WHY LADYBIRDS HAVE GENERALY BEEN SO INEFFECTIVE IN BIOLOGICAL CONTROL?

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INTRODUCTION

The vernacular names of coccinellid beetles in several languages suggest that these insects have always been recognized as useful predators even in the long distant past when humans had a semi-nomadic life-style (Exell, 1989). However clear mentions of their beneficial role only appeared in the eighteenth century when some eminent naturalists proposed that hothouses could be kept free of aphids with coccinellid beetles (Coppel and Mertins, 1977). In 1888, the introduction of *Rodolia cardinalis* (Mulsant) in California, from Australia, for the suppression of *Icerya purchasi* (Maskell) marked the real beginning of biological control. Since that time, several pests have been kept under control by these predators (Bartlett, 1978; Hodek, 1973). Nonetheless outstanding successes have only be achieved against coccid pests while ladybirds have generally failed to keep aphid populations under economic thresholds of damage (Bartlett, 1978; Greathead, 1989).

According to ecological studies of the relationships between prey and their natural enemies (Begon et al., 1986), aphidophagous ladybirds have at least two properties (i.e. searching ability and aggregation on host patches) that characterize good biological control agents. Larvae and adults of most ladybird species display a positive prey taxis: they randomly search plant surfaces and concentrate their effort on a small area after cathing a prey (Carter and Dixon, 1982; Kareiva and Odell, 1987). The resultant of this foraging behaviour is usually an aggregation of ladybirds in the most densely populated patches of prey. On the other hand, in terms of biological control, the reproductive response of ladybirds to aphid populations is probably too weak. Although little research interest has been paid to this subject. Wright and Laing (1980) and Mills (1982) showed that egg production is only correlated to a narrow range of aphid densities. As it is thought that such a response is controlled by satiation, doubts have been cast on the ability of ladybirds to control aphid population (Dixon, 1970; Mills, 1982; Wratten, 1973). Futher work, reported here, reinforce this lack of faith and suggest that the inefficiency of aphidophagous ladybirds as

Key words: Ladybirds, biological control, reproductive behaviour, reproductive numerical response, efficiency.

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biological control agents is a consequence of their ability to exploit unstable food resources.

REPRODUCTIVE STRATEGY OF LADYBIRD BEETLES

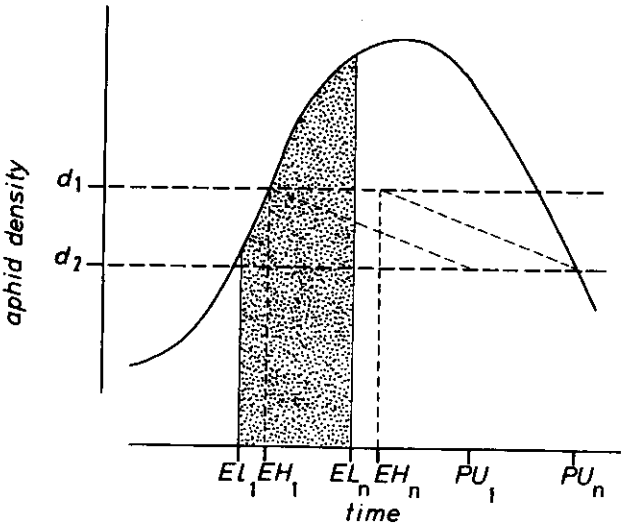

Fig. 1. The reproductive strategy of ladybirds: the period during wich egg laying is compatible with the requirements for the survival of larvae.
legend:
- symbols: EL = egg laying; EH = egg hatching; PU = pupation (indices 1 and n indicate the first and the last egg batch that meet the requirements for the survival of larvae); D_1 = aphid density for new born larvae; D_2 = aphid density for larvae immediately prior to pupation.
- the shaded area represents the period during which egg laying is compatible with the requirements for larval survival.

As ladybirds lay eggs near growing aphid colonies, it is hardly conceivable that forecasting the amount of food ultimately available for the offspring would be the cornerstone of their reproductive strategy. Taking into account that aphid populations persist for relatively short periods of time (Dixon, 1985) and in the light of studies on parasitoïds (Luck, 1990), it is more likely that the reproductive success of ladybirds is conditionned by the absolute necessity of minimizing the risk of competition between larvae. In addition, most aphidophagous ladybird beetles supposedly of economic importance have a developmental time of approximately one month in field conditions (Stewart et al., in press) while aphid colonies hardly last for a longer period of time as they fluctuate in response to quality changes of host plants (Dixon, 1985). In these conditions the life cycle of ladybirds must be tightly synchronized with the development of prey populations. More precisely, Dixon (1959) showed that new born larvae need a higher aphid density to survive than older ones and that the feeding success of these young larvae is also negatively correlated to prey size. Thus females must oviposit when the abundance of first and second instar aphids is

compatible with the survival of their first instar larvae. Later on, it is common sense that there must be enough aphids for the fourth instar larvae to complete their development to the pupal stage. A model taking these two conditions into account shows that reproduction should be restricted to a narrow period before the aphids reach peak abundance.(Fig. 1.; Hemptinne et al., 1990)

Surveys of populations of ladybirds and several species of aphids bring support to this model and indicate that eggs are overwhelmingly laid in aphid colonies early in their development (Hemptinne, Dixon and Coffin, in preparation).

