

Adaptive features of the predatory ladybird beetles in uncertain and competitive habitats

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The predatory species of ladybird beetles forage in habitats where aphid colonies show a patchy distribution in space and time. In an uncertain environment the numerical response of the females to aphid density suffers from unstable food source and sharing of the habitat by different ladybird species. As a result, the reproductive effort of a predatory ladybird species is threatened by the intraspecific and interspecific competitions. It is imperative that ladybird species should synchronize their reproduction and development of progeny with phenology of prey populations in order to overcome the risks of their habitats. This paper brings together the results of several studies to present an account of the adaptive mechanisms evolved by the predatory species of ladybirds to cope with the risks inherent in their life cycle.

MANY species of ladybird beetles (Insecta, Coleoptera, Coccinellidae) are predators of aphids, and other insects and mites. Some of these ladybird beetles are regarded as important natural control agents because of their ability to feed on large quantities of aphids¹. Several species of aphids are a menace to agriculture and horticulture²⁻⁴. As part of integrated pest management strategy, increasing efforts are being made to understand the ecology of predatory ladybird beetles in the development of successful biological control of pest aphids^{5,6}.

Field studies suggest that larvae and adults of most ladybird species search plant surfaces at random and concentrate their efforts on the restricted area where a prey is captured, i.e. they show a positive prey-taxis^{7,8}. As a consequence of this foraging behavior, ladybird beetles manage to exploit aphid colonies that have a patchy distribution and a short life span⁴. This tendency results in an aggregation of either conspecific larvae and adults or other species of ladybirds that share the same habitat and, therefore, are likely to interact with one another^{1,9,10}. In such a competitive environment, it is possible that the reproductive output of individual species is threatened by one or more of the following risks:

1. temporary nature of food supply – for instance, sudden collapse of aphid colonies before larval development is completed;
2. cannibalism of eggs and larvae; and
3. interspecific predation.

How predatory ladybirds overcome these inherent risks is the question this paper seeks to answer by reviewing the adaptive features of their reproductive behaviour, interspecific predations and cannibalism.

Reproductive behaviour

The reproductive behaviour of aphidophagous ladybird beetles is guided by the following facts: (i) the aphid populations persist for a relatively short period of time⁴; (ii) the developmental time of ladybirds and the life span of aphid colonies are approximately equivalent¹¹, and (iii) there is necessity of avoiding any competition between larvae for the limited food resource. Further, it has been shown that the newly born larvae need a higher aphid density to survive than the older ones, and that feeding success of these young larvae is negatively correlated to prey size¹². In these conditions it is conceivable that the life cycle of ladybirds should synchronize with the development of prey populations.

Field observations based on survey of different habitats occupied by *Adalia bipunctata* L. show that eggs are generally laid in aphid colonies early in their development^{12,13} and oviposition is limited to a short period of the early phase of population growth¹⁴. Similar results have been obtained for another ladybird species *Coccinella transversalis* (Fabricius) in bean crops infested by *Aphis craccivora* Koch¹ (Figures 1 and 2).

Laboratory observations further suggest that oviposition is strongly inhibited by the presence of conspecific larvae or other females¹⁴ (Figure 3). Such females not only produced less number of eggs but also took more time to lay eggs than control females. Interestingly, however, ovipositing females did not respond adversely to the presence of their own pupae and eggs. The possible cause of such an interference could be some form of signal, as reported in parasitoids⁵, to the ovipositing female, who gets the indication that the size of aphid colony is not suitable for egg laying.

A recent study⁶ suggests that an adult ladybird female lays an optimum number of eggs in an aphid colony. Since an aphid colony is a finite and temporary food source, the time of its existence is just enough for the larvae of ladybird to complete their development but not reproduce in that colony (Figure 4)¹⁶. This implies

