

Prey Consumption and Oviposition of the Aphidophagous Predator *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) in Relation to Prey Density and Adult Size

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Environ. Entomol. 30(6): 1182–1187 (2001)

ABSTRACT Effects of prey density and adult predator size on food consumption and oviposition were evaluated in an aphidophagous ladybird beetle, *Menochilus sexmaculatus* (F.), from tropical Asia. Both the functional response and reproductive numerical response showed an upper asymptote at 40 adult *Aphis craccivora* Koch/female/150 cm². Proportions of aphids consumed and eggs laid by female beetles were highest at lower aphid densities, i.e., five or 10 adult aphids. Ratio of eggs laid to aphids consumed, by dry weight, was highest at the lowest aphid density, i.e., five adult aphids. Larval food supply significantly influenced the size of adult females. After 24 h, smaller females consumed significantly fewer aphids and laid fewer eggs in comparison to larger females, but conversion efficiency from food to eggs remained the same irrespective of the difference in adult size. Results suggested that this ladybird species exploit prey efficiently at low density.

KEY WORDS *Menochilus sexmaculatus*, adult size, aphid prey, coccinellid predator, functional response, larval food supply

LADYBIRD PREDATORS OF aphids often feed on wide range of prey (Tao and Chiu 1971, Agarwala and Ghosh 1988, Hodek and Honek 1996) and forage in unstable habitats with variable prey density (Karieva 1984, Honek 1991). Although these predators usually aggregate in patches of high prey abundance (Mills 1982, Sakuratani et al. 1983, Obata and Johki 1990, Evans and Youssff 1992), short-lived aphid colonies may undergo rapid changes in density due to individual or combined actions of natural enemies, deterioration in host quality or climatic changes (Galecka 1966, Mohammed and Van Emden 1989, Helden et al. 1994, Dixon 1998). In such circumstances, development of larvae and reproduction of adult females are likely to suffer (Sundby 1966, Ng 1991). This is particularly true of ladybird predators because their developmental time is much longer than the developmental time of their aphid prey (Dixon 2000), and the fecundity of their females is closely related to the quantity and quality of aphid prey consumed (Hodek and Honek 1996, Sugiura and Takada 1998). Larval development on low food supply also significantly affects the size and reproduction of adults (Kaddou 1960, Smith 1965, Kawauchi 1990, Ng 1991). Size differences in adult predaceous ladybirds are common in nature (Hodek and Honek 1996), with smaller-sized ladybirds occurring frequently in fields (Obrycki et al. 1998). This reinforces the prediction that ladybird

beetles often live in habitats that are limited by food (Dixon 1997). Factors that affect prey consumption and reproduction in aphidophagous ladybirds are likely to affect their density in fields and, therefore, influence biological control.

Menochilus sexmaculatus (F.) is a common coccinellid predator of aphids in India, Japan, and other Far Eastern and Southern Asia countries (Tao and Chiu 1971, Agarwala and Ghosh 1988, Hussaein 1991), and it is known to have a prey range of 57 species of aphids (Agarwala and Yasuda 2000), five of coccids, one of Psyllidae (Sugiura and Takada 1998), and one of Lepidoptera (Jotwani and Verma 1969). This ladybird was introduced in North America to control the green bug, *Schizaphis graminum* (Rondani), on cereals (Cartwright et al. 1977). Prey preference studies suggested that the cowpea aphid, *Aphis craccivora* Koch, on bean plants, is one of the most suitable prey of this coccinellid predator (Okamoto 1978, Verma et al. 1983, Hussaein 1991, Omkar and Bind 1998, Sugiura and Takada 1998). In northern-eastern India, including subtropical areas of the Himalaya, this coccinellid frequently shares *A. craccivora* colonies on bean plants [*Dolichos lablab* (L.), *Vigna catjang* (Endlicher), *Vicia faba* (L.)] with other predators like *Coccinella transversalis* (F.), *Scymnus pyrocheilus* Mulsant (both Coccinellidae), and *Ischiodon scutellaris* Mulsant, a Syrphidae (Agarwala et al. 1987). Field studies on numerical response of *M. sexmaculatus* suggested that adults of this coccinellid became active at low aphid density/plant and closely synchronized their aggre-

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gation and reproduction with natural populations of the most preferred prey (Agarwala and Bardhanroy 1999), and eggs are chemically defended from intra-guild predation (Agarwala and Bardhanroy 1997, Agarwala et al. 1998, Agarwala and Yasuda 2001). Despite the advantages associated with using of this ladybird species as a biological control agent, there is a lack of information regarding its functional and reproductive numerical responses to changes in prey density, and influence of adult size on prey consumption and fecundity of females. This information will increase understanding about this predator's potential as a biological control agent of the pest aphids, and of cowpea aphid in particular.