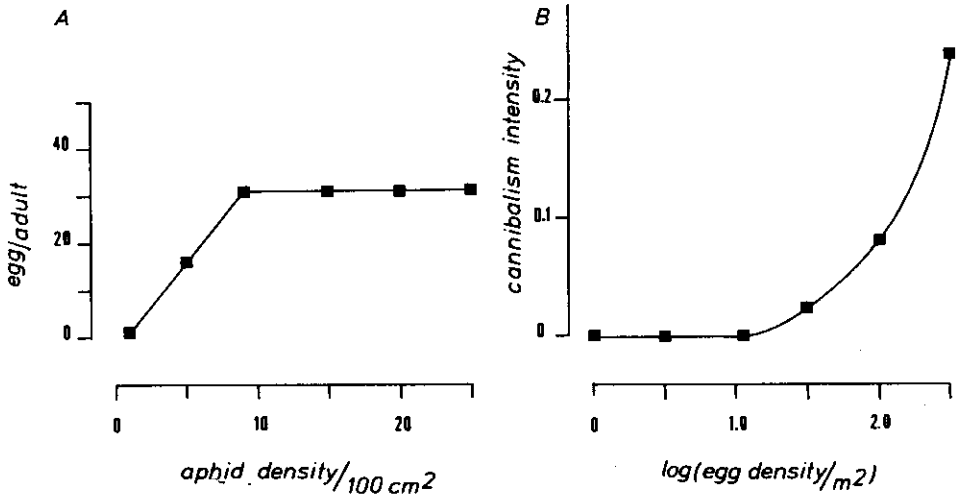

Fig. 2. The reproductive response of *Adalia bipunctata* (L.) to different densities of the aphid *Eucallipterus tiliae* (L.) in the field (A) and the relationship between the intensity of egg cannibalism and the density of two-spot eggs in field conditions (B). (redrawn from Mills, 1982).

The fact that the presence of honeydew or low aphid density elicit egg laying (Evans and Dixon, 1986) provides an explanation of how the ladybirds synchronize the beginning of their reproductive effort with the first stages of development of prey colonies. A possible effect of interference between ovipositing females and larvae, as it occurs in parasitoids (Beddington et al. 1976), is an attractive signal indicating that a group of aphids is no more suitable for egg laying. As a matter of fact, ladybird larvae are the most important threat for ladybird offspring. Firstly, in the field, larvae eat 19 to 33% of the eggs of their own species and this intraspecific cannibalism increases in intensity as egg density rises (Fig. 2B; Mills, 1982). Secondly, young larval instars serve as alternative food for older ones when the density of prey is low (Hodek, 1973; Takahashi, 1987). Therefore females would be well served by the ability to delay oviposition in the persence of conspecific larvae.

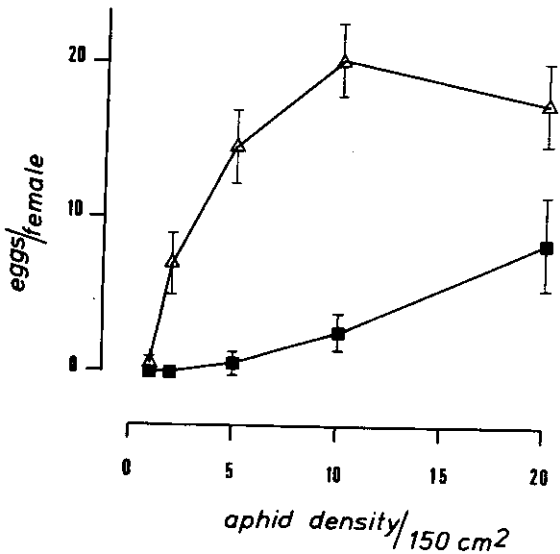

Fig. 3. Egg production of *A. bipunctata* at different aphid densities, in the presence (n = 15; dark symbols) and absence (n = 20; open symbols) of fourth instar larvae of the same ladybird species.
For each aphid density, the results are presented as a mean and a standard error.

