Entomologia Experimentalis et Applicata **94:** 141–147, 2000.

Egg production in response to combined alternative foods by the predator *Coccinella transversalis*

Edward W. Evans
Department of Biology, Utah State University, Logan, UT 84322-5305, USA (Fax: 435 797-1575)

Accepted: October 28, 1999

Key words: aphid honeydew, biological control, Coccinellidae, diet, oviposition, predation, reproduction

Abstract

Insect predators may commit to reproduction to varying degrees depending on the nature of the prey they consume. I compared egg production by females of the aphidophagous ladybird beetle *Coccinella transversalis* (F.) (Coccinellidae) maintained on differing diets. As expected, females laid most eggs on a diet of aphids (pea aphids, *Acyrthosiphon pisum* [Harris]). Upon being switched from a diet of aphids, females laid no eggs after the first 3 days when maintained on a water solution of sucrose, and laid almost no eggs when maintained on a diet of second-instar larvae of the moth *Helicoverpa armigera* (Hübner). However, females laid eggs in small numbers (on average, 2.7 eggs per day) when provided both sucrose and *Helicoverpa* larvae. Females laid similar numbers of eggs when aphid honeydew was substituted for sucrose in combination with *Helicoverpa* larvae; in both cases, egg production was only 10–15% of that on a diet of aphids. The production of small numbers of eggs from consumption of non-aphid foods may enhance the ability of aphidophagous ladybirds to optimize their timing of reproduction at short-lived colonies of their preferred aphid prey.

Introduction

Many ladybirds (Coleoptera: Coccinellidae) are considered primarily aphidophagous, with strong affinities for aphid prey (Gordon, 1985; Hodek & Honěk, 1996). Even so, these same species consume many other foods as well, including eggs and larvae of several orders of insects (Hodek, 1973; Hagen, 1987; Hodek & Honěk, 1996). In some instances, these predators may have potential as biological control agents of non-aphid prey (e.g., Yakhontov, 1938; Andow & Risch, 1985; Hazzard et al., 1991; Evans & England, 1996; Hilbeck et al., 1997; Mensah 1997), but much remains to be learned of the significance of such feeding habits for these predators. Hodek (1962, 1973) and Hodek & Honěk (1996) have stressed that, when consumed alone, prey other than an often quite restricted set of aphid species may be inadequate to support growth and development of immature ladybirds, or reproduction by adults. Instead, these prey may be similar to the plant nectar consumed by many ladybirds (Pemberton & Vandenberg, 1993) in serving as ‘alternative foods’; i.e., they merely sustain the predator temporarily until consumption of ‘essential foods’ (nutritionally adequate species of aphids) resumes.

Only limited experimental evidence has been gathered to date to test whether non-aphid foods that occur in the natural diet of aphidophagous Coccinellidae are adequate to support reproduction by the predators. The nearctic ladybird *Coleomegilla maculata* (DeGeer) reproduces on non-aphid prey with which it is naturally associated, including beetle and lepidopteran eggs (Hazzard & Ferro, 1991; Munyaneza & Obrycki, 1997; Phoofolo & Obrycki, 1997) and mites (Putnam, 1957). However, this ladybird is unusually broad in its natural diet (e.g., see Hodek & Honěk, 1996; Cottrell & Yeargan, 1998). Therefore its reproductive habits may differ from those of more narrowly aphidophagous ladybirds, such as those of the genus *Coccinella*. In fields of alfalfa (*Medicago sativa* L.) in North America, adults of both the native species *Coccinella transversoguttata* Brown and the introduced palaearctic species, *Coccinella septempunctata*

L., feed on larvae of the alfalfa weevil (*Hypera postica* [Gyllenhal]) and plant nectar as well as aphids. When placed on a diet of only weevil larvae or only sugar solution (a substitute for plant nectar) rather than aphids, adult females of both species cease reproductive activity. These predators will produce and lay eggs in modest numbers in the absence of aphids, however, when provided both alternative foods together (Richards & Evans, 1998; Evans et al. 1999; Giles et al. (1994) note that *C. maculata* also fails to reproduce on a diet of alfalfa weevils alone).