Materials and Methods

Insect Material. Males and ovipositing females of *M. sexmaculatus* were collected from bean plants, *V. catjang*, in fields at the University campus at Suryamaninagar, Tripura, in northeast India. These beetles were offered *A. craccivora* prey until females oviposited. Eggs from these females were kept in 9-cm petri dishes, one cluster of eggs in each, lined with filter paper in the bottom that was slightly dampened every 12 h. Hatched larvae were supplied an excess of cowpea aphids until the second molt when the larvae were transferred, one per petri dish, to new 9-cm petri dishes and kept until pupation. Aphids were obtained from a culture maintained on bean plants in a greenhouse. First-generation adult beetles of the laboratory rearing were kept, 20 each, in ventilated plastic boxes (16 cm length, 9 cm width, 12 cm height) in a sex ratio of 1:1 on a surplus supply of aphids. Corrugated paper and cut twigs of bean plants were provided in each box to facilitate laying of eggs. Eggs from first-generation beetles were used to initiate a culture of beetles for use in the experiments. The cultures were kept clean by replacing food and other contents every 24 h.

Prey Consumption and Oviposition in Relation to Prey Density. *M. sexmaculatus* females used in this experiment were controlled for their weight at emergence from the pupal case ($n = 60$, analysis of variance [ANOVA]: $F = 0.51$; $df = 5, 54$; $P = 0.77$) to eliminate size-related influences on prey consumption and oviposition by female beetles (Rhamlingam 1986, Dixon and Guo 1993). After eclosion from pupae, each of the females used in the experiment was kept on surplus of mixed instars of *A. craccivora*, and was allowed to mate with a male for 2 h. This was done every 48 h at the time of food change to maintain the reproductive vigour of the beetles. Ten-day-old *M. sexmaculatus* females (preoviposition period: mean \pm SE = 5.90 ± 0.34 d, $n = 16$) were starved for 16 h before use in the experiments to induce same hunger level. These females were kept individually in 9-cm petri dishes (approximate area: 150 cm^2) in an incubator at $20 \pm 1^\circ\text{C}$ and a photoperiod of 16:8 (L:D) h, and provided with one of the prey densities of 5, 10, 20, 30, 40, or 60 adult aphids. Numbers of aphids eaten and eggs produced by each *M. sexmaculatus* female were noted at 24 h

intervals for five consecutive days. This was repeated 10 times at each prey density.

Prey Consumption and Oviposition in Relation to Adult Size. Twenty hatched larvae were kept either on a low (10 aphids) or high (40 aphids) food supply during their development. Each larva was confined to a 9-cm petri dish and provided with 10 or 40 aphids comprised of second and fourth instars in 1:1 ratio. Larvae were weighed at the beginning and end of their development to assess differences in weight gain. Larvae kept on low food suffered 20% mortality during larval development and another 15% mortality occurred in the pupal stage. Thus, 13 adults were obtained from the initial 20 first instar larvae. Seven of these adults were females. All adult females were weighed upon emergence from pupae and measured for their lengths. These females, both from larval development on low ($n = 7$) and high ($n = 10$) food supply, were kept individually on an excess of aphids of mixed instars until first oviposition (preoviposition period: on low food: mean \pm SE = 9.57 ± 1.45 d, $n = 7$; on high food: mean \pm SE = 5.80 ± 0.45 d, $n = 10$; $t = 12.54$, $df = 15$, $P < 0.001$). At this stage, females were starved for 16 h and then each was provided with 40 adult aphids. Number of aphids eaten and eggs produced were recorded at the end of 24 h. This was done for five consecutive days for each female.