Table 1. Number of aphids eaten in the presence and absence of larvae at five prey densities over the final twenty four hours of experiments done to determine the numerical reproductive response of *A. bipunctata*.

Aphid density	n	Larvae absent x (SE)	%	Larvae present x (SE)	%
1	10	0.8(0.1)	80	1.0(0.0)	100
2	10	1.6(0.2)	70	1.0(0.0)	100
5	10	4.7(0.1)	70	4.9(0.3)	80
10	10	7.9(0.5)	0	8.2(3.1)	57
20	10	7.9(3.2)	0	10.7(5.3)	6

n, number of replicates.
%, percentage of replicates in what all the aphids were eaten.
x, mean number of aphids eaten.
SE, standard error of mean.

In laboratory conditions (at 20°C and under a photoperiod of 16HL;8HD), female two-spot ladybirds from the stock culture were kept individualy in a 9cm diameter Petri dish (+/− 150cm^2) together with 1, 2, 5, 10, or 20 aphids of equal size (average weight: 3.7 +/− 1.0mg). The aphids were changed daily and the beetles were allowed 48h to accommodate to the experimental conditions. The analysis of their reproduction over the next 24h revealed that the minimum threshold for egg production was approximately one aphid per 150cm^2. The average number of eggs laid peaked at 5 aphids/150cm^2 and there was no significant difference between the average number of eggs produced at 5, 10 and 20 aphids/150cm^2 (Fig. 3.). Measurements of aphid consumption suggest that the lower aphid densities were not sufficient to meet the nutritional requirements of mature females, which were only met at densities of 5 aphids/150 cm^2 or greater (Table 1.). Food supply controls the reproductive response as the number of eggs laid is correlated with the number of aphids eaten ($r = 0.75$; $P < 0.001$).

The reproductive numerical response was very different when four fourth instar larvae of *A. bipunctata* were introduced in each Petri dish at the end of the acclimatization period. The minimum threshold for egg production increased to 5 aphids/150cm^2 and although egg production increased with aphid abundance it is always lower than in the absence of larvae ($F = 10.022$; 1 and 4 df; $P < 0.05$; Fig. 3.). There was a slight increase in the number of aphids eaten and in the percentage of the cases in which all the aphids were consumed (Table 1.). The food supplies of 1, 2, 5 and 10 aphids daily were too low to satisfy the requirements of both larvae [10.2mg/larva at 20°C (Mills, 1979)] and females [30.0 mg/beetle at 20°C (Coffin, unpublished)]. In these conditions, it is likely that competition for food between larvae and female is the main factor affecting egg laying. On the other hand, such an effect cannot explain the low level of egg laying at 20 aphids/150cm^2. Therefore the presence of larvae in oviposition sites is a second regulatory factor of the reproductive behaviour of ladybird beetles.

In the course of these experiments and in the treatments with 20 aphids, it was also observed that the overall activity of females was significantly greater in the presence of larvae ($\chi^2 = 65.76$; 1 df; $P < 0.001$).

OVIPOSITION BEHAVIOUR

The oviposition behaviour of two-spot ladybirds has been explored in standard laboratory conditions (at 20°C and under a photoperiod of 16 HL:8 HD). Satiated one month old females were taken from the stock culture and placed singly in a 5cm diameter Petri dish. The number of eggs laid by beetles kept on their own was compared with that of females confined with one batch of eggs, three fourth instar larvae or three pupae of *A. bipunctata*.

The presence of larvae of two-spot ladybirds dramatically affected egg production (Table 2.). The average reduction with respect to the control was greatest after 3h. This is not a consequence of egg cannibalism by larvae, which ate fewer eggs than the control females (proportion comparison: $u = 5.21$; $P < 0.001$). The differences in oviposition progressively decreased with the passage of time and no significant differences are apparent after 48h. Females kept with larvae also layed their first batch of eggs later than control females (Kruskal-Wallis test: $H = 27.72$; $P < 0.001$). Ovipositing females apparently

Table 2. Number of eggs laid by females of *A. bipunctata* during 3, 6, 9, 24 or 48h when kept singly or with the immature stages of the same ladybird.

Treatment	Duration (h)				
	3	6	9	24	48
	x (SE)	x (SE)	x (SE)	x (SE)	x (SE)
Control	11.8(2.0)a	14.5(1.8)a	16.5(1.7)a	19.5(1.6)a	31.4(2.5)a
Eggs	9.1(1.7)a	13.1(1.4)a	14.7(1.4)a	18.3(1.8)a	32.0(2.9)a
Larvae	2.3(1.1)b	5.4(1.5)b	9.8(1.7)b	12.2(2.0)b	23.6(2.3)a
Pupae	6.8(2.0)a	11.9(2.3)a	14.8(2.2)a	17.5(1.9)a	29.1(2.9)a

Treatment, as described in text.
x, mean number of eggs.
SE, standard error of mean.
In each column, means followed by different letters differ significantly ($P < 0.01$ for the means at 3 and 6h; $P < 0.05$ for the means at 9 and 24h).

did not respond, in terms of number of eggs laid or time of first oviposition, to the presence of pupae and eggs.