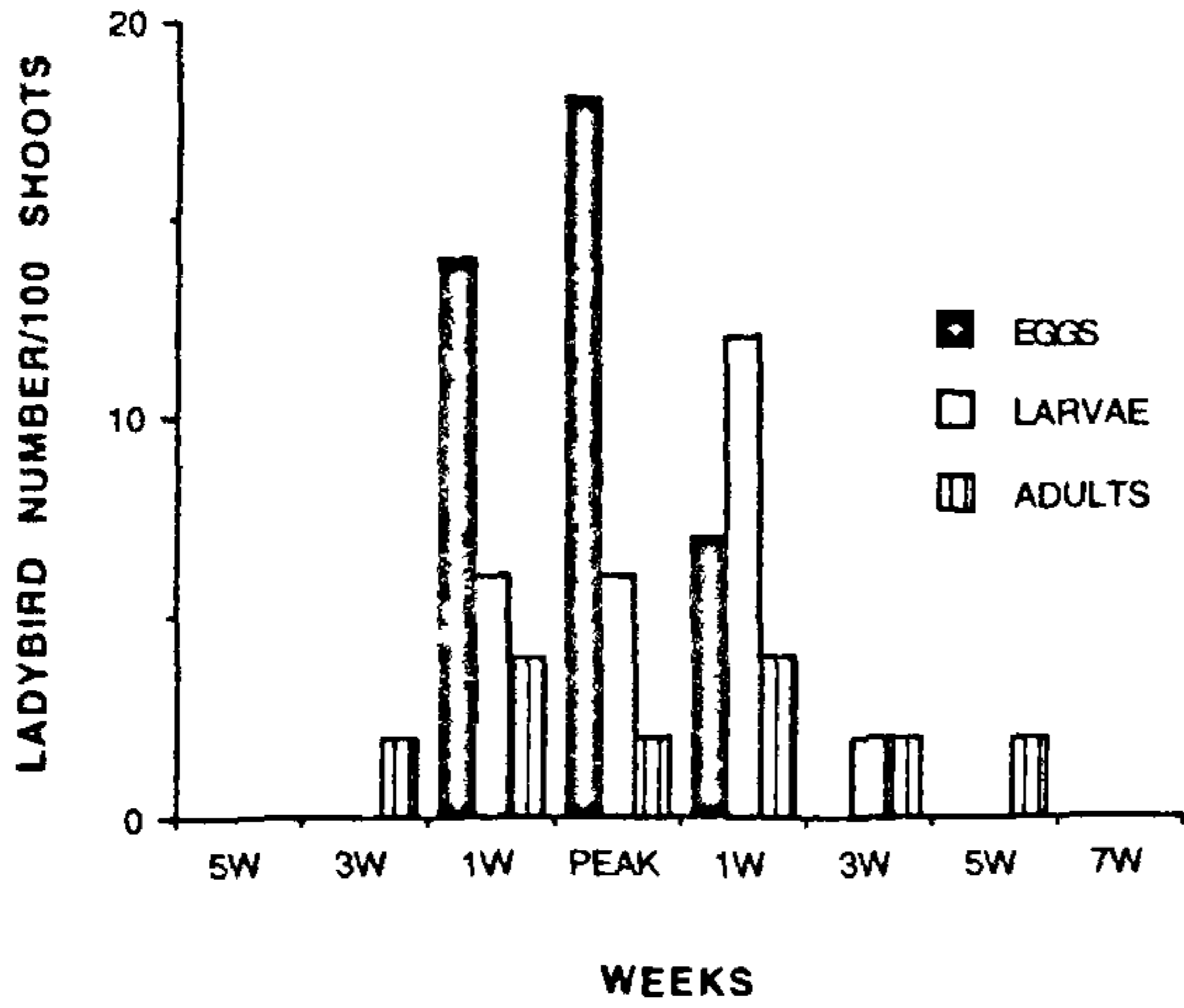


Figure 1. Distribution of ladybird eggs, larvae and adults of *Coccinella transversalis* in bean fields in time relative to peak abundance of aphid *Aphis craccivora*

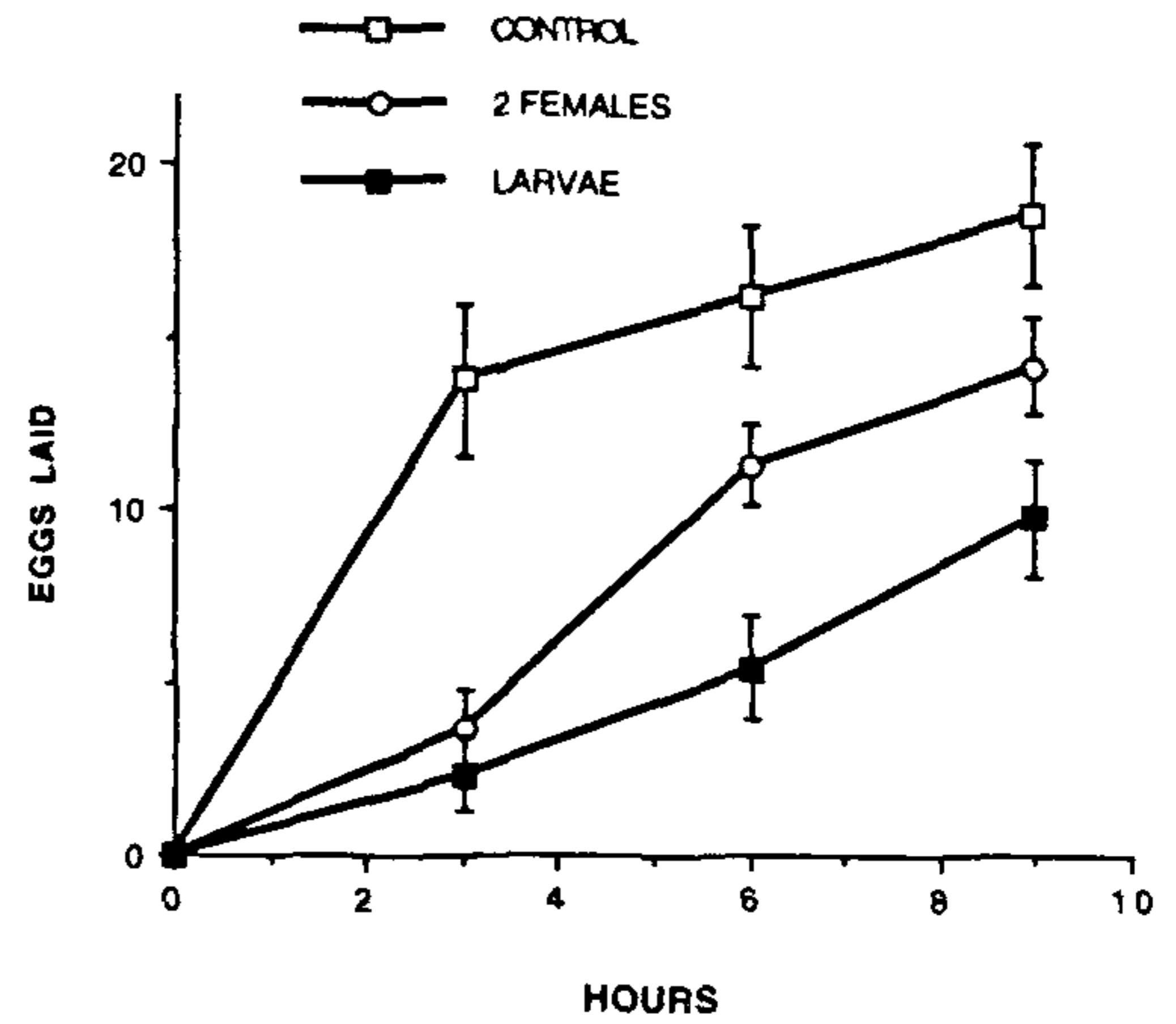


Figure 3. Average number of eggs laid by the females of ladybird *Adalia bipunctata* during 3, 6 and 9 h in 5 cm Petri dishes, in which they were kept singly, with another female or with three fourth-instar larvae (30 replicates for each treatment) (after ref. 14).

