Reproductive performance of four aphidophagous ladybirds on cowpea aphid, *Aphis craccivora* Koch

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Abstract: This study investigated prey consumption, egg production, percent progeny loss, reproductive, pre- and post-reproductive periods, reproductive time ratio, reproductive rate and bioconversion efficiency of four aphidophagous ladybirds, viz. *Cheilomenes sexmaculata* (Fabricius), *Coccinella septempunctata* Linnaeus, *Coccinella transversalis* Fabricius and *Propylea dissecta* (Mulsant) on *Dolichos lablab* Linnaeus infested with cowpea aphid, *Aphis craccivora* Koch. *C. sexmaculata* had the highest bioconversion efficiency, reproductive rate and reproductive time ratio followed in rank order by *P. dissecta*, *C. transversalis* and *C. septempunctata*. This study indicates that *C. sexmaculata* has a narrow ecological relationship with *A. craccivora*. The increased allocation of resources to reproduction as indicated through a high reproductive time ratio and high bioconversion efficiency of *C. sexmaculata* and *P. dissecta* suggest that they may be better adapted to compete for this prey with larger species like *C. transversalis* and *C. septempunctata*.

Key words: *Aphis craccivora*, *Cheilomenes sexmaculata*, *Coccinella septempunctata*, *Coccinella transversalis*, *Propylea dissecta*, prey suitability, reproductive performance

1 Introduction

Ladybirds (Col., Coccinellidae) are predators of phytophagous pests, such as aphids, diaspids, coccids, adelgids, aleyrodids, pentatomids, thrips and acarids (Hodek and Honek, 1996; Dixon, 2000). These prey species are, however, not equally suitable for growth, development and reproduction of ladybirds, with suitability differing in relation to habitat, nutritional requirements of the predator and the biochemical contents of their prey (Hodek, 1956, 1962; Blackman, 1965, 1967; Kalushkov and Hodek, 2001, 2004; Omkar and Srivastava, 2003; Omkar and Bind, 2004; Omkar and James, 2004; Pervez and Omkar, 2004). Prey were classified on the basis of their relative suitability into: essential (allowing complete immature development and reproduction), alternative (source of energy for survival while not allowing development and reproduction), and rejected or toxic (Hodek, 1962; Hodek and Honek, 1996). However, this classification was recently challenged as being too restrictive and lacking consideration of the ecological background of the predator (Rana et al., 2002).

Extensive studies were carried out on prey suitability for several coccinellid species (Hodek, 1956; Blackman, 1965, 1967; Agarwala et al., 1988; Hazzard and Ferro, 1991; Rogers et al., 1994; Kalushkov and Hodek, 2001, 2004; Omkar and Srivastava, 2003; Omkar and Bind, 2004; Omkar and James, 2004; Pervez and Omkar, 2004). In the field, aphid populations are targeted not only by one ladybird species but a guild of natural enemies dominated by a top predator (Polis et al., 1989; Polis and Holt, 1992). Studies on the role and status of different predators in a guild are needed to improve our understanding of predator–prey dynamics. One approach is to design such studies using different predators in single predator–single prey systems and thereafter compare the reproductive performance of individual predators. High performance may be an important factor for choosing efficient biocontrol agents for the prey species.

The cowpea aphid, *Aphis craccivora* Koch is a serious pest of leguminous crop plants in Southeast Asia (Tao and Chiu, 1971; Agarwala et al., 1987; Waterhouse, 1998). It is known to inject a powerful toxin, which can stunt or kill a plant in case of heavy infestations and also cause growth of black sooty mould because of the copious amount of honeydew secreted (Summers et al., 2004). Economic threshold levels for this pest have not yet been calculated although its heavy infestations require treatments. Cultural methods involving strip or border cutting during harvest, chemical methods involving organically certified insecticides such as neem products and pyrethrins and biological methods are part of the integrated pest management techniques for this pest (Summers et al., 2004). The ubiquitous presence of a multitude of natural enemies, such as parasitoids, ladybeetles, lacewings, big-eyed bugs, damsel bugs and syrphids, make them especially potential components of management without much efforts and interference.

