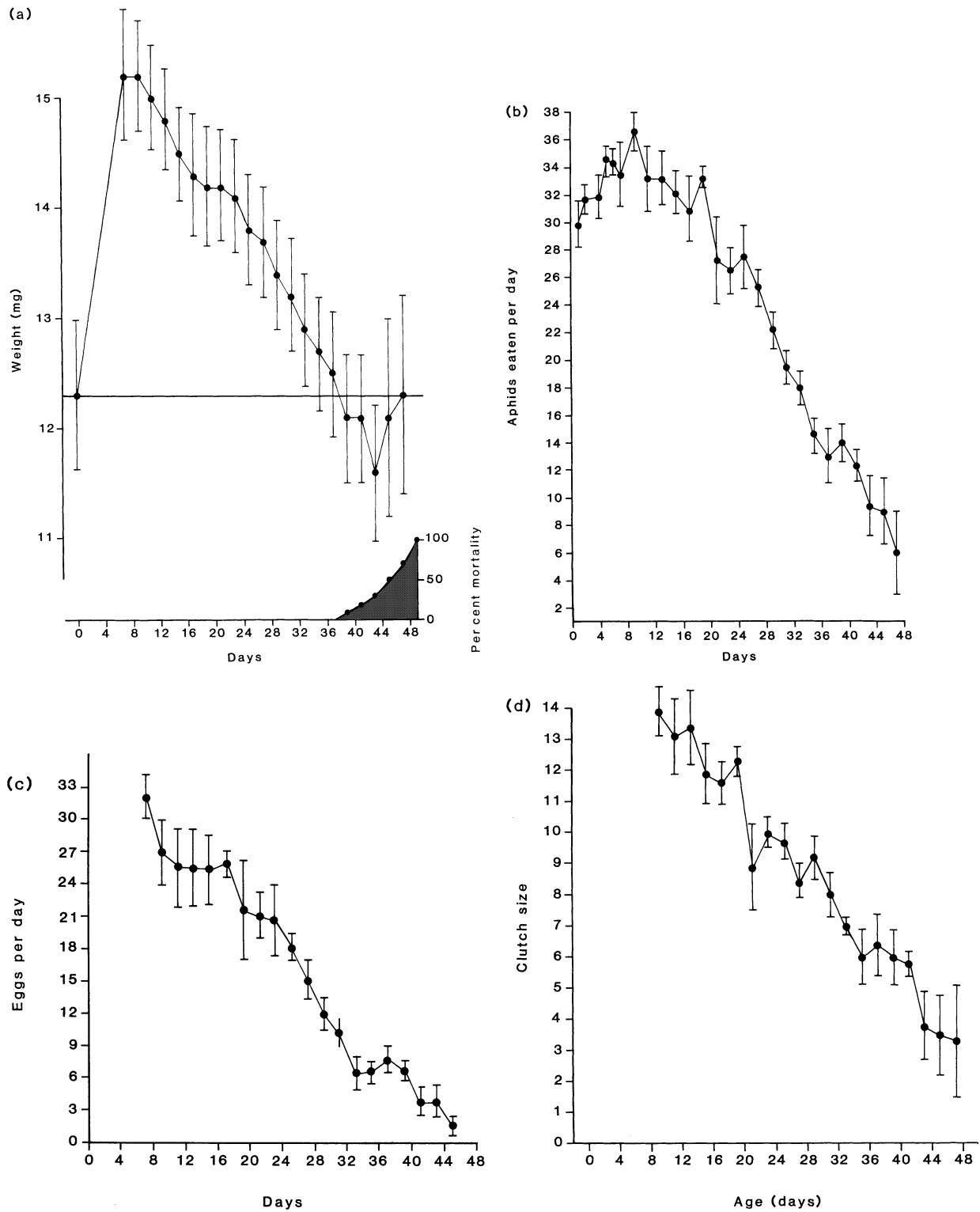


Fig. 2. Trends with age in (a) adult weight and mortality, (b) aphid consumption per day, (c) eggs laid per day, and (d) clutch size of *Menochilus sexmaculatus* fed an abundance of aphids daily.

Egg size. The mean weight of the eggs laid by the 12 *H. axyridis* was 0.228 ± 0.004 mg on the first day of reproduction, 0.221 ± 0.003 mg on the 11th day, 0.230 ± 0.002 mg on the 21st day, and 0.231 ± 0.003 mg on the 31st day, indicating that there was no significant change in average egg weight with increasing age in *H. axyridis* (ANOVA, $F=2.28$, d.f. = 3,44, NS).