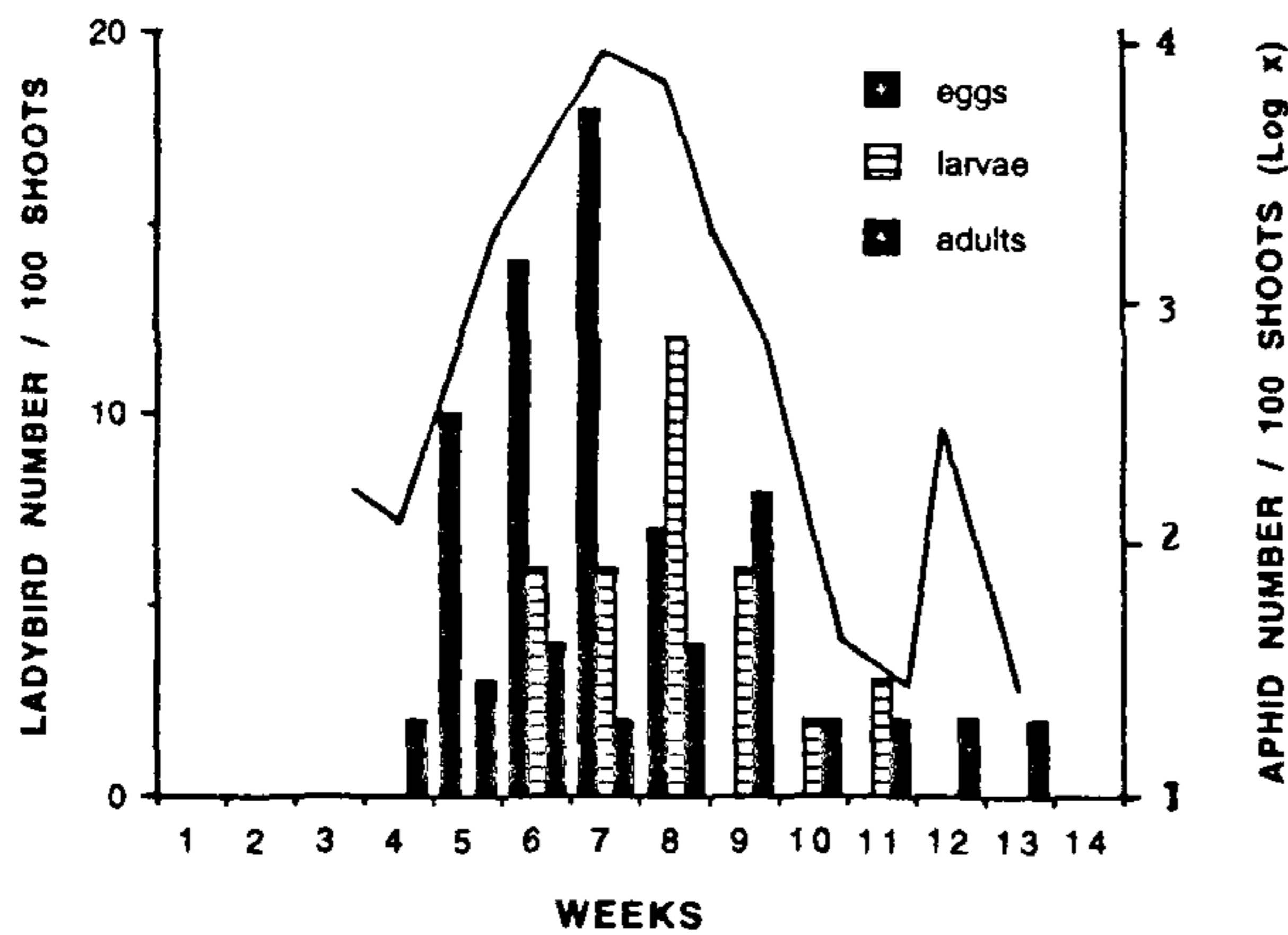


Figure 2. Number of aphid *A. craccivora* (—) and ladybird *C. transversalis* (histogram)/100 shoots recorded in bean field.

that the optimum number of eggs laid by an adult ladybird corresponds to the maximum offspring biomass which can be supported by aphid biomass. Thus the reaction of ovipositing females to the presence of conspecific larvae in an aphid colony seems to be adaptive because it allows females (i) to choose young aphid colonies – the presence of larvae indicates that the aphid colony has been present for some time, and (ii) to avoid situations where competition for food could threaten the development of their offspring. Under these circumstances adult ladybirds are likely to leave an aphid aggregate and begin search for a new colony soon after a certain number of eggs are laid. Further studies on these aspects are currently being pursued by many investigators.