Numerous studies investigating the suitability of *A. Craccivora* to ladybirds in terms of growth, development, survival and reproduction have been conducted, with this prey being recognized as a rejected or toxic prey in the earlier studies (Takeda et al., 1964; Okamoto, 1966; Hukusima and Kamei, 1970; Obatake and Suzuki, 1985). However, recent studies have disproved this (Omkar and Srivastava, 2003; Omkar and Bind, 2004; Omkar and James, 2004; Pervez and Omkar, 2004). This apparent contradiction in the suitability of *A. craccivora* has been attributed to the influence of different host plants (Hodek and Honek, 1996), with recent reports recognizing *A. craccivora* from *Dolichos lablab* Linnaeus (bean) to be suitable prey. The aim of the current study was to examine the reproductive performance of four aphidophagous ladybirds [viz. *Cheilomenes sexmaculata* (Fabricius), *Coccinella septempunctata* Linnaeus, *Coccinella transversalis* Fabricius and *Propylea dissecta* (Mulsant)] common to the predatory guild of *A. craccivora* on *D. lablab*. This may help to identify the most suitable biological control agent for the management of *A. craccivora*.

2 Materials and Methods

2.1 Stock maintenance

Adults of *C. sexmaculata*, *C. septempunctata*, *C. transversalis* and *P. dissecta* were collected from agricultural fields adjoining Lucknow, India and for maintaining the laboratory stock. Five pairs of conspecific adults of each species were kept in beakers (11.0 × 5.5 cm) containing corrugated filter paper for oviposition and supplied with *ad libitum* *A. craccivora* (from *D. lablab*). The eggs were collected and reared from egg-hatch to adult emergence on the above-mentioned prey [25 ± 2°C, 65 ± 5% relative humidity (RH), 14 : 10 h L : D].

2.2 Experimental design

Pairs, one male and one female, of newly emerged adults of each ladybird species were maintained separately in Petri dishes (9.0 × 1.5 cm) and fed 200 mg (approximately 400 individuals) of *A. craccivora* daily until the death of the female beetle. The weight of unconsumed aphids, duration of pre-oviposition, oviposition and post-oviposition periods, daily oviposition, weight of eggs laid, and number of eggs hatched were recorded every 24 h. Weights were measured using an electronic balance with 0.1 mg precision (SARTORIUS-H51, Westbury, New York, USA). The experiment was replicated 10 times ($n = 10$).

The number of eggs produced throughout a female's lifetime (fecundity), percent progeny loss (number of unviable eggs × 100/fecundity), pre-reproductive, reproductive (oviposition period), and post-reproductive periods, reproductive rate (fecundity/duration of oviposition period), reproductive time ratio (ratio of female reproductive to non-reproductive periods), predatory efficiency (number of prey consumed in a lifetime) and bioconversion efficiency (weight of eggs × 100/weight of prey consumed) were calculated. The data on percent progeny loss was transformed using arcsine square-root transformation prior to further analysis. All data were subjected to one-way anova and *post hoc* Tukey's test of significance was used for comparison of mean values using MINITAB-10.2 statistical software (Minitab Inc. 1994 Philadelphia, PA).