Pre-reproductive period. Neither the gonads of five 6-day-old female pupae, of average weight 30.9 ± 1.1 mg, nor the gonads of eight freshly emerged female adults, of average weight 31.6 ± 0.7 mg, of *H. axyridis* contained any eggs. When 10 newly emerged adults of *H. axyridis* were fed honey for 5 days then switched to a daily diet of an abundance of aphids, they took a similar length of time (9.2 ± 0.4 days) to start ovipositing once fed aphids as the 12 adults fed aphids in abundance from emergence (8.3 ± 0.3 days). That is, the time it takes to ovulate and mature eggs may determine the reproductive delay.

Other age-related factors

Fertility. A significantly greater percentage (80%) of the 1367 eggs laid by five females of *M. sexmaculatus* in the first 12 days of their reproductive life hatched than of the 225 eggs that they laid from day 32–42 of their reproductive life (57%) ($\chi^2 = 58.3$). In addition, each of the five females used showed the same trend ($\chi^2 = 6.7, 20.2, 11.8, 11.5, \text{ and } 8.6$). That is, early in reproductive life this ladybird beetle lays proportionately 1.4 times more fertile eggs than it lays towards the end of its life.

Assimilation. The ratio of the weight of faeces (101.8 mg) produced to the wet weight of aphids consumed (892.4 mg) in early life was significantly lower than that recorded (86 mg:367.1 mg) later in adult life in *C. transversalis* ($\chi^2 = 21.1$, $P < 0.001$). In addition, of the ratios for the four adults used to obtain the above data, three were also significant ($\chi^2 = 5.98, P < 0.05$; 3.46, NS; 7.5, $P < 0.05$; 4.46, $P < 0.05$). This indicates that the beetles became less efficient at assimilating food as they aged.

Similarly, in *H. axyridis*, the ratio of the weight of faeces produced to the wet weight of aphids consumed on the first day of reproduction was significantly lower than the ratio on the 31st day of reproduction, whether the ratio was determined using the aphids consumed on the same day or on the previous day (paired comparison: $t=4.1$, d.f. = 11, $P < 0.01$; $t=2.1$, d.f. = 11, $P < 0.05$).

Speed of walking. As the *H. axyridis* aged, their speed of movement declined at a rate of about $1.5 \text{ cm min}^{-1} \text{ day}^{-1}$ (Fig. 3), i.e. the performance of these beetles in terms of speed of movement is best in early adult life and decreases thereafter, especially rapidly after 30 days.

In addition to the changes observed in the rate of production of eggs with age, ladybirds also showed age-related trends in fertility, assimilation, and speed of movement, indicating that the organs of ladybirds deteriorate and that their efficiency declines with age.

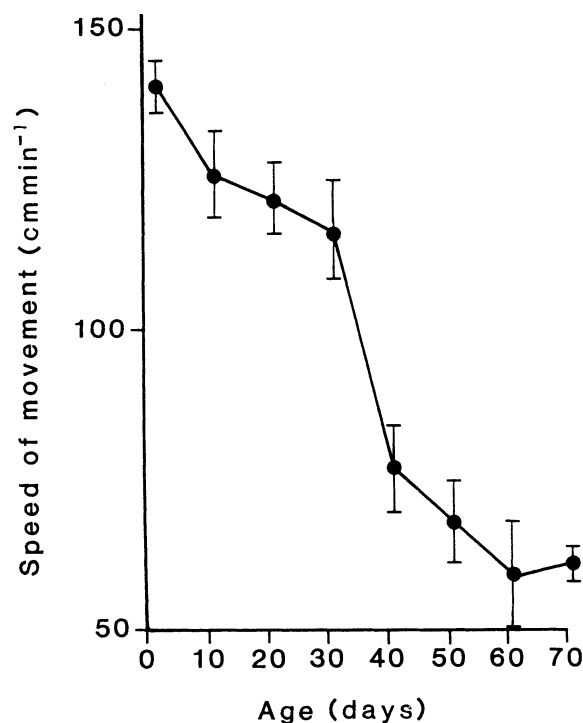


Fig. 3. Trend with age in the speed of locomotion of adult *Harmonia axyridis*.

Production

Although kept in a congenial environment and supplied with the same amount of food every day, production did not remain constant throughout adult life (Fig. 4). The function used by Kindlmann *et al.* (2001) to define the changes in production with age gave a very good fit to the data in Fig. 4. Thus, this study tends to support their assumption that production declines with age.

Discussion

In the laboratory, both *C. transversalis* and *M. sexmaculatus* had triangular fecundity functions, which were not shaped by survivorship. Although supplied with the same amount of food each day, after the onset of reproduction the beetles ate less and less with increasing age. The decline in egg production with age mirrored the decline in aphid consumption. This was associated with a decline in fertility, assimilation, and speed of locomotion with age, indicating that these beetles senesce and that this process shaped their fecundity schedule in the laboratory. Interestingly other studies have shown that reproduction has an adverse effect on the potential longevity of ladybirds (Dixon, 2000), which implies that reproduction and the rate of senescence are linked.