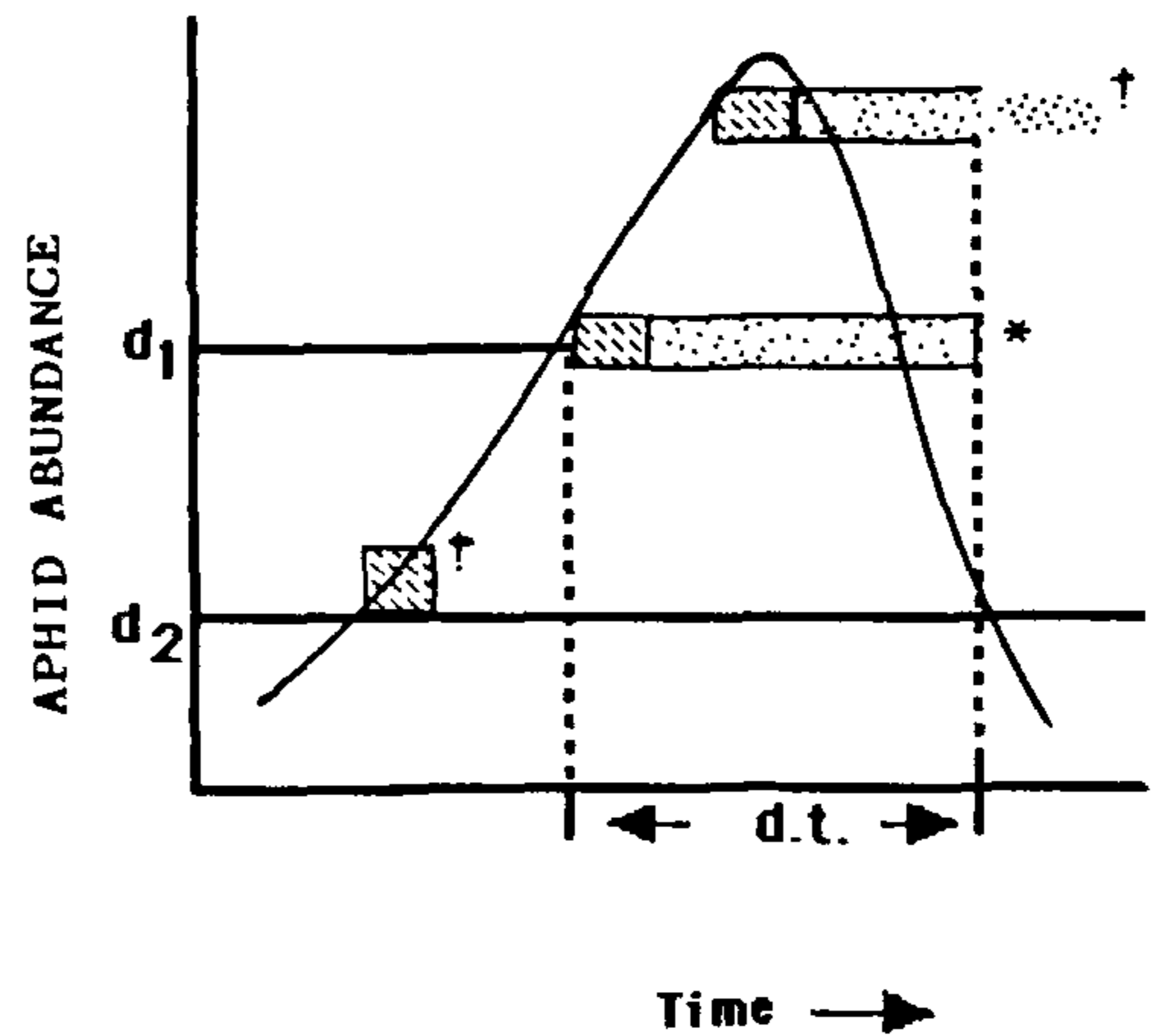


Figure 4. Reproductive behaviour of ladybirds: the period during which egg laying is compatible with the requirements for the survival of larvae. ▨ = egg laying, ▩ = larval development (open means that larvae cannot complete their growth; † unsuccessful; * successful reproductive effort, d_1 and d_2 = threshold densities for the survival of first- and fourth-instar larvae, respectively; d.t. = developmental time) (after ref. 16).

Cannibalism

An aphid colony is likely to be frequented by a succession of female ladybirds. As a result, larvae of different ages could forage on the same colony. Ladybirds which arrive late at an aphid colony are faced with optimization problem, i.e. the maximization of offspring production. Increase in predator density will bring about decrease in the number of prey available to each predator of

habitat (Holling type II response)¹⁷. As a result, there will be a lower rate of increase in predators and a higher rate of cannibalism. Laboratory experiments reveal that egg and larval cannibalism are inversely related to aphid abundance (Figure 5). Conspecific eggs are more likely to be encountered and eaten than larvae because the former is immobile and laid in a cluster¹⁸. Field observations also suggest a density-dependent egg cannibalism in ladybirds¹⁹. However, ladybirds have developed effective mechanisms to avoid the risk of cannibalism: (i) the female ladybird does not oviposit in or immediately around an aphid colony because the adults and larvae aggregate there^{20,21}; (ii) female ladybirds synchronize oviposition with the early development of aphid colonies, thus refraining from laying of eggs in the presence of larvae or even other females; and (iii) adult females are reluctant to eat their own eggs (Figure 6), and second-instar larvae have been seen to avoid eating sibling eggs²². This may be adaptive as it would reduce the chance of females eating their own eggs, whereas males are less likely to come across eggs they have sired. Non-sibling cannibalism, however, would still occur²¹, and in a situation of prey scarcity this could be an effective means by which adults could fuel their reproductive efforts and eliminate potential competitors. This mechanism can ensure future availability of food for themselves and their offspring.

