

FEMALE PROMISCUITY MAINTAINS HIGH FERTILITY
IN LADYBIRDS
(COL., COCCINELLIDAE)

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Most species of ladybird are promiscuous, both sexes mating a number of times during their reproductive lives. It is easy to understand why males should be promiscuous. Males produce large numbers of small, energetically cheap sperm. Consequently, a male's fundamental interest lies in maximising his reproductive output, by inseminating as many females as possible. Conversely, given Hodek's (1973) statement that one copulation is generally reported as being sufficient to allow the fertilisation of all a female's eggs, it is not easy to answer the question 'why are female ladybirds promiscuous?'. A female's prime motive must be to ensure that the relatively small number of large, nutrient-rich eggs (compared with sperm) that she produces are fertilised by sperm carrying good genes. Natural selection should therefore favour individuals with levels of promiscuity that maximise their reproductive output, in terms of both the number and fitness of progeny. This optimal promiscuity level will depend to a large extent on the costs and benefits of mating, which will vary from species to species. In the 2-spot ladybird, *Adalia bipunctata* (L.), mating lasts for several hours. During this time a female cannot oviposit and, although she can feed, rate and efficiency of aphid capture is likely to be reduced. Furthermore, movement will involve abnormal energy costs, as she has to carry the male on her back. In the laboratory, multiple-mated female 2-spots have shorter longevity than those permitted just a single mating (Majerus, pers. obs.). Against these costs must be set potential benefits of repeated mating. Mating has been shown to have a stimulatory effect on female oviposition rate, with the rate of oviposition being greatest in the day or two after mating, and then declining to a constant rate, unless elevated by another mating (Sem'yanov, 1970). It has also been suggested that female promiscuity may be a bet-hedging strategy. A female whose progeny are sired by a number of different males has an increased probability that at least some of these offspring are fathered by genetically fit males (Majerus, in press). An added consideration, at least in the 2-spot ladybird, is the amelioration of inbreeding depression. In the 2-spot, mating with close relatives has been shown to be a considerable disadvantage in terms of both the fertility and viability of eggs produced (Lus, 1947; Majerus & Kearns, 1989). By mating with a succession of different males, a female reduces the chances that all her progeny are the result of mating with a close relative. In addition, as sperm may be stored in a female's spermatheca for a considerable length of time, repeated mating will provide the

potential for sperm competition: that is to say the competition, within a single female, between sperm from two or more males, for the fertilisation of the ova (Parker, 1970). Assessment of the balance between the costs and benefits of mating for female 2-spot ladybirds obviously depends crucially on the contention that a single mating is sufficient to allow the fertilisation of all a female's eggs.

I here describe a series of experiments to test this proposition in three species of coccinellid.

METHODS

Stocks of the 2-spot ladybird, the 14-spot ladybird (*Propylea 14-punctata* (L.)) and the cream-streaked ladybird (*Harmonia 4-punctata* (Pontopiddan)), were collected from Cambridge (2-spot and 14-spot) and the King's Forest, Suffolk (cream-streaked). Mating pairs from the stocks were isolated to generate progeny, which were then isolated immediately after eclosion. Female progeny from the families produced were then removed in twos, one being assigned to a 'repeated mating' class, the other to a 'single mating' class. These females were retained in isolation for two weeks after eclosion before being put with a male. Males were chosen randomly from stocks of reproductively mature males which were known to be between two and six weeks old (from eclosion), and which had not mated in the previous seven days.

Single mating females were given one male on the fourteenth day after eclosion. Those that paired within two hours and remained paired for more than one hour (23 of 25 for the 2-spot; 21 of 25 for the 14-spot; 24 of the 25 for the cream-streaked) were retained for further experimentation. The same initial procedure was used for the first mating of females assigned to the repeated mating class. The same criteria were used before placing females in the experiment; 22 of 25 2-spot, 22 of 25 14-spot and 23 of 25 cream-streaked ladybirds met the criteria. Thereafter, a male, randomly selected from the stock, was put with each repeated mating female, each day between 8.00 a.m. and 8.30 a.m., and removed the same day between 6.30 p.m. and 7.00 p.m. (or if the pair were in copula at this time, as soon as they parted thereafter). Matings were recorded for each female. The two females from a family were only used in the experiment when both met the criteria for the initial mating.

The females of both classes were placed in clean Petri-dishes each morning, and were fed on an excess of pea aphids (*Acyrothosiphon pisum*) cultured on broad beans (*Vicia faba*). Eggs were counted and left in the laboratory at approximately 21°C. The number of eggs which turned grey after three days were counted. Turning grey, rather than hatching, was taken as the criterion of fertility, because of the high level of sibling egg cannibalism exhibited by some coccinellids (Hurst & Majerus, 1993; Hurst *et al.*, in prep.). However, hatch rates were

also recorded for all egg batches. Females were retained in the experiment until they died, or until they had laid 1000 eggs.

For analysis, eggs were split chronologically into sets of 50. One egg, on the periphery of each clutch, was arbitrarily designated as the first from that clutch, and others were numbered left to right and away from this first egg. This allowed eggs from these clutches, which covered the cusp from one set of 50 eggs to the next, to be assigned to a set.

Any female that failed to produce at least 250 eggs before death was excluded from the analysis, as was the other female from her family. In addition, females which produced low initial hatch rates, i.e. less than 70% from the first 50 eggs, were excluded from the analysis.