***Table 1.** Reproductive performance of four ladybirds on the bean aphid,* Aphis craccivora

Ladybird species	Prey consumption	Egg production (total no. of eggs)	Progeny loss (%)	Pre-reproductive period (days)	Reproductive period (days)	Post-reproductive period (days)	Reproductive time ratio	Reproductive rate (eggs per female per day of oviposition)	Bioconversion efficiency
P. dissecta	1760.40 ± 16.55 a	941.80 ± 24.99 a	5.52 ± 0.81 a	8.40 ± 1.08	45.20 ± 0.77 a	2.10 ± 1.10	4.62 ± 0.34 c	20.85 ± 0.48 b	17.45 ± 0.88 c
C. sexmaculata	2801.50 ± 18.25 b	1998.20 ± 145.87 c	9.82 ± 0.83 b	6.50 ± 0.85	67.60 ± 1.62 d	5.90 ± 1.52	5.58 ± 0.35 d	29.42 ± 1.73 c	27.12 ± 1.97 d
C. transversalis	4494.00 ± 148.18 c	914.80 ± 21.61 a	4.80 ± 0.71 a	10.30 ± 0.95	58.40 ± 1.71 c	11.70 ± 2.75	2.68 ± 0.10 b	15.78 ± 0.57 a	7.80 ± 0.27 a
C. septempunctata	4541.70 ± 116.33 c	1060.70 ± 25.86 a	25.27 ± 0.73 c	14.90 ± 1.73	50.70 ± 1.07 b	12.80 ± 2.78	1.87 ± 0.10 a	20.99 ± 0.60 b	9.87 ± 0.36 b
F-value	204.87	46.37	87.75	89.96	52.06	53.73	35.67	32.96	62.72

Values are mean ± SE.
Values followed by different letters indicate significant differences at $P < 0.001$.
Percent progeny loss = number of unviable eggs × 100/fecundity; reproductive rate = fecundity/duration of oviposition period; reproductive time ratio = ratio of adult female reproductive/non-reproductive periods.

3 Results

The egg production of *C. sexmaculata* was significantly higher than that of the other three ladybird species ($F_{3,36} = 46.37$; $P < 0.001$; table 1). Comparison of mean values revealed insignificant differences between the mean egg production of *P. dissecta*, *C. septempunctata* and *C. transversalis*. Percent progeny loss was greatest for *C. septempunctata* and least for *C. transversalis* ($F_{3,36} = 87.75$; $P < 0.001$; table 1). The pre-reproductive ($F_{3,36} = 89.96$; $P < 0.001$), reproductive ($F_{3,36} = 52.06$; $P < 0.001$) and post-reproductive ($F_{3,36} = 53.73$; $P < 0.001$) periods differed significantly between ladybird species. *C. sexmaculata* had maximum reproductive period while *C. septempunctata* had the longest non-reproductive period. The reproductive time ratio differed significantly ($F_{3,36} = 35.67$; $P < 0.001$) and was highest for *C. sexmaculata* followed by *P. dissecta*, *C. transversalis* and *C. septempunctata*. The reproductive rate was highest for *C. sexmaculata* and lowest for *C. septempunctata* ($F_{3,36} = 32.96$; $P < 0.001$). *C. septempunctata* and *C. transversalis* had a higher prey consumption ($F_{3,36} = 204.87$; $P < 0.001$), but lower bioconversion efficiency than *C. sexmaculata* ($F_{3,36} = 62.72$; $P < 0.001$) (table 1).

4 Discussion

Cheilomenes sexmaculata showed exceptionally high reproductive performance on *A. craccivora* in terms of egg production, reproductive period, reproductive rate, reproductive-time ratio and bioconversion efficiency, with the other three species lagging behind significantly. This suggests that although all four ladybird species co-exist as predators of *A. craccivora*, there is a high probability that *C. sexmaculata* dominates the guild. Female *C. sexmaculata* in the presence of *C. transversalis* oviposited as well as consumed less prey; however, the reverse study was not conducted (Agarwala et al., 2003). Detailed studies on intraguild predation between the experimental ladybird complex have however not yet been dealt with in detail. A recent study on prey suitability of *C. sexmaculata* using seven prey species revealed *A. craccivora* to be the most suitable prey in terms of immature survival, development and adult reproduction (Sugiura and Takada, 1998; Omkar and Bind, 2004), further supporting the existence of a strong ecological relationship between *C. sexmaculata* and *A. craccivora*. Although no formal studies exist on the field distribution of ladybird species in *A. craccivora* fields in the Indian subcontinent, general self-observations of field indicate high incidence of *C. sexmaculata*, further supporting the results of this study.