Predation

Ladybirds like *Adalia bipunctata* (L.), *A. decempunctata*

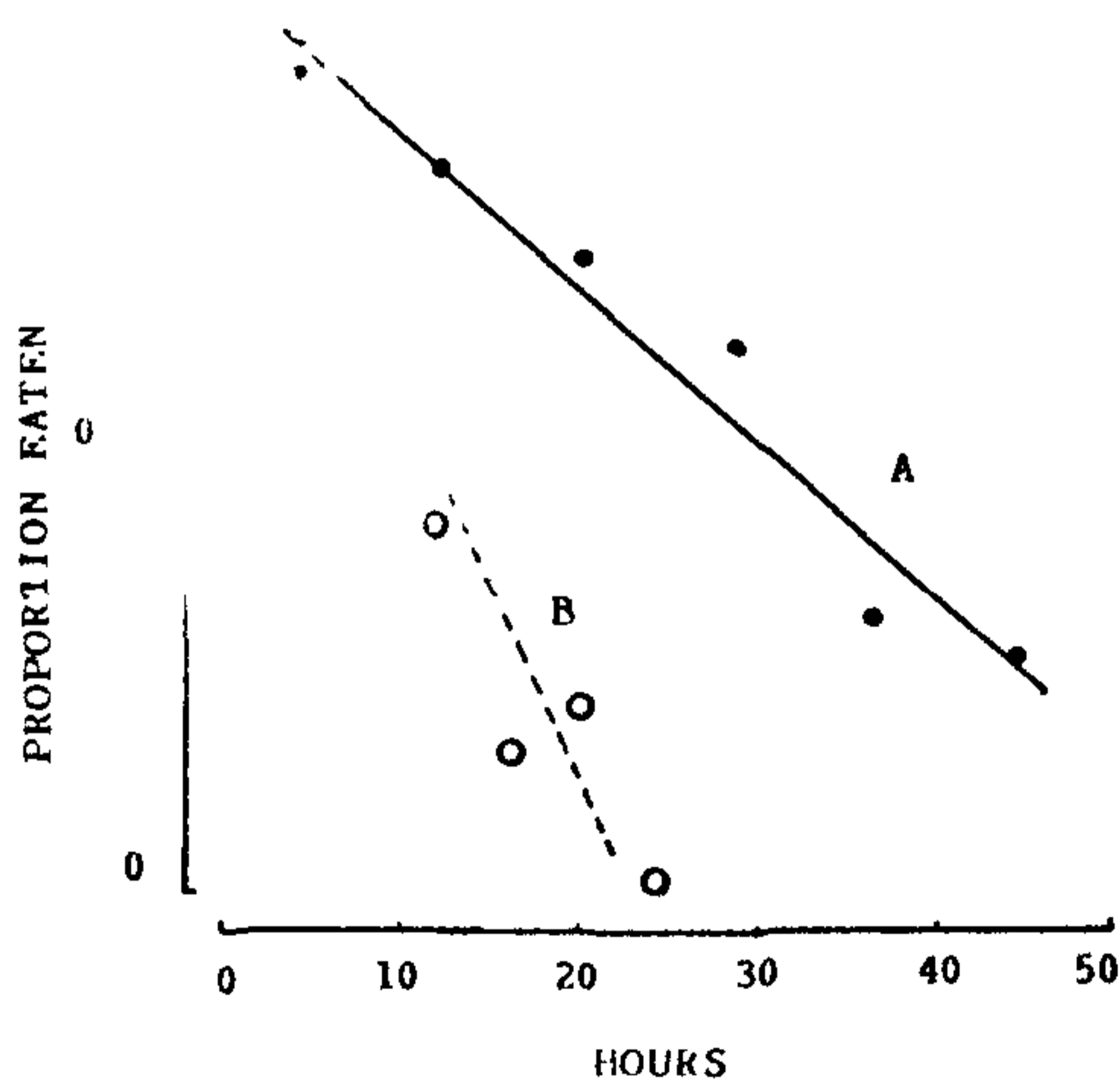


Figure 5. The proportion of the clutches of eggs (A, ●) and third-instar larvae (B, ○) of *Adalia bipunctata* eaten by its fourth-instar larvae in relation to aphid density after 1, 5 and 24 h (eggs: $r^2 = 0.95$; $y = 1.007 - 0.0017x$; larvae: $r^2 = 0.91$, $y = 1.003 - 0.044x$; means of 20 observations) (after ref 18)

(L.), *Coccinella septempunctata* L. and *C. undecimpunctata* L. commonly coexist in the same habitat¹. In their coexistence their eggs and larvae are likely to occur in the same aphid colony¹⁰. Laboratory experiments indicate that the different species of ladybirds interact with one another, leading to predation of some of them (Figure 7)¹⁸.

Available results suggest that interspecific predations are asymmetrical. Starving larvae and adults of *A.*

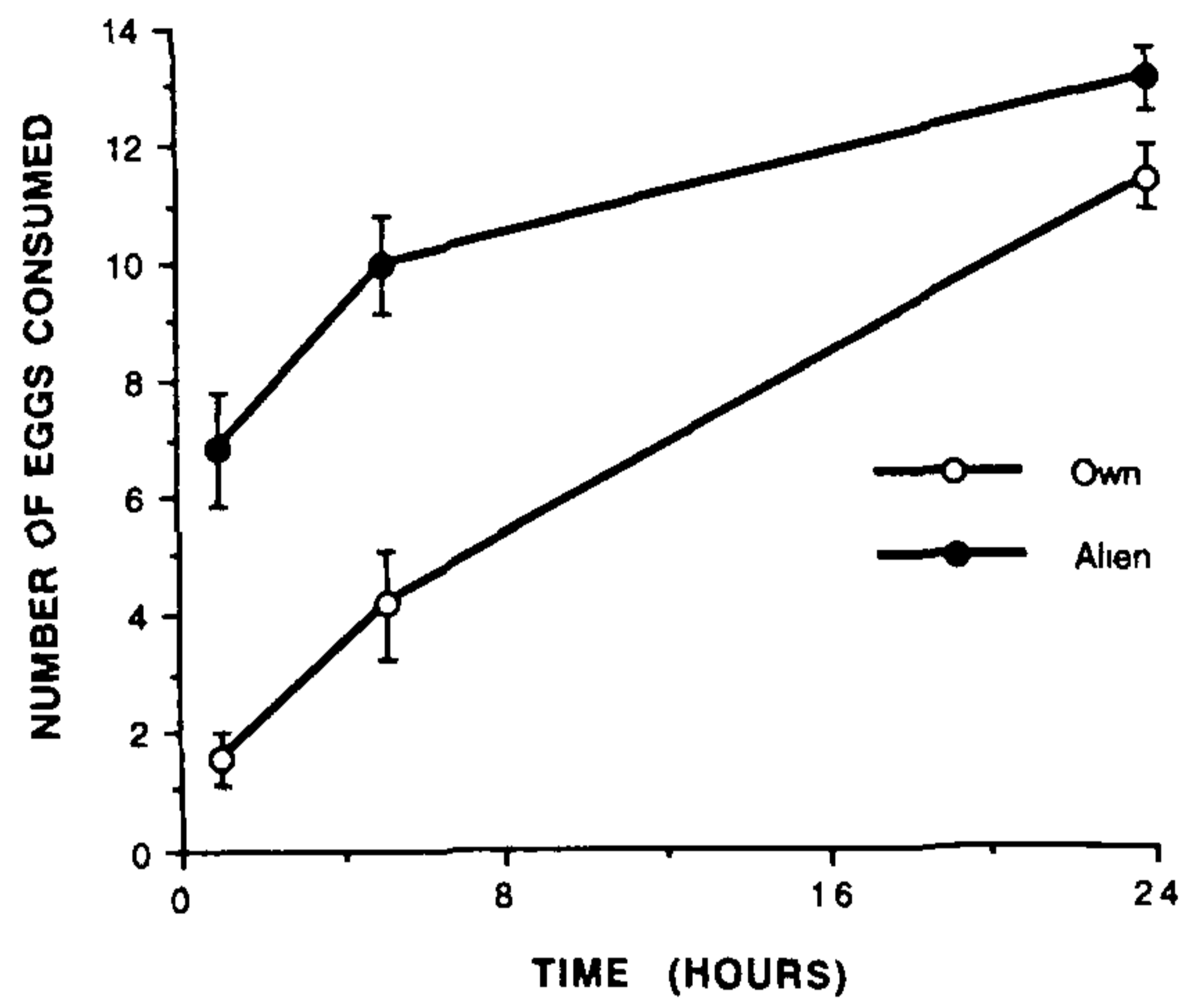


Figure 6. The mean number (\pm SE) of their own and alien eggs eaten by female *Adalia bipunctata* after 1, 5 and 24 h (after ref. 22).