Also of interest, and contrary to what is assumed to happen in most insects, the ladybird beetles used in this

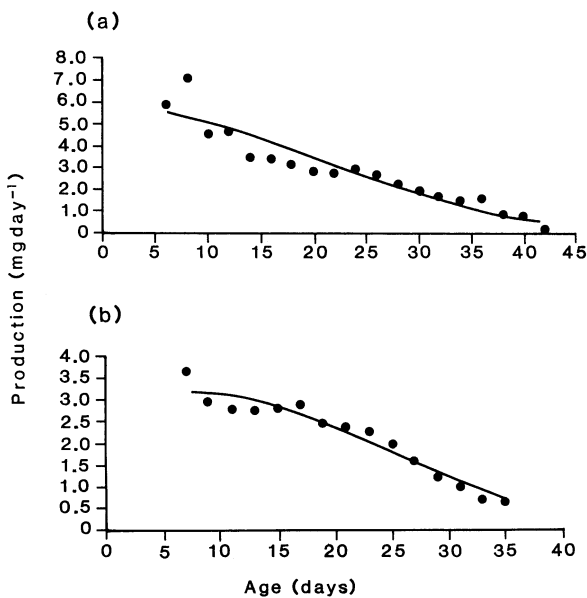


Fig. 4. The trends in production recorded during adult reproductive life in (a) *Coccinella transversalis* and (b) *Menochilus sexmaculatus* when fed an abundance of aphids daily. The lines were calculated using the function used by Kindlmann *et al.* (2001) to define changes in production in adult insects with age.

study did not cease growing on becoming adult. Initially they showed a 20–40% increase in weight then their weight declined back to close to their initial weight. The gonads of freshly emerged adults of *H. axyridis* did not contain any eggs. It is likely that the pre-reproductive delays recorded in this study are the periods of time required by these beetles to develop an egg from ovulation at 25 °C. The period required is likely to be temperature dependent. Thus it is likely that the striking changes in adult weight observed in this study reflect changes in the size of the gonads. The fact that the weight of an adult at the end of its life was close to its initial weight tends to support this contention and indicate that the soma does not grow. Not knowing this could lead to the conclusion that these beetles are calling on reserves (capital) to supplement income when producing eggs, especially late in adult life (cf. Boggs, 1997). In reality, they are income breeders but this is obscured by the fact that it takes time to produce an egg from an oocyte. In not first putting the incoming energy into storage, it is possible that ladybirds have maximised their reproductive conversion efficiency (unit of offspring output per unit input).

The total numbers of aphids eaten and eggs laid during adult life for each of these ladybird beetles are known. On emergence from pupae, adults of the two spot ladybird *Adalia bipunctata* contain little by way of fat reserves, and male and female beetles contain the same amount of fat (Yasuda & Dixon, 2002). Even if these fat reserves are used for egg production, they can contribute very little as the total weight of eggs produced by *C. transversalis* and *M. sexmaculatus* was 4.6 and 5.8 times their body weight at emergence respectively. This study has also revealed that

on emergence from pupae, *H. axyridis* had no eggs in its gonads. Assuming that these observations apply to ladybird beetles in general, it is possible to calculate the efficiency with which they convert aphids into eggs. On a wet weight basis, this is 10.4 and 8.4% for *C. transversalis* and *M. sexmaculatus* respectively. Interestingly, the smaller species has the lower reproductive efficiency, which is to be expected as its respiratory costs per unit weight are higher.

This laboratory study on three species of ladybird beetle is consistent in that they all showed signs of senescence, and that in *C. transversalis* and *M. sexmaculatus* the triangular fecundity function was shaped by senescence. That is, there is strong evidence to support the contention that the efficiency with which insects can acquire and process food deteriorates with age and it is this that is largely responsible for the triangular shape of the fecundity schedule. This is consistent with the expectation that selection is likely to favour those individuals that invest more in early reproduction even if this has an adverse effect on their potential longevity, because fewer individuals will survive to reproduce in the second half of life than in the first (Williams, 1974). In the field, conditions are likely to be considerably more adverse than the conditions experienced by the beetles in this study and as a consequence the survival of the older beetles, in particular, is likely to be reduced further. Although this is likely to result in greater variability in the shape and timing of the trends, the implication of the results presented is that senescence is an important factor shaping the fecundity schedules of insects in the field, especially in income breeders. Clearly, senescence and survival are inter-related. This study tends to support the view that investment in early reproduction, through senescence, could also be important in determining the shape of the survivorship curve of adults in the field.

The assumption made by Kindlmann *et al.* (2001) that production declines throughout adult life as a consequence of senescence, appears to be well supported by this study. This is because the efficiency with which ladybird beetles harvest and process prey and produce eggs declines with age. That is, senescence shapes and is shaped by other life-history traits (Williams, 1992).

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