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Intrinsic advantages of *Cheilomenes sexmaculata* over two coexisting *Coccinella* species (Coleoptera: Coccinellidae)

OMKAR, AHMAD PERVEZ, GEETANJALI MISHRA, SHEFALI SRIVASTAVA, SATYENDRA K. SINGH and AVANISH K. GUPTA

Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, India

Abstract Development, survival and reproductive performance of coexisting ladybird species, *viz. Cheilomenes sexmaculata*, *Coccinella septempunctata*, and *Coccinella transversalis*, of the tribe Coccinellini were studied and compared to assess their coexistence and ecological relationships. High values of life history parameters, *viz*. developmental rate, immature survival, fecundity, egg viability, reproductive rate and conversion of efficiency of ingested food were recorded for *C. sexmaculata* followed by *C. transversalis* and *C. septempunctata* suggesting that the former has intrinsic advantages over the latter two species. This could possibly counterbalance its disadvantages, like relatively smaller size and weight, thereby making it competitive. The developmental period increased with increase in body size. Exceptionally high fecundity after single mating has been recorded in *C. sexmaculata*. The egg viability, however, was lower than in both *Coccinella* species.

Key words *Cheilomenes sexmaculata*, *Coccinella septempunctata*, *Coccinella transversalis*, size, reproductive rate, bioconversion efficiency
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Introduction

Ladybirds (Coleoptera: Coccinellidae) vary in size both within and between the species and between sexes within a species. Normally, two or more ladybird species of varying sizes and body weights coexist. However, the species will compete strongly for prey resource under limited food conditions. It is likely that the larger size predatory stages between and within species will dominate over the smaller ones (Yasuda *et al*., 2001). Seemingly, larger related species are more competent (van Buskirk & Yurewicz, 1998), less vulnerable (Crowl & Covich, 1990; Wissinger, 1992), and have greater longevity (Bradshaw & Holzapfel, 1992; Neems *et al*., 1998) and survivorship (Calow & Townsend, 1981). However, if the smaller species are able to coexist while competing with the bigger ones, it is likely that they possess some intrinsic advantages.

The size variation between species is dependent on the ecological niche, including food and habitat, besides genotypes. The smaller ladybird species, such as *Stethorus* and *Scymnus*, are predominantly mite feeders, while a high proportion of very large species prey on chrysomelids and lepidopterous larvae (Dixon, 2000). The coccidophagous species are relatively smaller in size than aphidophagous ones (Dixon, 2000). The small size of coccidophagous ladybirds might be an evolutionary consequence as they feed on scales and mealy bugs, which are almost immobile (Dixon & Stewart, 1991). This suggests that body size could have direct associations or trade-offs with life attributes and performance and a direct effect on the evolution and adaptation of species. Thus, if life attributes and performance of some closely related species are compared, associations and trade-offs between life attributes and body size of species can be expected. This could enhance our understanding of the impact of body size on perfor-

Correspondence: Omkar, Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow - 226007, India. Tel: +91 0522 2740382; e-mail: omkaar55@hotmail.com

mance of closely related ladybird species.

Cheilomenes sexmaculata (Fabricius) is a common ladybird of Oriental region and known to have a prey range of 57 aphid species (Agarwala & Yasuda, 2000). It has a wide range of essential prey, which is prey that can support both development and adult survival, with best performance on aphid, *Aphis craccivora* Koch (Omkar & Bind, 2004). It is of global importance and was introduced in North America for the biocontrol of cereal aphid, *Schizaphis graminum* (Rondani) (Cartwright *et al*., 1977). In North India, it coexists with other aphidophaga, including *Coccinella transversalis* Fabricius and *Coccinella septempunctata* Linnaeus, which are also generalist predators with a wide prey range (Omkar & Pervez, 2004; Srivastava & Omkar, 2003). Recently, comparative reproductive behavior of *C. sexmaculata* and *C. transversalis* was studied (Omkar, 2004). All the three ladybirds belong to the tribe Coccinellini and possess great potential for their utilization as biocontrol agents of aphid pests. However, smaller in size, *C. sexmaculata* is a major component of Indian coccinellid fauna, which suggests that it may possess certain intrinsic advantages. The experiments were thus designed to compare certain life-attributes of these ladybird species and to check the validity of the above assumption.