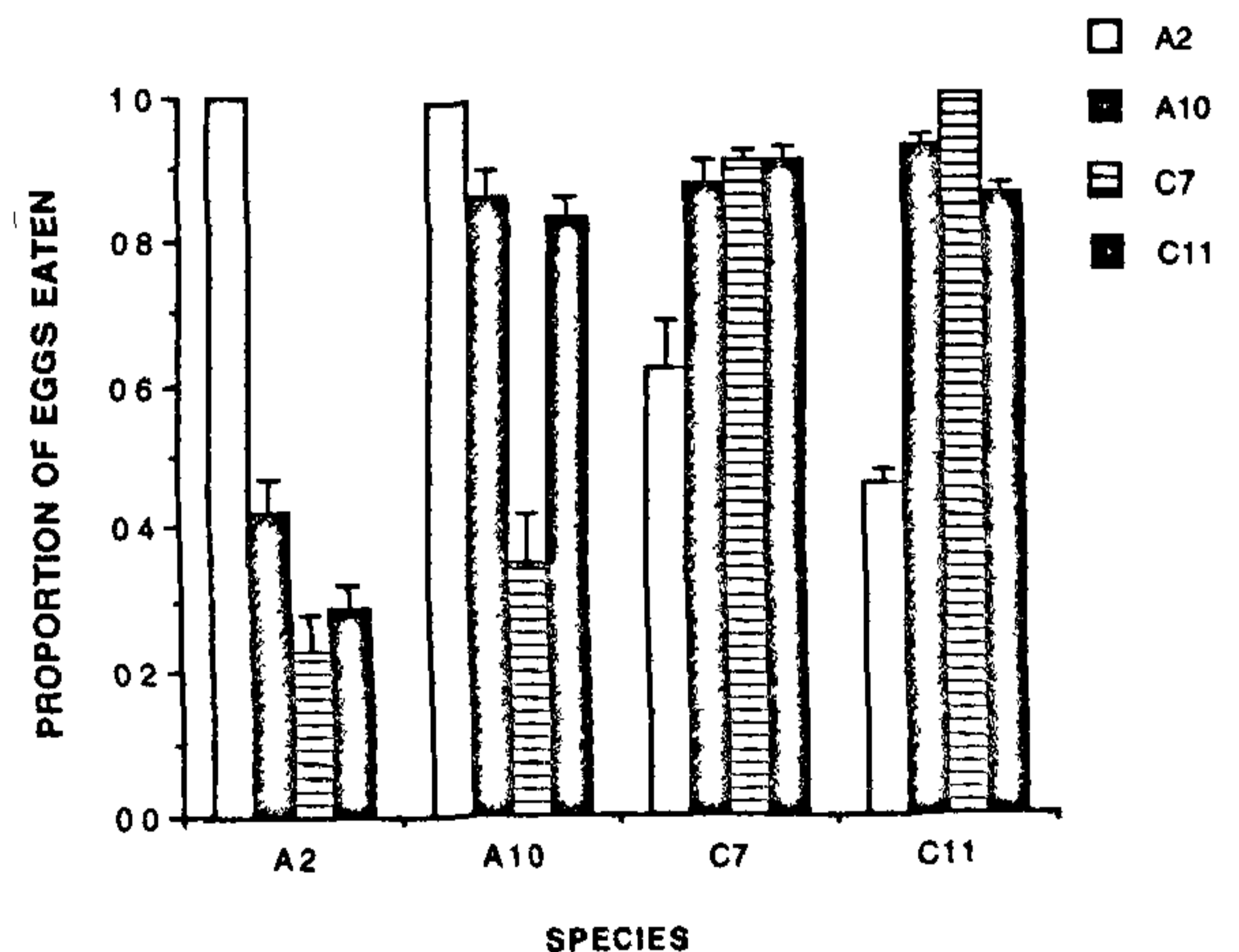


Figure 7. The proportion of eggs of their own and three other species eaten by larvae of four species of ladybirds (the four species are: *Adalia bipunctata* = A2, *A. decempunctata* = A10, *Coccinella septempunctata* = C7 and *C. undecimpunctata* = C11; 2- or 3-day-old fourth-instar larvae of the four species starved for 24 h prior to experiment; larvae were offered equal weight of eggs of the four species, n varies between 20 and 30) (after ref. 18)

bipunctata and *C. septempunctata* ate significantly fewer eggs of their own species when painted with a water extract of the eggs of other species. Thus, the eggs of both these species are protected to some extent from predation. The protective chemical used in this case was water-soluble (Figure 8)¹⁸.

The results of further experiments have confirmed¹⁹ that eating of the eggs of other species is not without risk, and that smaller species is better defended than larger species. An interesting study on the interaction between *A. bipunctata* (smaller species) and *C. septempunctata* (larger species) provides a good example. Larvae of the latter species fed on *A. bipunctata* eggs showed a significant increase in mortality than the larvae of former species fed on *C. septempunctata* eggs. The available information on interspecific predation is limited to a few of a large number of known ladybird species^{1,23}. More results in future studies on a number of other species would strengthen the current thinking on interspecific predation and its possible impact on the reproductive behaviour of ladybird beetles.