The Australasian ladybird, *Coccinella transversalis* (F.), is another primarily aphidophagous predator (Bishop & Holtkamp, 1982; Agarwala & Ghosh, 1988; Pope, 1988). However, it also feeds on eggs and young larvae of *Helicoverpa armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae), major pests of Australian cotton (Room, 1979; Mensah, 1997), and likely on cotton nectar as well (Adjei-Maafo & Wilson, 1983). Here I examine egg production by *C. transversalis* females maintained on a diet of *Helicoverpa* larvae or sugar solution alone or in combination, versus on a diet of aphids. Comparison of the results with those of previous feeding studies of adult aphidophagous ladybirds permits more general assessment of the adequacy of non-aphid, ‘alternative’ foods for reproduction in this group of predators.

I also examine egg production of ladybirds maintained on a diet lacking aphids, wherein fresh aphid honeydew (upon which the predators readily feed in nature; e.g., see references in Evans & Richards, 1997), rather than simple sugar solution, is provided in combination with *Helicoverpa* larvae. The presence of aphid honeydew and/or associated odors serves as a cue for oviposition by aphidophagous ladybirds (Evans & Dixon, 1986). Hence the combination of honeydew and a non-aphid prey might be especially effective in supporting egg production even in the absence of aphid consumption. The potential importance of such honeydew consumption for lady beetle reproduction, however, has not been investigated previously.

Materials and methods

Insects. Female ladybirds used as experimental subjects were collected as adults in early summer 1997 near Canberra, Australia, from lucerne (alfalfa) fields (in which they feed especially on aphids, including the pea aphid *Acyrthosiphon pisum* [Harris], but in which *Helicoverpa* larvae occur as well; Bishop & Holtcamp, 1982; Milne & Bishop, 1987). The beetles were placed initially (for up to 2 weeks) in a refrigerator before being transferred to a constant temperature chamber at 20 °C and L14:D10, where they were held first in groups of mixed sex and supplied with pea aphids in excess (reared in a greenhouse on broad beans, *Vicia faba* L.), and where eggs were laid frequently.

Thereafter, females were placed individually in petri dishes (5 cm diameter) with a cotton-stoppered vial of water. These females were provided experimental diets, which in some instances included larvae of *Helicoverpa armigera* and/or pea aphid honeydew. Larvae of *H. armigera* were obtained from a laboratory colony maintained on artificial diet (Daly & Fisk, 1995). Fresh aphid honeydew was provided each day by previously placing opened petri dishes for 24–48 h beneath bean plants infested with aphids. Before ladybirds were transferred to these dishes, live aphids and shed exoskeletons that had fallen in were removed, leaving droplets of honeydew (plus traces of aphid exoskeletons) on the bottom and sides of the petri dish.

Experimental design. Individual female ladybirds were assigned randomly to receive one of five experimental diets (supplied daily): (a) twenty adult pea aphids, (b) twenty second-instar larvae of *H. armigera*, (c) sugar solution only (sucrose dissolved in the water supply at a concentration of 150 g per l), (d) twenty second-instar larvae of *H. armigera* plus sugar solution, or (e) twenty second-instar larvae of *H. armigera* plus aphid honeydew. Initial trials established that when females were offered twenty adult aphids or second-instar *H. armigera* larvae, live prey (generally five to ten individuals) were still present one day later. Comparison of replicates with female ladybirds plus *Helicoverpa* larvae versus with larvae alone revealed considerable cannibalism among larvae, but indicated that on average the lady beetles consumed five larvae per day; females provided twenty adult aphids consumed on average thirteen per day. Six females were maintained on each of the five diets for 10 days. Females were transferred each day to new petri dishes stocked with new water vials and foods (prey, sugar solution and honeydew).

Egg production by females was recorded twice a day. Occasionally, some of the newly laid eggs were cannibalized by adults or consumed by *Helicoverpa* larvae between checks. Such eggs could be identified and counted from their chewed remains or from the yellow spot they left.

All females were weighed immediately prior to the start of the experiment. These initial weights were compared with those after rearing on experimental diets for 7 days; the percentage change in weight was calculated as the difference in weight (weight at day 7 minus initial weight) divided by initial weight.