Efficiency of Converting Food into Eggs. Data on prey consumption and egg production in both experiments were used to determine the ratio of eggs produced to aphids consumed (dry mass) to know the conversion efficiency of *M. sexmaculatus* females at different prey density and influence of adult size. For this purpose, fresh (FW) to dry weight (DW) conversions of adult aphids and eggs were determined by drying at 40°C for 10 d (adult aphids: $\text{DW} = 0.183 \times \text{FW}$ of aphids (mg), $n = 77$, $r^2 = 0.56$, $P < 0.001$; eggs: $\text{DW} = 0.0358 \times \text{FW}$ of eggs (mg), $n = 80$, $r^2 = 0.32$, $P < 0.001$). All weights in this study were taken in a microbalance sensitive to $0.01 \mu\text{g}$.

Data Analyses. For the purpose of clarity regression lines of functional response and reproductive numerical response were drawn based on mean values of aphids consumed and eggs produced, respectively. However, the raw data of these experiments were subjected to one factor ANOVA for interaction between the prey density and the effects, both for prey consumption and egg production. Data of the second experiment were subjected to Student's *t*-test in respect of size of adult females, aphids eaten and eggs produced, and ratio of eggs produced to aphid consumed by *M. sexmaculatus* females. All proportion data were arcsine roots transformed before statistical analysis. Comparison between the treatments, when necessary, was made by Scheffé test. A significance level of 0.05 was used to reject the null hypothesis.

Results

Functional Response. Mean number of aphids eaten by a *M. sexmaculatus* female per day increased gradually from low to higher densities. However, in terms

Table 1. Proportions (arcsine root transformed) of aphids consumed and eggs produced by a *M. sexmaculatus* female per day at increasing prey density ($n = 10$ replicates for each prey density)

Prey density	Mean \pm SE proportions of	
	Aphids eaten	Eggs produced
5	0.843 \pm 0.019 ^a	0.868 \pm 0.018 ^a
10	0.844 \pm 0.014 ^a	0.671 \pm 0.066 ^b
20	0.748 \pm 0.096 ^b	0.636 \pm 0.008 ^b
30	0.762 \pm 0.033 ^b	0.611 \pm 0.039 ^b
40	0.792 \pm 0.039 ^b	0.643 \pm 0.059 ^b
50	0.583 \pm 0.072 ^c	0.459 \pm 0.051 ^c

Different letters following means in a column indicate significant differences by Scheffé test ($P < 0.05$).

of proportion of aphids eaten to the prey density, aphid consumption was significantly higher at lower prey densities of five and 10 aphids. Thereafter the mean proportion of aphids consumed decreased with increasing prey densities and was significantly lower at 60 aphids/female than at 40 aphids/female (ANOVA: $F = 25.61$; $df = 5, 54$; $P < 0.0001$, Table 1). Regression analysis suggest that a curvilinear response is a better statistical fit to the data ($Y = 2.64 + 1.31X - 0.011X^2$, $r^2 = 0.98$, $P < 0.001$, Fig. 1) than a linear response with a flat maximum ($Y = 4.33 + 0.63X$, $r^2 = 0.91$, $P < 0.01$).

Numerical Response. Mean number of eggs laid by a *M. sexmaculatus* female per day increased gradually from lower to higher densities until an upper asymptote was recorded at a prey density of 40 aphids/female/150 cm². Egg production at higher density of 60 aphids/female was not significantly different from the asymptote. In terms of the ratio of number of eggs produced to number of prey present, however, it was recorded to be highest at the lowest prey density i.e., five aphids. The ratio was significantly lower for 60 aphids/female than for 40 aphids/female (ANOVA:

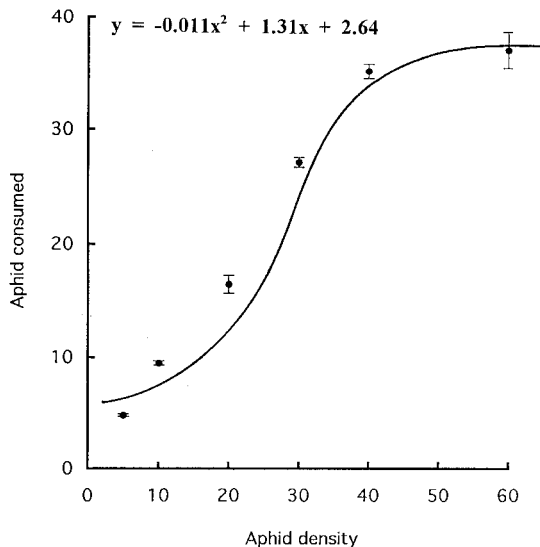


Fig. 1. Functional response in terms of mean \pm SE number of aphids consumed by an *M. sexmaculatus* female per day at increasing aphid density.