Propylea dissecta had a higher bioconversion efficiency, reproductive rate and reproductive time ratio than the two *Coccinella* species, however, the egg production of the three species was similar. Despite the larger size of the *Coccinella* species, their egg production was relatively lower than *C. sexmaculata*. It is generally assumed that species with greater size should be more fecund as bigger egg batches are expected (Stewart et al., 1991; Dixon and Guo, 1993). The relatively poor performance of *Coccinella* spp. may have resulted from comparatively lower suitability of the constituents of *A. craccivora* to the physiology of *Coccinella* spp. (Omkar and Srivastava, 2003; Omkar and James, 2004). The chemical components of aphids probably reduce oogenesis or prevent complete vitellogenesis, thus leading to reduced reproductive output (Iperti, 1966). The high bioconversion efficiency of *C. sexmaculata* and *P. dissecta* provides a probable competitive advantage to these species.

Aphis craccivora from numerous host plants has been considered less than suitable prey for ladybirds (Okamoto, 1966; Hukusima and Kamei, 1970; Obatake and Suzuki, 1985). The lower placement of *A. craccivora* in the suitability list of *C. septempunctata* (Omkar and Srivastava, 2003) could perhaps explain its poor performance in the present study, which is despite its previously reported higher preference for the aphid in terms of consumption (Omkar et al., 1997). However, the reason for the poor performance of *C. transversalis* is not clear and needs to be further investigated.

An interesting aspect of the study was the reproductive-time ratio signifying the compartmentalization of life history and the allocation of resources to various phases of life, in the present case, reproductive and non-reproductive periods. A major proportion of life was allocated for reproduction in *C. sexmaculata* and *P. dissecta* and less so in *C. transversalis* with the lowest allocation in *C. septempunctata*. The higher resource allocation to the reproductive phase in *C. sexmaculata* and *P. dissecta*, which are smaller in size, perhaps also points towards a better survival strategy. It is also possible that these smaller species may be investing more in reproduction to compete with the larger ones having a better predation efficiency (Calow and Townsend, 1981; Crowl and Covich, 1990; Wissinger, 1992).

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References

Agarwala, B. K.; Das, S.; Bhaumik, A. K., 1987: Natural food range and feeding habits of aphidophagous insects in north east India. J. Aphidol. **1,** 18–22.

Agarwala, B. K.; Das, S.; Choudhuri, M. S., 1988: Biology and food relations of *Micraspis discolor* (F.): an aphidophagous coccinellid of India. J. Aphidol. **2,** 7–17.

Agarwala, B. K.; Bardhanroy, P.; Yasuda, H.; Takizawa, T., 2003: Effects of conspecific and heterospecific competitors on feeding and oviposition of a predatory ladybird: a laboratory study. Entomol. Exp. Appl. **106,** 219–226.

Blackman, R. L., 1965: Studies on specificity in Coccinellidae. Ann. Appl. Biol. **56,** 336–338.

Blackman, R. L., 1967: The effects of different aphid foods on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. Ann. Appl. Biol. **59,** 207–219.

Calow, P.; Townsend, C. R., 1981: Resource utilization and growth. In: Physiological Ecology. Ed. by Townsend, C. R.; Calow, P. Sunderland, MA: Sinauer Associates; 220–244.

Crowl, T. A.; Covich, A. P., 1990: Predator-induced life-history shifts in a fresh water snail. Science **247,** 949–951.

Dixon, A. F. G., 2000: Insect Predator–Prey Dynamics, Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge, UK.

Dixon, A. F. G.; Guo, Y., 1993: Egg and cluster size in ladybird beetles (Coleoptera: Coccinellidae): The direct and indirect effects of aphid abundance. Eur. J. Entomol. **90,** 457–463.

Hazzard, R. V.; Ferro, D. N., 1991: Feeding responses of adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of Colarado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphidiidae). Environ. Entomol. **20,** 644–651.

Hodek, I., 1956: The influence of *Aphis sambuci* L. as prey of the ladybird beetle *Coccinella septempunctata* L. Vest. Cs. Spol. Zool. **20,** 62–74.

Hodek, I., 1962: Essential and alternative food in insects 11. International Congress Entomol. Vienna 1960 **2,** 696–697.

Hodek, I.; Honek, A., 1996: Ecology of Coccinellidae. Dordrecht Boston London: Kluwer Academic Publishers.