Statistical analyses. Percentage changes in weight were analysed using analysis of variance (ANOVA; SAS Institute, 1996). Linear contrasts were employed to test predictions that (i) females would best maintain their weight (by feeding most readily and remaining most active reproductively) when provided aphids versus other diets (diet a versus b, c, d, and e), (ii) females would better maintain body weight when provided aphid honeydew versus sugar solution in addition to *Helicoverpa* larvae (diet e versus d), (iii) females would better maintain weight when provided both a source of sugar and larvae versus larvae alone (diets d and e versus b) and (iv) females would better maintain weight when provided larvae (with or without sugar solution or honeydew) versus sugar solution only (diets b, d, and e versus c).

Daily egg production was analysed both for the first 3 days of the experiment (when effects of aphid consumption prior to the experiment could be expected to be strongest; Richards & Evans, 1998), and for the final 7 days. Because females in each treatment laid eggs readily during the first 3 days, the data for these days could be analyzed using analysis of variance. Linear contrasts were used to test the predictions that egg production would be (i) highest on a diet of aphids versus on other diets (diet a versus b, c, d, and e), (ii) higher when females were provided both the alternative prey (*Helicoverpa* larvae) and a source of sugar versus only one or the other (diets b and e versus b and c), and (iii) higher when females were provided larvae with aphid honeydew (and attendant odor cues) versus larvae with sugar solution (diet e versus d). In contrast to females during the first 3 days, a number of females in some treatments laid few or no eggs during the following 7 days. Therefore non-parametric Wilcoxon tests were used to test the above predictions.

Results

Weight. At the onset of the experiment, individual ladybirds weighed 26.3 ± 0.8 mg (mean ± s.e.; ANOVA for differences among treatments: $F_{1,25} = 0.45$, $P=0.77$). One week later, weights of those females that continued to be provided aphids (diet a) had increased modestly, but weights of females provided *Helicoverpa* larvae (with or without sugar solution or aphid honeydew) had declined, as had weights of females provided sugar solution only (Figure 1; ANOVA of percentage change in weight with linear contrasts: females fed aphids versus all others, $F_{1,25} = 28.46$, $P<0.0001$). Among females provided *Helicoverpa* larvae, percentage loss in weight was very similar between individuals also provided aphid honeydew versus sugar solution (Figure 1: diet d versus e; $F_{1,25} = 0.03$, $P=0.86$). Percentage loss in weight did not differ significantly between these two groups of females combined and those females provided *Helicoverpa* larvae alone (Figure 1: diets d and e versus b; $F_{1,25} = 1.59$, $P=0.22$), nor did it differ between all three groups combined of females provided *Helicoverpa* larvae and those provided sugar solution only (Figure 1: diets b, d, and e versus c; $F_{1,25} = 0.31$, $P=0.58$). Overall, body weights of females other than those fed aphids declined by an average of 17.6% over the first 7 days of the experiment (Figure 1).

Oviposition. Associated with differences in body weight that developed over time between females fed aphids and those fed other foods were differences in rates of egg production and oviposition. Females in all five treatments laid eggs in moderate to large numbers during the first 3 days of the experiment (Table 1). As predicted, females provided aphids laid especially large numbers of eggs (linear contrast between these females and all others, $F_{1,25} = 4.32$, $P=0.048$). No significant differences in egg production occurred, however, between females provided *Helicoverpa* plus sugar solution or aphid honeydew versus those provided only *Helicoverpa* or only sugar solution (diets d and e versus b and c; $F_{1,25} = 0.01$, $P=0.93$), or females provided *Helicoverpa* plus aphid honeydew versus *Helicoverpa* plus sugar solution (diet e versus d; $F_{1,25} = 1.54$, $P=0.23$).