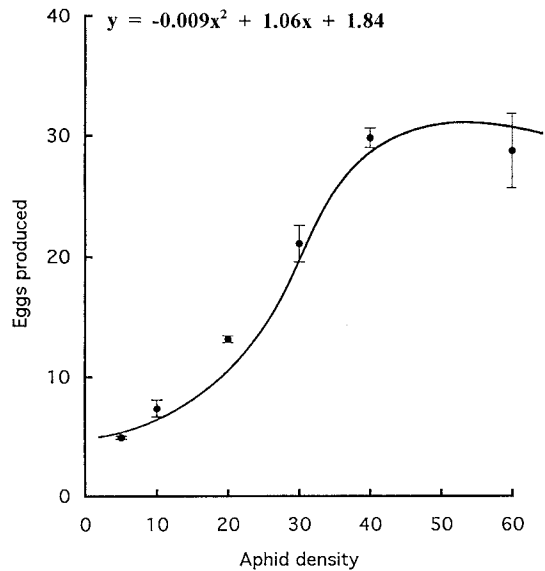


Fig. 2. Numerical response in terms of mean \pm SE number of eggs laid by an *M. sexmaculatus* female per day at increasing aphid density.

$F = 15.88$; $df = 5, 54$; $P < 0.0001$, Table 1). Regression analysis suggest that a curvilinear response provided a better statistical fit to the data ($Y = 1.84 + 1.06X - 0.009X^2$, $r^2 = 0.92$, $df = 59$, $P < 0.001$, Fig. 2) than a linear response with a flat maximum ($Y = 4.06 + 0.49X$, $r^2 = 0.88$, $df = 59$, $P < 0.001$).

Ratio of Eggs to Aphids. The dry mass of eggs produced per dry mass of aphids consumed by an *M. sexmaculatus* female per day was highest at the lowest prey density (Fig. 3). The results suggest that the efficiency of conversion of prey consumed to eggs produced was particularly high at very low prey density and varied little among other prey densities (ANOVA: $F = 12.25$; $df = 5, 54$; $P < 0.0001$).

Effects of Adult Size. There was a marked difference in size of adult females which completed development in low and high larval food supply (Table 2). Small-sized females from low larval food supply consumed significantly fewer aphids ($t = 4.23$, $df = 15$, $P = 0.007$) and produced fewer eggs per day ($t = 3.12$, $df = 15$, $P = 0.007$) in comparison to females from high larval food supply (Fig. 4 A and B). However, there was no statistical difference in the ratio of eggs produced to per aphid consumed by dry mass between the females from low and high food supply ($t = 1.16$, $df = 15$, $P = 0.265$, Fig. 4C).

Discussion

Feeding and oviposition patterns of individual predators reflect the adaptiveness of their populations to foraging conditions in fields. Host-plant restricted aphid colonies are often irregularly distributed in space and time (Honek 1987, Agarwala and Bhattacharya 1995, Dixon 1998). As a result, at any instant, number of aphids available in a patch as a food for

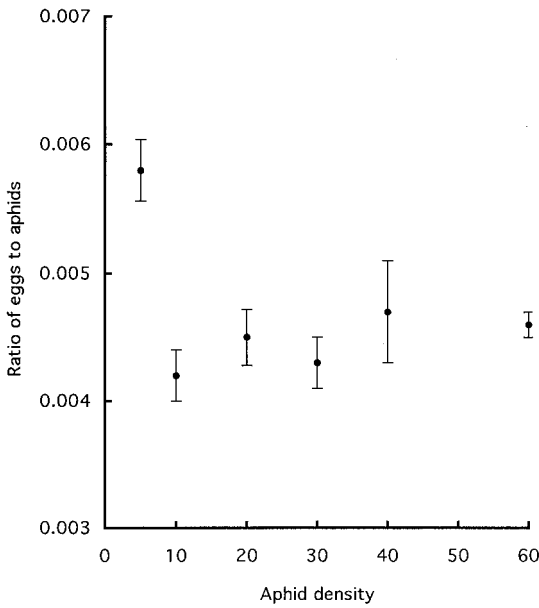


Fig. 3. Mean ± SE of ratio of eggs laid to aphid consumed, by dry weight, by *M. sexmaculatus* females at different prey density.

predators may vary. In such environments, predators able to adjust to variable food resources will have greater impact on prey population.