RESULTS

The mean number of matings by the repeated mating females were: 25.09 for the 2-spot ladybird ($n = 18$); 18.75 for the 14-spot ladybird ($n = 15$); and 15.78 for the cream-streaked ladybird ($n = 17$). The mean number of eggs laid, the mean fertility for each sequential set of 50 eggs, and the mean hatch rates for each sequential set of 50 eggs, are given in Table 1.

In all three species, the fertility rates, and hatch rates, from females that had mated once, began to decline after about 100 eggs. For the 2-spot, significant levels of fertility (at least 10% of eggs hatching) were maintained until about 550 eggs had been laid, and some level of fertility even longer, the last egg to develop and hatch successfully from a single mating female being the 839th that she had laid, some 57 days after she had mated. For the 14-spot ladybird, the declines in fertility and hatch rates were more rapid, significant levels of fertility only being maintained up to about 350 eggs, and no eggs developing after 500. For the cream-streaked ladybird, the drop in fertility and hatch rate was sharper still, with a rapid decline after about 200 eggs, significant levels of fertility only being maintained to 250 eggs, and none hatching after 450.

By comparison, in all three species, high levels of fertility (over 70%) and hatch rate (69% or over) were maintained throughout the experiment for the repeated mating females. All three species show a slow but significant decline in fertility and hatch rate throughout the experiment, with the effect being least marked in the 2-spot ladybird and most obvious in the 14-spot ladybird.

DISCUSSION

The results show conclusively that female promiscuity is a potent factor in maintaining high egg fertility. The contention that one copulation is sufficient to allow the fertilisation of all a female's eggs (Hodek, 1973) does not hold for the three species considered here. Females which have mated once either use up all the sperm, or the

TABLE 1. — THE EFFECT OF MATING ON FERTILITY AND EGG HATCH RATE IN THREE SPECIES OF COCCINELLID.

		Sets of eggs (50 eggs per set)																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Adalia bipunctata</i>																					
single mating:	fertility	0.91	0.99	0.92	0.87	0.79	0.65	0.61	0.50	0.42	0.32	0.18	0.08	0.04	0.01	0.00	0.00	0.01	0.00	0.00	0.00
	hatch rate	0.90	0.92	0.84	0.80	0.74	0.62	0.58	0.48	0.41	0.31	0.17	0.08	0.04	0.01	0.00	0.00	0.01	0.00	0.00	0.00
repeated mating:	fertility	0.93	0.99	0.98	0.97	0.99	0.96	0.94	0.97	0.96	0.95	0.97	0.92	0.90	0.91	0.90	0.92	0.90	0.83	0.82	0.82
	hatch rate	0.90	0.89	0.90	0.91	0.92	0.89	0.88	0.90	0.87	0.88	0.86	0.84	0.83	0.83	0.81	0.80	0.80	0.76	0.74	0.75
<i>Propylea 14-punctata</i>																					
single mating:	fertility	0.96	0.98	0.92	0.86	0.77	0.43	0.13	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	hatch rate	0.94	0.93	0.87	0.80	0.70	0.41	0.12	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
repeated mating:	fertility	0.98	0.98	0.96	0.88	0.90	0.88	0.86	0.87	0.87	0.85	0.77	0.77	0.79	0.80	0.80	0.78	0.75	0.72	0.77	0.74
	hatch rate	0.96	0.90	0.91	0.81	0.84	0.79	0.79	0.78	0.78	0.81	0.69	0.71	0.74	0.72	0.73	0.71	0.70	0.68	0.72	0.71
<i>Harmonia 4-punctata</i>																					
single mating:	fertility	0.93	0.98	0.93	0.78	0.26	0.20	0.07	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	hatch rate	0.89	0.94	0.87	0.69	0.24	0.19	0.07	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
repeated mating:	fertility	0.95	0.97	0.98	0.95	0.92	0.94	0.90	0.93	0.92	0.88	0.87	0.85	0.82	0.85	0.81	0.83	0.83	0.81	0.79	0.76
	hatch rate	0.91	0.88	0.91	0.84	0.81	0.83	0.81	0.86	0.84	0.79	0.77	0.76	0.77	0.74	0.72	0.75	0.75	0.75	0.71	0.69

sperm loses its capacity for fertilisation through death or weakness. The former possibility, that females may become exhausted of sperm, has been proposed previously by de Jong *et al.* (1993) for the 2-spot ladybird, although they provide no experimental data on the point.

However, irrespective of whether a female's store of sperm from a single mating gradually becomes used up as she lays batches of eggs, or alternatively sperm has a limited potent life in females, the promiscuous behaviour of these female ladybirds is obviously adaptive, having a very considerable effect on the fertility and hatch rates of eggs produced.

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Notes on Placochilus seladonicus (Fall.) (Hem., Miridae) in Britain. — The host of this pretty plant-bug is Field Scabious (*Knautia arvensis* (L.) Coulter), the flowers of which the bluish females closely match. Shirt (1987, *British Red Data Books: 2. Insects*, NCC) designates *Placochilus seladonicus* as 'Category 1 - Endangered' but Kirby (1992, *A review of the scarce and threatened Hemiptera of Great Britain*, JNCC, Peterborough) considered that it should not be so categorised, on the grounds that its status is insufficiently known and that it may be a recent colonist in Britain.

The bug was first found in Britain on 3.ix.1977, at a site having a few scattered examples of its host-plant. This was on the Lower Greensand in Bedfordshire where a disused railway track ran beside a filled-in sand quarry at Leighton Buzzard (Nau, 1979,