During the next 7 days of the experiment, females on contrasting diets differed significantly from each other in daily egg production (Table 1). Females provided aphids laid far more eggs per day than other females (Wilcoxon test: $Z=3.96$, $P<0.0001$); while egg production of aphid fed females was similar to that of the first 3 days, egg production dropped to low levels among the remaining females. Among these latter females, those provided *Helicoverpa* plus solu-

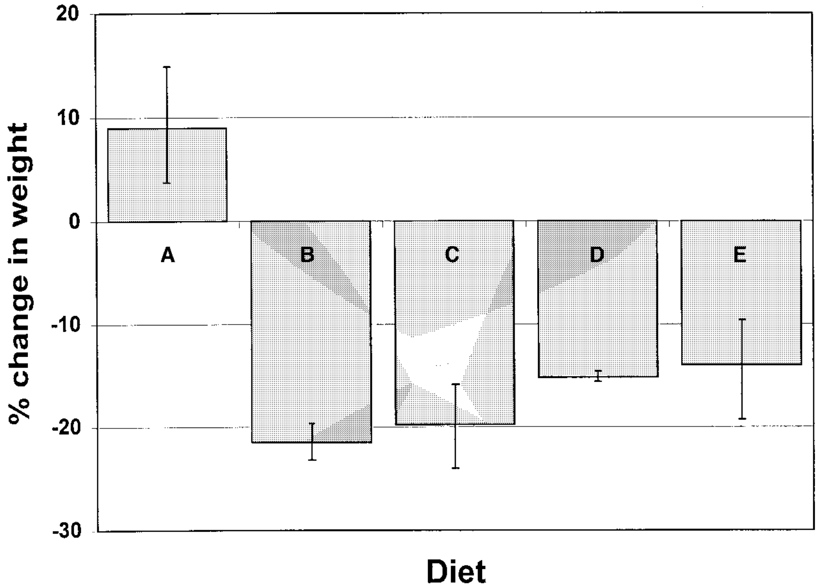

Figure 1. The percentage gain or loss (mean ± 1 s.e.) in body weight over 7 days of females of *C. transversalis* maintained on a diet of (A) pea aphids, (B) *Helicoverpa* larvae, (C) sugar solution, (D) *Helicoverpa* and sugar solution, and (E) *Helicoverpa* and pea aphid honeydew.

Table 1. Number of eggs laid per day [mean (s.e.)] in the first 3 days and the final 7 days that female ladybirds were maintained on differing diets, as described in the Methods section (n = six females per treatment)

Diet	First 3 days	Final 7 days
Aphids (a)	27.3 (8.1)	20.0 (3.8)
Helicoverpa only (b)	17.1 (6.2)	0.4 (0.2)
Sugar solution only (c)	9.8 (4.8)	0.0 (–)
Helicoverpa + sugar (d)	18.2 (6.2)	2.7 (1.3)
Helicoverpa + honeydew (e)	7.6 (4.4)	2.0 (1.2)

tion or aphid honeydew laid significantly more eggs than those provided only *Helicoverpa* or only sugar solution (diets d and e versus b and c; Wilcoxon test: Z=2.36, P= 0.018). Of females provided *Helicoverpa*, those also provided aphid honeydew did not differ significantly from those also provided sugar solution (diet e versus d; Wilcoxon test: Z=0.08, P=0.93).

Discussion

Female ladybirds laid no eggs (beyond the first 3 days) when provided only sugar solution, and almost no eggs when provided *Helicoverpa* larvae alone. However, they laid significantly more eggs (on average, two to three eggs per day) on a diet of both the larvae and a source of sugar (sucrose or aphid honeydew) than on a simple diet of the larvae or sugar alone. But even so, females on these non-aphid diets laid fewer eggs than females maintained on a diet of aphids. When provided *Helicoverpa* larvae plus sugar solution, for example, females laid only 14% as many eggs (after the first 3 days) as the females provided aphids. Overall, these results are similar to those reported for *Coccinella* species from western North America that fed on weevil larvae and/or sugar solution (Richards & Evans, 1998; Evans et al., 1999). More generally, the suitability of mixed diets for oviposition by other groups of ladybirds has received little attention (Hodek & Honěk, 1996; but see Phoofolo & Obrycki, 1997).