A number of studies have demonstrated the effects of prey quantity on the consumption, survival, and reproduction of aphidophagous predators (Kaddou 1960, Smith 1965, Kawauchi 1979, Evans and Yousff 1992, Ives et al. 1993, Yasuda and Ishikawa 1999). Most coccinellid predators, as well as other predators of aphids, are reported to show Holling's (1965) functional response type II (Mogi 1969, Kawauchi 1979, Sinha et al. 1982, Hodek and Honek 1996). Such a response is typical of predators foraging in unstable prey populations and this means rapid utilization of food by predators even at lower densities. In the current study, *M. sexmaculatus* females displayed similar response. An upper asymptote was recorded at 40 aphids/female. Increase in prey consumption at higher densities is limited by satiation in predators (Mills 1982, Hodek and Honek 1996). Changes in time scale, searching area and habitat quality of the prey may also cause variations in the functional response of a predator. However, there are only a few studies in

Table 2. Weight and length of adult females at emergence from the pupal case when their larvae developed on low and high food availability

Larval food supply	n	Size of females at birth (mean ± SE)	
		Weight, mg	Length, mm
Low	7	9.71 ± 0.48	3.87 ± 0.17
High	10	15.44 ± 0.22	5.69 ± 0.10
Student's <i>t</i> -test	df = 15	<i>t</i> = 12.017	<i>t</i> = 11.02
		<i>P</i> < 0.001	<i>P</i> < 0.001

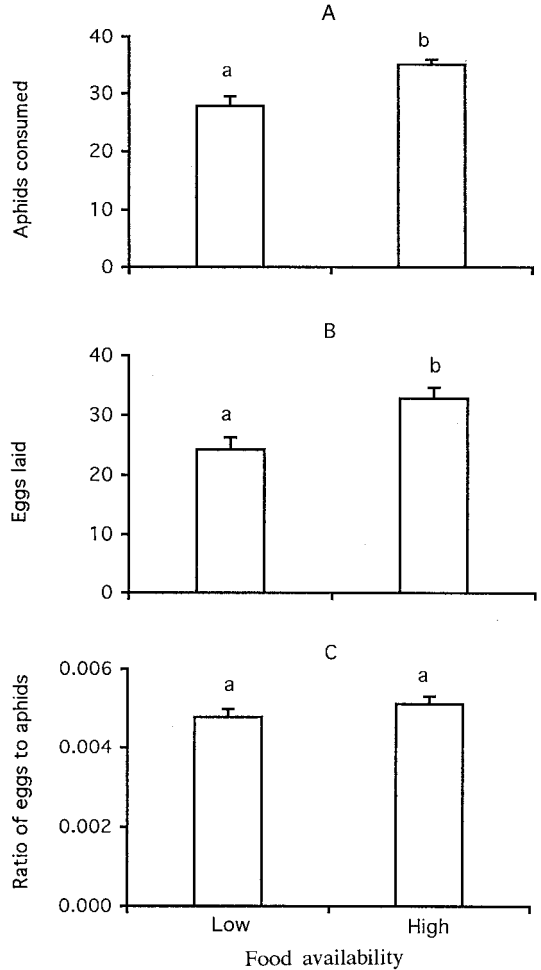


Fig. 4. Influence of size of females on the mean ± SE number of aphids eaten (A), eggs laid (B) and ratio of eggs laid to aphids consumed, by dry weight, (C) when their larvae were developed on different food supply. Bars with different letters indicate significant differences by Student's *t*-test (*P* < 0.05).

this direction (Carter and Dixon 1982, Ferran and Dixon 1993, Ives et al. 1993, Yasuda and Ishikawa 1999).

Reproductive numerical response of *M. sexmaculatus* females to prey density was almost similar to the functional response. Such a correspondence in the shapes of the functional and numerical responses is suggestive of the dependence of predator's rate of increase on their successful searching and eating preys. This vindicates the models explained by Hassell (1978), Taylor (1984) and Ferran and Dixon (1993), and reviewed by Hodek and Honek (1996).