Materials and methods

Stock maintenance

Adults of *C. sexmaculata*, *C. transversalis* and *C. septempunctata* were collected from local agricultural fields adjoining Lucknow, India and brought to the laboratory. For the stock, groups of five pairs of conspecific adults were kept in the beakers containing corrugated filter paper on *ad libitum* supply of their suitable prey diet, that is *Lipaphis erysimi* (Kaltenbach), *A. craccivora* and *Aphis gossypii* (Glover) for *C. septempunctata*, *C. sexmaculata* and *C. transversalis*, respectively, as determined previously in the laboratory (Omkar & Srivastava, 2003; Omkar & James, 2004; Omkar & Bind, 2004). The eggs obtained from the ladybirds were collected on filter papers and reared from egg-hatch to adult emergence on ad libitum supply of suitable prey at laboratory conditions of 25 ± 2℃ temperature, 65% ± 5% RH, 14:10 (L:D) photoperiod.

Body length, body weight and walking speed

The body length and body weight of adult females of the above three ladybird species were measured. The body length of 5-day-old adult females were measured by placing the female on a point on the graph paper, holding it firmly but gently and allowing it to extend naturally; the distance between the tip of the head and the abdomen was measured (n = 10). To determine body weight, the adult females were weighed (0.1 mg precision) separately in ten replicates (n = 10) using electronic balance (SARTORIUS-H51). To determine walking speed, the same 5-day-old female of each ladybird species was placed on a 100 cm long glass rod and the distance travelled by each in a minute was recorded (n = 10).

Pre-adult development and survival

One hundred eggs of each ladybird species were taken from the stock and the hatched larvae reared singly from egg-hatch till adult emergence on their respective suitable prey in muslin covered glass beakers (6.5 × 9.5 cm). The incubation period, first, second, third and fourth larval period, pre-pupal and pupal periods along with number of life stages surviving were recorded. The percent survival (number of pupae × 100/number of first instars hatched) and adult emergence (number of adults emerged × 100/ number of pupae) were calculated. The experiment was replicated ten times with 100 eggs per replicate resulting in 1 000 eggs per species. The body size in terms of length and weight was fitted against the developmental rate (1/developmental period, i.e. the period in days from oviposition to adult emergence) using linear regression analysis. The data were subjected to one-way ANOVA followed by post hoc Tukey's test of significance using statistical software MINITAB (2000) on a personal computer.

Performance of ladybirds in response to single mating

A sexually mature 10-day-old female was allowed to mate once with a sexually mature 10-day-old male in a Petri dish (1.5 × 9.0 cm). After the termination of mating, the female was isolated and reared in a Petri dish on *ad libitum* supply of suitable aphids till her death. The pre-oviposition, oviposition and post-oviposition periods, fecundity, egg viability and mean reproductive rate were recorded. The fecundity and egg viability were subjected to non-linear regression analysis to determine the relationship using MINITAB (2000) on a personal computer.

Reproductive response of ladybirds in response to lifetime mating

Four hundred respective aphids were provided daily per adult female of all three ladybird species for lifetime, and the number of aphid consumed were recorded. These females were allowed to mate daily and oviposition was recorded. Aphids and eggs were weighed separately using an electronic balance (SARTORIUS-H51) and the wet weight of prey biomass consumed (number of aphids consumed during lifetime × weight of single aphid) and wet weight of egg biomass produced (number of eggs laid in lifetime × weight of a single egg) were calculated. The efficiency of conversion of ingested food (ECI) into egg biomass was calculated [egg biomass laid (in mg) × 100/ prey biomass consumed (in mg)]. Reproductive attributes, *viz*. pre-oviposition, oviposition and post-oviposition periods, fecundity, percent egg viability, and mean reproductive rate were also recorded. The experiment was replicated ten times (n = 10). The data pertaining to pre-oviposition, oviposition and post-oviposition periods, fecundity, percent egg viability and mean reproductive rate were subjected to one-way ANOVA. The post hoc Tukey's test of significance was done to compare the mean values using statistical software MINITAB (2000) on personal computer.

Results

Body length, body weight and walking speed

Cheilomenes sexmaculata was the smallest and the lightest among the three ladybird species, followed by *C. transversalis* and *C. septempunctata* (Table 1). The size of all three ladybirds varied significantly in terms of body length (F = 22.04; df = 2, 27; P < 0.001) and body weight (F = 2748; df = 2, 27; P < 0.001). *C. transversalis* walked the fastest followed by *C. sexmaculata* and *C. septempunctata* (F = 5.32; df = 2, 27; P < 0.05; Table 1).