The cessation of egg production and oviposition by *Coccinella* spp. when feeding on only non-aphid prey contrasts with the active reproduction of *Coleomegilla maculata* when feeding on eggs of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Hazzard & Ferro, 1991; Munyaneza & Obrycki, 1997), and of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae) (Phoofolo & Obrycki, 1997). Early feeding studies by Putnam (1957, 1964) and Smith (1965), however, revealed that females of this ladybird are unusual in their propensity to produce eggs on diverse foods (including spider mites and artificial diets). Although not naturally consumed by ladybirds, eggs of the lepidopteran *Ephestia* (*Anagasta) kuehniella* Zeller (a pest of stored products) also provide a suitable diet for eliciting high rates of oviposition in the coccinellids *Harmonia axyridis* (Pallas) and *Semiadalia undecimnotata* (Schneider) (Schanderl et al., 1988; see also Ettifouri & Ferran, 1993; Ferran et al., 1997). Thus, the practical challenge of inducing active egg production in mass rearing of ladybirds as biocontrol agents may be met in some cases with provision of non-aphid prey rather than aphids or artificial foods. Nevertheless, for many aphidophagous ladybirds such as those of the genera *Coccinella* and *Hippodamia*, it has proved quite difficult to induce egg production when aphids are not included in the diet (Racioppi et al., 1981; Hagen, 1987; Hodek & Honěk, 1988).

Recent studies have revealed that ladybird reproductive activity is highly sensitive to chemical cues produced both by the prey and by other ladybirds (Evans & Dixon, 1986; Hemptinne et al., 1992, 1993; Merlin et al., 1996a,b; Ruzicka, 1997; Doumbia et al., 1998). In the present study, the number of eggs laid by females did not differ significantly when aphid honeydew rather than simple sugar (sucrose) was provided in combination with *Helicoverpa* larvae. Thus, although the presence of aphid honeydew may stimulate oviposition of mature eggs (Evans & Dixon, 1986), it does not appear to have special effect (beyond that associated with sugar alone, as might be obtained from consuming plant nectar, for example) in stimulating the maturation of eggs when female ladybirds consume non-aphid prey.

The results reported here and those reported previously (Richards & Evans, 1998; Evans et al., 1999) confirm that for adults of oligophagous ladybirds such as *Coccinella* that are closely associated with aphid prey, non-aphid prey such as lepidopteran or coleopteran larvae are indeed 'alternative foods' in the sense proposed by Hodek (1962, 1973) and Hodek & Honěk (1996). Thus, when consumed as the sole item in the diet, these prey sustain the predators but they do not support egg production. Nevertheless, when a diet of such foods is enhanced by provision of sugar, eggs are produced in low numbers. It is intriguing to note that enhancement of egg production by sugar consumption has also been reported in adults of parasitic Hymenoptera (England & Evans, 1997) and Lepidoptera (Wheeler, 1996) in which larvae rather than adults otherwise acquire the nutrients used for egg production (sugar is a natural adult food for these insects, but it is generally thought of as a food burned as fuel rather than as a food promoting egg production). In the case of aphidophagous ladybirds, such enhancement may allow these predators to produce eggs even when aphids are absent or occur in very low numbers (a situation likely to prevail often as these mobile predators continually seek out short-lived local outbreaks of aphids; Dixon, 1998). Produced upon consumption of non-aphid prey and a source of sugar such as nectar, such eggs would then be available for immediate oviposition as dispersing females discover aphids early in colony growth. Such ability to respond immediately may be of considerable significance for these predators, as optimal conditions for ladybird reproduction may vanish rapidly as the aphid colony matures (Hemptinne et al., 1992; Kindlmann & Dixon, 1993).

Acknowledgements

I thank CSIRO Entomology, Canberra, for hosting me and providing space and equipment; J. Daly, P. De Barro, A. Grabowski, S. Grosse, P. Hart, M.-L. Johnson, W. Milne, K. Olsen, W. Wanjura, and P. Wellings for their very kind assistance; and A. F. G. Dixon, J.-L. Hemptinne, I. Hodek, W. Milne, and an anonymous reviewer for commenting on the manuscript. Support was also provided by the Utah Agricultural Experiment Station.

References

Adjei-Maafo, I. K. & L. T. Wilson, 1983. Factors affecting the relative abundance of arthropods on nectaried and nectariless cotton. Environmental Entomology 12: 349–352.

Agarwala, B. K. & A. K. Ghosh, 1988. Prey records of aphidophagous Coccinellidae in India. A review and bibliography. Tropical Pest Management 34: 1–14.