Results of this study show that proportion of prey eaten and the ratio of number of eggs produced to number of prey eaten by *M. sexmaculatus* females were maximum at lower prey densities used, i.e., five or 10 aphids, and this was significantly higher than the proportion achieved at the prey density of 40 aphids. At

higher prey density, the ratios of number of eggs produced to number of aphids consumed attained saturation threshold. This finding appears to be in agreement with preference of ladybird predators for laying eggs when aphid colonies are still small or growing (Hemptinne et al. 1992, Hironori and Katsuhiko 1997, Agarwala and Bardhanroy 1999), and their tendency to attain an optimum number of eggs laid within aphid colonies (Kindmann and Dixon 1993, 1999).

Variable prey availability in time and space could result in variation in adult size of predators (Barbult 1988, Zhou et al. 1995). Differences in adult size affect the fitness of males and females in terms of mating, searching behavior, food consumption, fecundity and longevity (Kessler 1971; Zheng et al. 1993a, 1993b; Ohgushi 1996; Richardson and Baker 1997). In a competitive environment of arthropod predators of aphids, size difference in adult females could be disadvantageous to smaller individuals in terms of lower fecundity and reduced longevity, in particular at high food density. The results of this study show that larvae developing on low food supply resulted in significantly smaller adult females in comparison to adult females of larvae that developed on high food supply. The difference in size of these females was also reflected by significant differences in prey consumption and fecundity; smaller adults consumed less food and produced fewer eggs at constant food availability. However, the ratio of eggs produced to per capita aphid consumed was not affected by the difference in size of adult females. This suggested that despite disadvantages associated with being smaller in size, the size difference in adult females did not affect their efficiency of converting food into eggs. This is particularly relevant to smaller-sized ladybirds, which occur frequently in fields (Obrycki et al. 1998).

Acknowledgments

This study was supported by research grants from the Ministry of Science & Technology, Government of India, and the Japanese Society for Promotion of Science to B.K.A. We are thankful to S. Bhattacharya for her help in conducting some of the experiments.

References Cited

- Agarwala, B. K., and P. Bardhanroy. 1997. Oviposition behaviour and reproduction efficiency in ladybird beetles: a case study of *Menochilus sexmaculatus* (Fabr.). *J. Aphidol.* 11: 1-10.
- Agarwala, B. K., and P. Bardhanroy. 1999. Numerical response of ladybird beetles (Col., Coccinellidae) to aphid prey (Hom., Aphididae) in a field bean in north-east India. *J. Appl. Entomol.* 123: 401-405.
- Agarwala, B. K., S. Bhattacharya, and P. Bardhanroy. 1998. Who eats whose eggs? Intra-versus interspecific interactions in starving ladybird beetles predaceous on aphids. *Ethol. Ecol. Evol.* 10: 361-368.
- Agarwala, B. K., and S. Bhattacharya. 1995. Adaptive features of predatory ladybird beetles in uncertain and competitive habitats. *Curr. Sci.* 69: 587-591.
- Agarwala, B. K., A. K. Bhaumik, and S. Das. 1987. Natural food range and feeding habits of aphidophagous insects in north-east India. *J. Aphidol.* 1: 18-22.
- Agarwala, B. K., and A. K. Ghosh. 1988. Prey records of aphidophagous Coccinellidae in India. A review and bibliography. *Trop. Pest Manage.* 14: 1-14.
- Agarwala, B. K., and H. Yasuda. 2000. Competitive ability of ladybird predators of aphids: a review of *Cheilomenes sexmaculata* (Fabr.) (Coleoptera: Coccinellidae) with a worldwide checklist of prey. *J. Aphidol.* 14: 1-20.
- Agarwala, B. K., and H. Yasuda. 2001. Overlapping oviposition and chemical defense of eggs in two co-occurring species of ladybird predators of aphids. *J. Ethol.* 19: 47-53.
- Barbult, B. 1988. Body size, ecological constraints, and the evolution of life history strategies. *Evol. Biol.* 22: 261-286.
- Carter, M. C., and A.F.G. Dixon. 1982. Habitat quality and the foraging behaviour of coccinellid larvae. *J. Anim. Ecol.* 51: 865-878.
- Cartwright, B., R. D. Eikenbary, J. W. Johnson, T. N. Farris, and R. D. Morrison. 1977. Field release and dispersal of *Menochilus sexmaculatus*, an important predator of the greenbug, *Schizaphis graminum*. *Environ. Entomol.* 6: 699-704.
- Dixon, A.F.G. 1997. Patch quality and fitness in predatory ladybirds. *Ecol. Stud.* 130: 205-223.
- Dixon, A.F.G. 1998. Aphid ecology: an optimization approach. Chapman and Hall, London.
- Dixon, A.F.G. 2000. Insect predator-prey dynamics, ladybird beetles and biological control. Cambridge University Press, Cambridge.
- Dixon, A.F.G., and A. Guo. 1993. Egg and cluster size in ladybird beetles (Coleoptera: Coccinellidae): the direct and indirect effects of aphid abundance. *Eur. J. Entomol.* 90: 457-463.
- Evans, E., and N. N. Yousff. 1992. Numerical responses of aphid predators to varying prey density among Utah alfalfa fields. *J. Kans. Entomol. Soc.* 65: 30-38.
- Ferran, A., and A.F.G. Dixon. 1993. Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). In R. J. Chambers, A.F.G. Dixon, I. Hodek, and J.-M. Rabasse [eds.], *Behavioural ecology of aphidophagous insects*. *Eur. J. Entomol.* 90: 383-402.
- Galecka, B. 1966. The role of predators in the reduction of two species of potato aphids, *Aphis nasturtii* Kalt. and *A. frangulae* Kalt. *Ekol. Pol.* 14: 245-274.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ.
- Helden, A., A.F.G. Dixon, and N. Carter. 1994. Environmental factors and morphological discrimination between spring and summer migrants of the grain aphid, *Sitobion avenae* (Homoptera: Aphididae). *Eur. J. Entomol.* 91: 23-28.
- Hemptinne, J.-L., A.F.G. Dixon, and J. Coffin. 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238-245.
- Hironori, Y., and S. Katsuhiko. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 153-163.
- Hodek, I., and A. Honek. 1996. *Ecology of Coccinellidae*. Kluwer Academic, Dordrecht, The Netherlands.
- Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45: 3-60.
- Honek, A. 1987. Effect of plant quality and microclimate on population growth and maximum abundances of cereal aphids, *Metopolophium dirhodum* (Walker) and *Sitobion*