That ladybirds use bitter-tasting alkaloids as a defence against predation by ants and birds²⁴⁻²⁸ shows the chemical defence ability of the ladybird eggs. It would appear from the results that defence is based on odour rather than on colour. Recent studies suggest that clustered eggs of either *Coccinella transversalis* (Fabricius) or *Menochilus sexmaculatus* (Fabricius) are significantly less likely to be eaten by the larvae and adults of the rival species than the eggs offered singly (Agarwala, Bhattacharya and Bardhan Roy, in preparation). However, clustering of eggs does not prove to be a deterrent in cannibalism. In this context it is interesting to note that

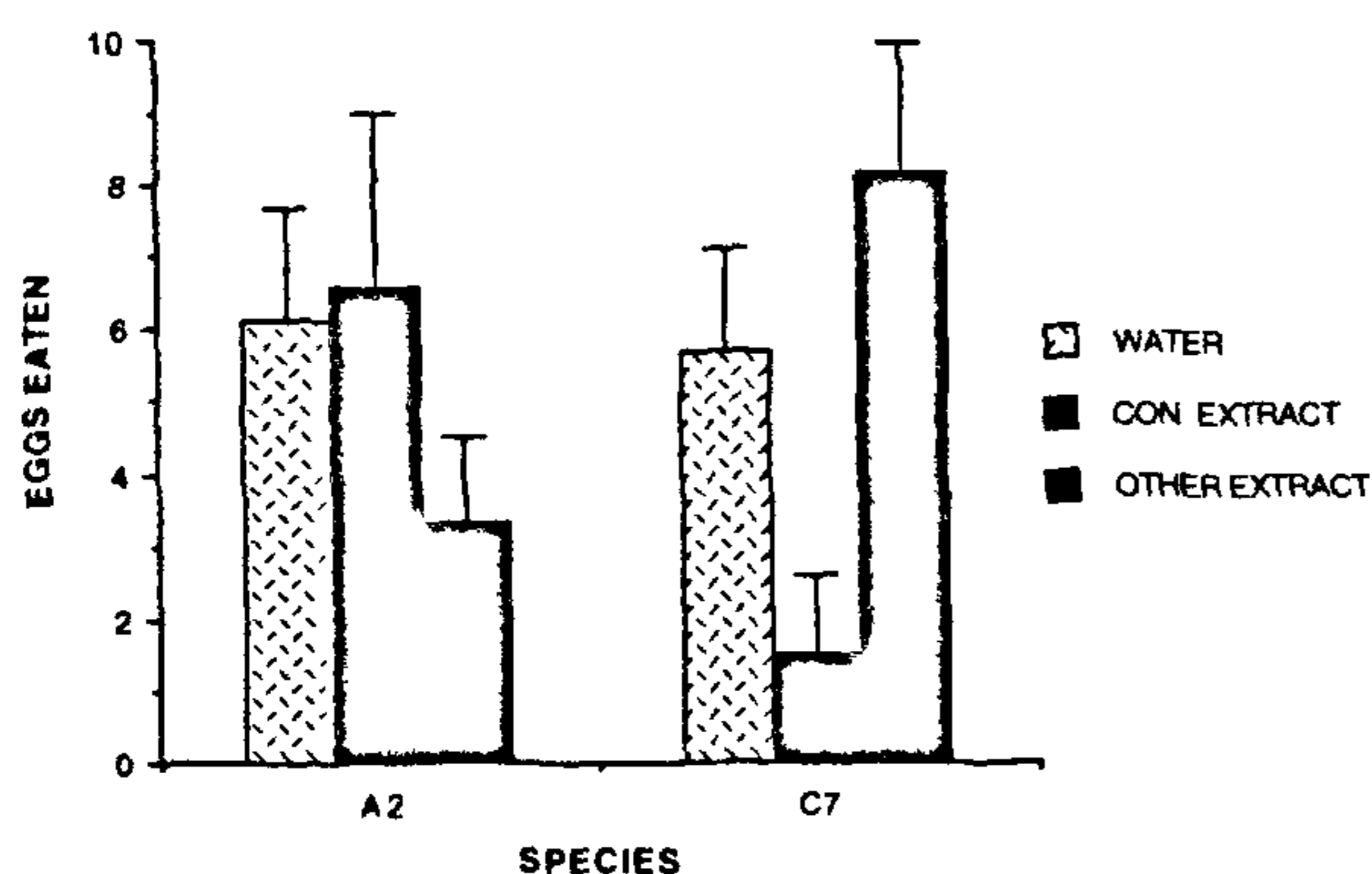


Figure 8. The effect on egg cannibalism in *Adalia bipunctata* and *Coccinella septempunctata* of painting eggs with water extract of conspecific eggs (concentrated extract) and a water extract of other species eggs (other extract) (1 mg of egg crushed in 0.15 ml of distilled water, centrifuged for 2 min and 0.05 ml of the supernatant painted on a batch of 10 eggs with a micropipette; eggs left dry for 2 h; 10 eggs offered to a starving fourth-instar larvae, experiments last 24 h; $n = 20$) (after refs 18 and 22).

alkaloids are present in the eggs, larvae, pupae and adults of ladybirds. The effectiveness of alkaloids in deterring ants is concentration-dependent²⁵. Thus, clustering of eggs in ladybirds appears to be an anti-predatory device and, therefore, is another instance of adaptation for self-preservation. It would be useful to examine and define the chemical defence in ladybirds in future studies.

Conclusions

Aphid populations undergo seasonal changes in abundance. This ensures a strong selection pressure in ladybird beetles, who can successfully synchronize their development and reproduction with the phenology of aphid populations. As a result, ladybird species are able to maintain an optimum number of eggs and larvae in each aphid colony.

As aphid colony is a temporary habitat, a female ladybird chooses a young aphid colony for oviposition so that the resulting larvae could complete development. This behaviour of female ladybirds takes care of the new-born larvae, whose survival is dependent on an abundance of young aphids²⁹. However, the number of eggs laid by a female has a finite relationship with prey abundance (reproductive numerical response) because (i) a satiated female is less active and, therefore, does not oviposit, and (ii) early hatching of larvae in aphid colony serves as a deterrent signal to the egg laying of females. Consequently, an optimal oviposition by a female ladybird is obvious in the early phase of aphid population development^{6,14}. Such a reproductive strategy ensures that ladybird biomass production is proportional to the aphid biomass likely to be available in an aphid colony.