Andow, D. A. & S. J. Risch, 1985. Predation in diversified agroecosystems: relations between a coccinellid predator *Coleomegilla maculata* and its food. Journal of Applied Ecology 22: 357–372.

Bishop, A. L. & R. H. Holtkamp, 1982. The arthropod fauna of lucerne in the Hunter Valley, New South Wales. General and Applied Entomology 14: 21–32.

Cottrell, T. E. & K. V. Yeargan, 1998. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environmental Entomology 27: 1402–1410.

Daly, J. C. & J. H. Fisk, 1995. Decrease in tolerance to fenvalerate in resistant *Helicoverpa armigera* after pupal diapause. Entomologia Experimentalis et Applicata 77: 217–222.

Dixon, A. F. G., 1998. Aphid Ecology. An Optimization Approach. Chapman and Hall, London, UK.

Doumbia, M., J.-L. Hemptinne, & A. F. G. Dixon, 1998. Assessment of patch quality by ladybirds: the role of larval tracks. Oecologia 113: 197–202.

England, S. & E. W. Evans, 1997. Effects of pea aphid (Homoptera: Aphididae) honeydew on longevity and fecundity of the alfalfa weevil (Coleoptera: Curculionidae) parasitoid *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae). Environmental Entomology 26: 1437–1441.

Ettifouri, M. & A. Ferran, 1993. Influence of larval rearing diet on the intensive searching behaviour of *Harmonia axyridis* (Col.: Coccinellidae) larvae. Entomophaga 38: 51–59.

Evans, E. W. & A. F. G. Dixon, 1986. Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. Journal of Animal Ecology 55: 1027–1034.

Evans, E. W. & S. England, 1996. Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. Ecological Applications 6: 920–930.

Evans, E. W. & D. R. Richards, 1997. Managing the dispersal of ladybird beetles (Col.: Coccinellidae): use of artificial honeydew to manipulate spatial distributions. Entomophaga 42: 93–102.

Evans, E. W., A. T. Stevenson, & D. R. Richards, 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. Oecologia 121: 107–112.

Ferran, A., J. Gambier, S. Parent, K. Legendre, R. Tournière, and L. Giuge, 1997. The effect of rearing the ladybird *Harmonia axyridis* on *Ephestia kuehniella* eggs on the response of its larvae to aphid tracks. Journal of Insect Behavior 10: 129–144.

Giles, K. L., J. J. Obrycki, and T. A. DeGooyer, 1994. Prevalence of predators associated with *Acyrthosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. Biological Control 4: 170–177.

Gordon, R. D., 1985. The Coccinellidae (Coleoptera) of America north of Mexico. Journal of the New York Entomological Society 93: 1–912.

Hazzard, R. V. & D. N. Ferro, 1991. Feeding responses of adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of the Colorado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphididae). Environmental Entomology 20: 644–651.

Hazzard, R. V., D. N. Ferro, R. G. Van Driesche, & A. F. Tuttle, 1991. Mortality of eggs of Colorado potato beetle (Coleoptera: Chrysomelidae) from predation by *Coleomegilla maculata* (Coleoptera: Coccinellidae). Environmental Entomology 20: 841–848.

Hagen, K. S., 1987. Nutritional ecology of terrestrial insect predators. In: F. Slansky & J.G. Rodriguez (eds), Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York, pp. 533–577.

Hemptinne, J.-L., A. F. G. Dixon, & J. Coffin, 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. Oecologia 90: 238–245.

Hemptinne, J.-L., A. F. G. Dixon, J.-L. Doucet, & J.-E. Petersen, 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. European Journal of Entomology 90: 451–455.

Hilbeck, A., C. Eckel, & G. G. Kennedy, 1997. Predation on Colorado potato beetle eggs by generalist predators in research and commercial potato plantings. Biological Control 8: 191–196.

Hodek, I., 1962. Essential and alternative foods in insects. In: H. Strouhal & M. Beier (eds), Transactions of the XIth International Congress of Entomology, vol. 2. Organisationskomittee des XI Internationalen Kongress für Entomologie, Vienna, pp. 697–698.