Hukusima, S.; Kamei, M., 1970: Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Res. Bull. Fac. Agric. Gifu Univ. **29,** 53–66.

Iperti, G., 1966: Comportement naturel des Coccinelles aphidiphages du Sud-Est de la France. Leur type de specificite, leur action predatrice sur *Aphis fabae* L. Entomophaga **11,** 203–210.

Kalushkov, P.; Hodek, I., 2001: New essential aphid prey for *Anatis ocellata* and *Calvia quatuordecimguttata* (Coleoptera: Coccinellidae). Biocont. Sci. Technol. **11,** 35–39.

Kalushkov, P.; Hodek, I., 2004: The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. BioControl **49,** 21–32.

Obatake, H.; Suzuki, H., 1985: On the isolation and identification of canavanine and ethanolamine contained in the young leaves of black locus, *Robinia pseudoaccacia*, lethal for the ladybeetle, *Harmonia axyridis*. Tech. Bull. Fac. Agric. Kagawa Univ. **36,** 107–115.

Okamoto, H., 1966: Three problems of prey specificity of aphidophagous coccinellids. In: Ecology of Aphidophagous Insects. Ed. by Hodek, I. Prague: Academia; The Hague: Dr W. Junk; 45–46.

Omkar; Bind, R. B., 2004: Prey quality dependent growth, development and reproduction of a biocontrol agent, *Cheilomenes sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). Biocont. Sci. Tech. **14,** 665–673.

Omkar; James, B. E., 2004: Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae). J. Appl. Ent. **128,** 150–157.

Omkar; Srivastava, S., 2003: Influence of six aphid prey species on development and reproduction of a ladybird beetle, C*occinella septempunctata*. BioControl **48,** 379–393.

Omkar; Srivastava, S.; James, B. E., 1997: Prey preference of a lady beetle, *Coccinella septempunctata* Linnaeus (Coleoptera : Coccinellidae). J. Adv. Zool. **18,** 96–97.

Pervez, A.; Omkar, 2004: Prey dependent life attributes of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant). Biocont. Sci. Tech. **14,** 385–396.

Polis, G. A.; Holt, R. D., 1992: Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol. **7,** 151–154.

Polis, G. A.; Myers, C. A.; Holt, R. D., 1989: The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. Syst. **20,** 297–330.

Rana, J. S.; Dixon, A. F. G.; Jarosik, V., 2002: Costs and benefits of prey specialization in a generalist insect predator. J. Anim. Ecol. **71,** 15–22.

Rogers, C. E.; Jackson, H. B.; Eikenbary, R. D., 1994: Responses of an imported coccinellid, *Propylea 14-punctata* to aphids associated with small grains in Oklahoma. Environ. Entomol. **1,** 198–202.

Stewart, L. A.; Hemptinne, J.-L.; Dixon, A. F. G., 1991: Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. Funct. Ecol. **5,** 380–385.

Sugiura, K.; Takada, H., 1998: Suitability of seven aphid species as prey of *Cheilomenes sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). Japan J. Appl. Ent. Zool. **42,** 7–14.

Summers, C. G.; Godfrey, L. D.; Rethwisch, M.; Haviland, D. R., 2004: *UC IPM Pest Management Guidelines: Alfalfa*. UC ANR Publication 3430, Insects and Mites. http://www.agrifor.ac.uk/browse/cabi/2d4766799c57b502e512fbfca0fa4a28.html.

Takeda, S.; Hukusima, S.; Yamada, H., 1964: Seasonal abundance in coccinellid beetles. Res. Bull. Fac. Agric. Sci. Gifu Univ. **19,** 55–63.

Tao, C. C.; Chiu, S. C., 1971. Biological control of citrus, vegetables and tobacco aphids. Spec. Publ. Taiwan Agric Res. Inst **10,** 1–10.

Waterhouse, D. F., 1998: Biological Control of Insect Pests: Southeast Asia Prospects. Canberra: Australian Centre for International Agricultural Research.

Wissinger, S. A., 1992: Niche overlap and the potential for competition and intraguild predation between size-structured populations. Ecology **73,** 1431–1444.

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