DISCUSSION

Temporal changes in aphid abundance (Dixon, 1985) pose a considerable challenge to ovipositing aphidophagus ladybirds. They should synchronize their reproduction with the early development of aphid colonies because the survival of new born larvae is very dependent on the abundance of young aphids (Dixon, 1959). Besides, oviposition late in aphid population development could result in the older larvae being short of food and failing to complete their growth. Thus, there is only a short period suitable for egg laying at the beginning of the development of an aphid population when these two constraints are met (Hemptinne et al., 1990). Field surveys of populations of several species of aphids indicate that oviposition tends to be concentrated over a few days before the aphid populations reach peak abundance (Hemptinne, Dixon and Coffin, in preparation) whereas ladybirds can lay eggs for at least three months without interruption (Hodek,1973). There are thus strong indications that ladybirds prefer to oviposit in an aphid colony early in its development. This analysis implies that the food supply is not the only factor controlling egg production in ladybird beetles (Gutierrez and Baumgaertner, 1984) and that females should be able to assess the potential of an aphid colony for supporting their offspring before laying eggs. At first sight the presence of ladybird larvae is a powerful clue to the quality of breeding sites. It indicates that there would be a risk of egg cannibalism (Mills, 1982) and that new born larvae would probably face tough competition for food from older larvae (Hodek, 1973; Takahashi, 1987). In addition, it could also be symptomatic of an aphid population in a late stage of

development. Laboratory experiments reported here confirm that larvae affect the reproductive behaviour of female ladybirds.

Ladybirds responded by increased oviposition to increase in prey abundance up to a maximum of 5 aphids/150cm^2; above this *A. bipunctata* is fully satiated and egg production is constant and independent of prey abundabce (Mills, 1982). The shapes of the numerical response determined in the laboratory and the field (Fig. 2A) (Mills, 1982; Wright and Laing, 1980) are identical although done under quite different conditions. In the present study the reproductive numerical response was affected by the presence of larvae. The larvae could have competed for food with the females when only 1, 2 and 5 aphids were avaible, whereas that is less likely when 10 aphids were provided and when 20 aphids were given there was enough food for both larvae and females (Mills, 1979). The modification of the numerical response is thus partly a consequence of an interaction between larvae and females which does not involve competition for food. This is supported by the observations that females showed a reduced oviposition rate in the presence of larvae of their own species. This inhibition of egg laying lasts for 3h after which the oviposition increases dramatically, presumably because females are unable to refrain from egg laying any longer.

The presence of larvae also provokes a higher level of activity in the females. The activity of predators is influenced both by the hunger (Holling, 1966) and the presence of other predators in the area. Hassel et al. (1976) reported that on encountering another individual of its own species, a searching predator may react by leaving the area. As approximately 50% of the 20 aphids provided to the females kept with larvae were uneaten (Table 1.), hunger does not seem to be the cause of the enhanced activity reported here. The more likely causal factor is once again an interaction between females and larvae.

Ladybird beetles have been used successfully several times for the biological control of coccid pests (Bartlett, 1978; Hodek, 1973) whereas their role as biological control agents of aphid populations has been disappointing. The following analysis of the reproductive behaviour of *A. bipunctata* provides an explanation for this. Their reproductive numerical response is confined to a narrow range of aphid densities and above approximately 10 aphids/150cm^2 egg production becomes independent of prey abundance as the ladybirds are satiated (Mills, 1982). This in itself has a destabilizing effect on the prey-predator relationship and implies that *A. bipunctata* will not be able to control prey populations once they reach the low levels at which the beetles are satiated (Crawley, 1975; Dixon, 1970; Wratten, 1973). A second factor is the impact of egg cannibalism which increases dramatically as egg density rises (Fig. 2B; Mills, 1982). Whatever the adaptative value of egg cannibalism (Fox, 1975), it is nevertheless wasteful in terms of reproductive effort. Thus it would be advantageous if females avoided breeding in locations where cannibalism and competition threaten the survival of their offspring. The laboratory experiments reported here support this hypothesis as females on the verge of oviposition will withold eggs and more than likely leave a place after encountering larvae. As a consequence the aggregative response of ladybirds to prey density is curtailed which in addition to satiation at low prey densities accounts for their poor efficiency as biological control agents.

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