A lower reproductive response, thus, serves to maximize the fitness of ladybirds in terms of successful development of eggs that are laid in an aphid colony. However, a ladybird population has inherent dangers in its ecology: their positive prey-taxis in foraging and the likelihood of sharing of an aphid colony by populations of other ladybird species with a similar phenology pose considerable challenge to eggs and larvae from cannibalism and predation. Spatial distribution of ladybirds ensures that adults keep arriving at a patch of aphid colonies, resulting in predator pressure, both intraspecific and interspecific, on eggs and larvae. The pressure of intraspecific predation or cannibalism is avoided (i) in part by lower numerical response, which ensures that the optimal number of ladybird eggs laid in a particular colony should be lower, thereby not offering an opportunity of density-dependent cannibalism¹⁹ and (ii) by the reluctance of a female to eat its own eggs, and also its inhibition in laying eggs in the presence of conspecific larvae. The ability of a ladybird to assess the quality of aphid colony diminishes the chances of egg and larval cannibalism.

Interspecific predation is subdued partly because ladybird eggs afford protection through chemical defence. Clustering of eggs in predatory ladybirds seems to be strongly adaptive. These devices not only result in increased fecundity in less time³⁰, so vital for its reproductive strategy, but also, more importantly, improve the chances of egg survival in two ways: (i) the defence acts as a distasteful deterrent to its predators^{31,32}, and (ii) some of the eggs in a cluster are inaccessible to parasites and predators³³.

The various accounts mentioned here suggest that ladybird beetles have evolved a combination of mechanisms that ensure their occurrence in an environment which suffers from limitations of temporary existence of prey and risks of predations. Some grounds of the reproductive strategy of ladybirds in response to cannibalism and predation have already been worked out but the hypothesis that clustered eggs are chemically defended against ladybird predators needs verification. Also there is a need to understand more precisely the prey-predator interactions in terms of factors which maximize the fitness of ladybird beetles in an uncertain habitat.

1. Hodek, I., *Biology of Coccinellidae*, Academic Press, Prague, 1973.
2. Ghosh, A. K., *Indian Agric.*, 1974, **18**, 1-214.
3. Blackman, R. L. and Eastop, V. F., *Aphids on the Worlds' Crop. An Identification Guide*, Wiley, Chichester, 1984.
4. Dixon, A. F. G., *Aphid Ecology*, Blackie, Glasgow, 1985.
5. Kindlmann, P. and Dixon, A. F. G., *J. Evol. Biol.*, 1992, **5**, 677-690.
6. Kindlmann, P. and Dixon, A. F. G., *Eur. J. Entomol.*, 1993, **90**, 443-450.
7. Carter, M. C. and Dixon, A. F. G., *J. Anim. Ecol.*, 1982, **51**, 865-878.
8. Kareive, P. and Odell, G., *Am. Nat.*, 1987, **130**, 232-270.
9. Agarwala, B. K. and Ghosh, A. K., *Trop. Pest Manage.*, 1988, **34**, 1-14.
10. Evans, E. W., *Oecologia*, 1991, **87**, 401-408.
11. Obrycki, J. J. and Tauber, M. J., *Ann. Entomol. Soc. Am.*, 1981, **74**, 31-36.
12. Hemptinne, J.-L. and Naisse, J., in *Ecology and Effectiveness of Aphidophaga SPB*, Academic Publishing, The Hague, 1988.
13. Hemptinne, J.-L. and Dixon, A. F. G., in *Behaviour and Impact of Aphidophaga SPB*, Academic Publishing, The Hague, 1992.
14. Hemptinne, J.-L., Dixon, A. F. G. and Coffin, J., *Oecologia*, 1992, **90**, 238-245.
15. Beddington, J. R., Hassell, M. P. and Lawton, J. H., *J. Anim. Ecol.*, 1976, **45**, 165-185.
16. Agarwala, B. K., in *Reproductive Strategy in Aphidophagous Ladybeetles (Coccinellidae) of India*, ICAR Final Technical Report, 1993.
17. Hassell, Michael P., *The Dynamics of Arthropod Predator-Prey Systems*, Princeton University Press, Princeton, New Jersey, 1978.
18. Agarwala, B. K. and Dixon, A. F. G., *Ecol. Entomol.*, 1992, **17**, 303-309.
19. Mills, N. J., *Ann. Appl. Biol.*, 1982, **101**, 144-148.
20. Bank, C. J., *Anim. Behav.*, 1957, **5**, 12-24.
21. Osawa, N., *Res. Popul. Ecol.*, 1989, **31**, 153-160.
22. Agarwala, B. K. and Dixon, A. F. G., *Eur. J. Entomol.*, 1993, **90**, 45-50.
23. Majerus, M. and Kearns, P., *Ladybirds*, Richmond Publishing, England, 1989.
24. Rothschild, M., *Trans. R. Entomol. Soc. London*, 1961, **113**, 101-122.
25. Pasteel, J. M., Deroe, C., Tursch, B., Braekman, J. C., Daloz, D. and Hootele, C., *J. Insect. Physiol.*, 1973, **19**, 1771-1784.
26. Mueller, R. H., Thompson, M. E. and Dipardo, R. M., *J. Org. Chem.*, 1984, **49**, 2217-2231.
27. Rothschild, M., Moore, B. P. and Brown, M. V., *Biol. J. Linn. Soc.*, 1984, **23**, 375-380.
28. Marples, N. M., Brakfield, P. M. and Cowie, R. J., *Ecol. Entomol.*, 1989, **14**, 79-84.
29. Dixon, A. F. G., *J. Anim. Ecol.*, 1959, **28**, 259-281.
30. Courtney, S. P., *Am. Nat.*, 1984, **123**, 276-281.
31. Fisher, R. A., *The Genetical Theory of Natural Selection*, Dover, New York, 1958.
32. Stamp, N. E., *Am. Nat.*, 1980, **115**, 367-380.
33. Damman, H. and Cappuccino, N., *Ecol. Entomol.*, 1991, **16**, 163-167.

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