Hodek, I., 1973. Biology of Coccinellidae. Czechoslovak Academy of Science, Prague.

Hodek, I. & A. Honěk, 1988. Sampling, rearing and handling of aphid predators. In: A. K. Minks & P. Harrewijn (eds), Aphids, Their Biology, Natural Enemies and Control, volume 2B. Elsevier, Amsterdam, pp. 311–321.

Hodek, I. & A. Honěk, 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Kindlmann, P. & A. F. G. Dixon, 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. European Journal of Entomology 90: 443–450.

Mensah, R. K, 1997. Yellow traps can be used to monitor populations of *Coccinella transversalis* (F.) and *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) in cotton crops. Australian Journal of Entomology 36: 377–381.

Merlin, J., O. Lemaitre, & J.-C. Grégoire, 1996a. Oviposition in *Cryptolaemus montrouzieri* stimulated by wax filaments of its prey. Entomologia Experimentalis et Applicata 79: 141–146.

Merlin, J., O. Lemaitre, & J.-C. Grégoire, 1996b. Chemical cues produced by conspecific larvae deter oviposition by the coccidophagous ladybird beetle, *Cryptolaemus montrouzieri*. Entomologia Experimentalis et Applicata 79: 147–151.

Milne, W. M. & A. L. Bishop, 1987. The role of predators and parasites in the natural regulation of lucerne aphids in eastern Australia. Journal of Applied Ecology 24: 893–905.

Munyaneza, J. & J. J. Obrycki, 1997. Reproductive response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle (Coleoptera: Chrysomelidae) eggs. Environmental Entomology 26: 1270–1275.

Pemberton, R. W. & N. J. Vandenberg, 1993. Extrafloral nectar feeding by ladybird beetles (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 95: 139–151.

Phoofolo, M. W. & J. J. Obrycki, 1997. Comparative prey suitability of *Ostrinia nubilalis* eggs and *Acyrthosiphon pisum* for *Coleomegilla maculata*. Biological Control 9: 167–172.

Pope, R. D., 1988. A revision of the Australian Coccinellidae (Coleoptera). Part 1. Subfamily Coccinellinae. Invertebrate Taxonomy 2: 633–735.

Putnam, W. L., 1957. Laboratory studies on the food of some coccinellids (Coleoptera) found in Ontario peach orchards. Canadian Entomologist 89: 572–579.

Putnam, W. L., 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. Canadian Entomologist 96: 1149–1155.

Racioppi, J. V., R. L. Burton & R. Eikenbary, 1981. The effects of various oligidic synthetic diets on the growth of *Hippodamia convergens*. Entomologia Experimentalis et Applicata 30: 68–72.

Richards, D. R. & E. W. Evans, 1998. Reproductive responses of aphidophagous lady beetles (Coleoptera: Coccinellidae) to non-aphid diets: an example from alfalfa. Annals of the Entomological Society of America 91: 632–640.

Room, P. M., 1979. Parasites and predators of *Heliothis* spp. (Lepidoptera: Noctuidae) in cotton in the Namoi Valley, New South Wales. Journal of the Australian Entomological Society 18: 223–228.

Ruzicka, Z., 1997. Recognition of oviposition-deterring allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). European Journal of Entomology 94: 431–434.

SAS Institute, 1996. SAS/STAT software: changes and enhancements for Release 6.12. Cary, NC, USA.

Schanderl, H., A. Ferran & V. Garcia, 1988. L'élevage de deux coccinelles *Harmonia axyridis* et *Semiadalia undecimnotata* à l'aide

d'oeufs d'*Anagasta kuehniella* tués aux rayons ultraviolets. Entomologia Experimentalis et Applicata 49: 235–244.
Smith, B. C., 1965. Effects of food on the longevity, fecundity, and development of adult coccinellids (Coleoptera: Coccinellidae). Canadian Entomologist 97: 910–919.
Wheeler, D., 1996. The role of nourishment in oogenesis. Annual Review of Entomology 41: 407–431.
Yakhontov, V. V., 1938. Practical results of an experiment. A biological method of controlling pests of lucerne and cotton. Review of Applied Entomology Series A 26: 238–239.