- avenae* (F.) (Hom., Aphididae). J. Appl. Entomol. 104: 304–313.
- Honek, A. 1991. Environment stress, plant quality and abundance of cereal aphids (Hom., Aphididae) on winter wheat. J. Appl. Entomol. 112: 65–70.
- Hussain, M. Y. 1991. *Menochilus sexmaculatus* Fabr. (Coleoptera: Coccinellidae): its biology, prey requirement and artificial diet. J. Plant Prot. 8: 153–160.
- Ives, A. R., P. Karieva, and R. Perry. 1993. Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. Ecology 74: 1929–1938.
- Jotwani, M. G., and K. K. Verma. 1969. *Chilomenes sexmaculata* (Fabr.) as a predator of sorghum stem borer *Chilozonellus* (Swinnoe). Indian J. Entomol. 31: 84–85.
- Kaddou, I. K. 1960. The feeding behaviour of *Hippodamia quindesignata* (Kirby) larvae. Univ. Calif. Publ. 16: 181–230.
- Karieva, P. 1984. Predator-prey dynamics in spatially structured population: manipulating dispersal in a coccinellid-aphid interaction. Lect. Notes Biomath. 54: 368–389.
- Kawauchi, S. 1979. Effects of prey density on the rate of prey consumption, development and survival of *Propylea japonica* Thunberg (Coleoptera: Coccinellidae). Kontyu 47: 204–212.
- Kawauchi, S. 1990. Studies on the comparative ecology of three aphidophagous coccinellids. Kurume Univ. J. 39: 239–305 (in Japanese with English summary).
- Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Paradosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food shortage. Oecologia 8: 93–109.
- Kindlmann, P., and A.F.G. Dixon. 1993. Optimal foraging in ladybird beetles and its consequences for their use in biological control. Eur. J. Entomol. 90: 443–450.
- Kindlmann, P., and A.F.G. Dixon. 1999. Strategies of aphidophagous predators: lessons for modeling insect predator-prey dynamics. J. Appl. Entomol. 123: 397–399.
- Mills, N. J. 1982. Satiation and the functional response: a test of a new model. Ecol. Entomol. 7: 305–315.
- Mogi, M. 1969. Predation response of the larvae of *Harmonia axyridis* Pallas (Coccinellidae) to the different prey density. Jpn. J. Appl. Entomol. Zool. 13: 9–16.
- Mohammed, B. M., and H. F. Van Emden. 1989. Host plant modification to insecticide susceptibility in *Myzus persicae* (Sulz.). Insect Sci. Appl. 10: 699–703.
- Ng, S. M. 1991. Voracity, development and growth of larvae of *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) fed on *Aphis spiraecola*, pp. 199–206. In L. Polgar, R. J. Chambers, A.F.G. Dixon, and I. Hodek [eds.], Behaviour and impact of aphidophaga. SPB Academic, The Hague.
- Obata, S., and Y. Johki. 1990. Distribution and behaviour of adult ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Entomophaga 31: 303–311.
- Obrycki, J. J., K. L. Giles, and A. M. Ormord. 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. Oecologia 117: 279–285.
- Ogushi, T. 1996. Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle. Ecol. Entomol. 21: 47–55.