Pre-adult development and survival

The pre-imaginal stages of *C. sexmaculata* developed fastest followed by *C. transversalis* and *C. septempunctata* (Table 1). However, the developmental period (F = 9.36; df = 2, 27; P < 0.001) was shortest and the percent survival highest (F = 295.3; df = 2, 27; P < 0.001) in *C. sexmaculata*. The developmental rate decreased linearly with increaseing in body size in terms of body length ($y = -0.0038x + 0.1035$; r^2 = 0.3077) and body weight ($y = -0.0004x + 0.0889$; r^2 = 0.3306) of the three ladybird species (Figs. 1, 2).

Reproductive response of ladybirds in response to single mating

Coccinella sexmaculata laid the maximum number of eggs, while *C. septempunctata* the least after being subjected to single mating (Table 2). The oviposition period

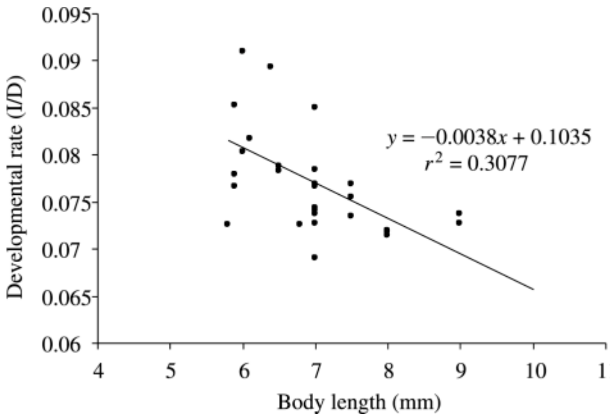

Fig. 1 Relationship between size (in length) and developmental rate for three ladybird species.

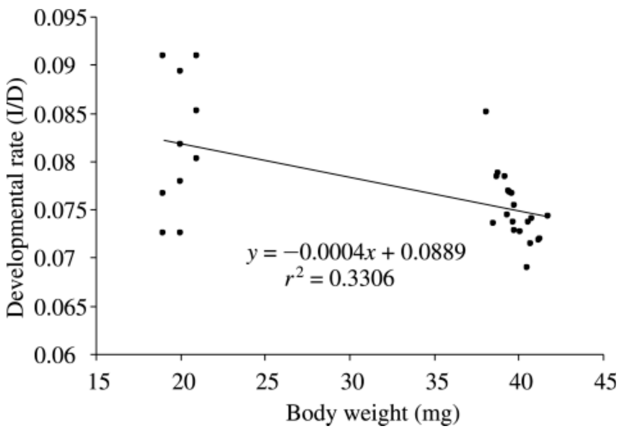

Fig. 2 Relationship between size (in weight) and developmental rate for three ladybird species.

Table 1 Body length, body weight, walking speed development time and survival of three ladybird species.

Species	Body length (mm)	Body weight (mg)	Walking speed (cm/min)	Development period (days)	Survival (%)
C. sexmaculata	6.08 ± 0.30 a	20.00 ± 0.82 a	177.55 ± 20.57 b	12.31 ± 1.06 a	85.00 ± 7.07 a
C. transversalis	7.05 ± 0.37 b	39.12 ± 0.56 b	181.15 ± 27.56 b	13.01 ± 0.57 ab	24.00 ± 6.99 c
C. septempunctata	7.70 ± 0.82 c	40.63 ± 0.70 c	148.95 ± 23.85 ab	13.73 ± 0.39 bc	73.48 ± 2.80 b
F-value	22.04**	2748**	5.32*	9.36**	295.3**

Values are mean ± SD; *P < 0.05; ** P < 0.001; different letters in the column denote the data to be statistically significant (Tukey's test: mean = 3.51; df = 2, 27; n = 10).

was longest in *C. sexmaculata* and shortest in *C. transversalis*. Despite the long oviposition period in *C. sexmaculata*, it had the highest reproductive rate. The percent egg viability, however, was highest in *C. transversalis* and lowest in *C. sexmaculata*. The calculated values of reproductive rate reveal *C. sexmaculata* to be the best in performance. The fecundity has a negative relationship with egg viability ($y = -0.0159x + 100.85$; $r^2 = 0.7255$; $P < 0.001$; Fig. 3) in three ladybird species.