- Okamoto, H. 1978. Laboratory studies on food ecology of aphidophagous lady beetles (Coleoptera: Coccinellidae). Mem. Fac. Agric. Kagawa Univ. 29: 1–94.
- Omkar, and R. B. Bind. 1998. Prey preference of a ladybird beetle *Cheilomenes* (= *Menochilus*) *sexmaculata* (Fabr.). J. Aphidol. 12: 63–66.
- Rhahlingam, M. 1986. Seasonal variations in ovariole number/ovary in *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). Proc. Indian Nat. Sci. Acad. 52: 619–623.
- Richardson, J.M.L., and R. L. Baker. 1997. Effect of body size and feeding on fecundity in the damselfly *Ischnura verticalis* (Odonata: Coenagrionidae). Oikos 79: 477–483.
- Sakuratani, Y., Y. Sugiura, M. Ishida, S. Kuwahara, and T. Sugimoto. 1983. Aggregative response of adults of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) to aphid population density. Mem. Fac. Agric. Kinki Univ. 16: 49–54.
- Sinha, T. B., R. K. Pandey, R. Singh, C.P.M. Tripathi, and A. Kumar. 1982. The functional response of *Coccinella septempunctata* Linn., a coccinellid predator of mustard aphid, *Lipaphis erysimi* Kalt. Entomol. 7: 7–10.
- Smith, B. C. 1965. Effect of food on the longevity, fecundity and development of adult coccinellids. Can. Entomol. 97: 760–768.
- Sugiura, K., and H. Takada. 1998. Suitability of seven aphid species as prey of *Cheilomenes sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae). Jpn. J. Appl. Entomol. Zool. 42: 7–14.
- Sundby, R. A. 1966. A comparative study of the efficiency of three predatory insects, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), *Chrysopa carnea* St. (Neuroptera: Chrysopidae) and *Syrphus ribesii* L. (Diptera: Syrphidae) at two different temperatures. Entomophaga 11: 395–404.
- Tao, C. C., and S. C. Chiu. 1971. Biological control of citrus, vegetables and tobacco aphids. Sp. Publ. Taiwan Agric. Res. Inst. 10: 1–110.
- Taylor, R. J. 1984. Predation. Chapman and Hall, New York.
- Verma, S. N., V. P. Gargav, and S. Mittal. 1983. Host preference of six spotted ladybird beetle, *Menochilus sexmaculatus* (Fabr.). Indian J. Plant Prot. 11: 66–69.
- Yasuda, H. and H. Ishikawa. 1999. Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle. J. Appl. Entomol. 123: 585–589.
- Zheng, Y., K. M. Danne, K. S. Hagen, and T. E. Mittler. 1993a. Influence of larval dietary supply on the fecundity of the lacewing *Chrysoperla carnea*. Entomol. Exp. Appl. 67: 9–14.
- Zheng, Y., K. S. Hagen, K. M. Daane, and T. E. Mittler. 1993b. Influence of larval dietary supply on the food consumption, food utilization efficiency, growth and development of the lacewing *Chrysoperla carnea*. Entomol. Exp. Appl. 67: 1–7.
- Zhou, X., A. Honek, W. Powell, and N. Carter. 1995. Variations in body length, weight, fat content and survival in *Coccinella septempunctata* at different hibernation sites. Entomol. Exp. Appl. 75: 99–107.

Received for publication 6 December 2000; accepted 23 July 2001.