Performance of ladybirds in response to lifetime mating

Coccinella sexmaculata performed the best in terms of high values of reproductive performance after being subjected to lifetime mating (Table 3). It started egg-laying just after 3.70 days post-emergence, which is significantly earlier than the two *Coccinella* species ($F = 51.14$; df = 2, 27; $P < 0.001$;). The fecundity ($F = 4.43$; df = 2, 27; $P < 0.001$), reproductive rate ($F = 15.64$; df = 2, 27; $P < 0.001$) and efficiency of conversion of ingested food ($F = 28.28$; df = 2, 27; $P < 0.001$) was significantly higher than the both *Coccinella* species (Table 3). *C. sexmaculata* was most efficient in converting the prey biomass into egg biomass, followed by *C. septempunctata* and *C. transversalis*.

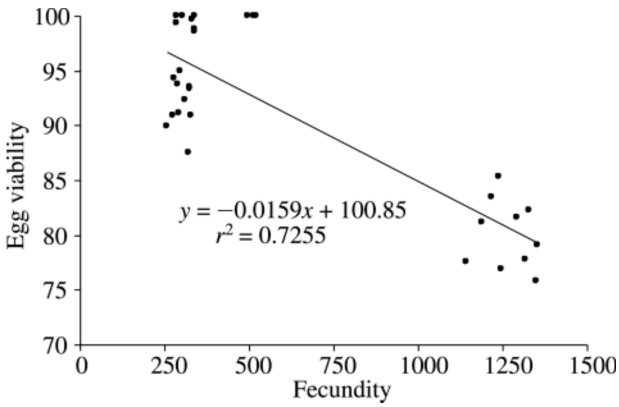

Fig. 3 Relationship between fecundity and egg viability when ladybirds were subjected to single mating.

Table 2 Reproductive attributes of three ladybird species after single mating.

Species	Oviposition period (days)	Fecundity	Egg viability (%)	Reproductive rate (eggs/day)
C. sexmaculata	53.30 ± 3.86 a	1267.60 ± 71.90 a	80.10 ± 3.15 a	23.87 ± 2.03 a
C. transversalis	16.50 ± 2.17 c	375.50 ± 94.80 b	99.64 ± 0.56 c	22.72 ± 4.81 a
C. septempunctata	22.30 ± 2.63 b	297.70 ± 23.60 c	91.92 ± 2.28 b	13.48 ± 1.70 b
F-value	442.81*	591.62*	188.28*	32.37*

Values are mean ± SD; *$P < 0.001$; different letters in the column denote the data to be statistically significant (Tukey's test: mean = 3.51; df = 2, 27; n =10).

Table 3 Reproductive attributes of three ladybird species after lifetime mating.

Species	Pre-oviposition period (days)	Oviposition period (days)	Fecundity	Egg viability (%)	Reproductive rate	Efficiency of conversion of ingested food
C. sexmaculata	3.70 ± 1.41 a	61.90 ± 18.60 ab	1898.20 ± 649.20 a	90.02 ± 2.68 b	31.83 ± 7.00 a	12.90 ± 4.40 a
C. transversalis	9.70 ± 1.06 c	67.80 ± 4.52 ab	1399.60 ± 74.60 b	96.39 ± 0.97 a	20.71 ± 1.60 c	4.92 ± 0.27 b
C. septempunctata	8.40 ± 1.64 b	69.80 ± 4.18 ab	1764.10 ± 153.24 ab	87.88 ± 3.32 c	25.37 ± 2.82 b	6.03 ± 0.59 b
F-value	51.14**	1.32	4.43*	30.34**	15.64**	28.28**

Values are mean ± SD; *$P < 0.05$; *$P < 0.001$; different letters in the column denote the data to be statistically significant (Tukey's test: mean = 3.51; df = 2, 27; n = 10).

Discussion

The significantly high values for life history parameters, such as developmental rate, immature survival, reproductive rate, conversion of efficiency of ingested food and so on, for *C. sexmaculata* suggest that this ladybird possesses certain intrinsic advantages. This explains its coexistence with the bigger *Coccinella* species sharing a common prey resource. Despite being smaller in size, *C. sexmaculata* is a major component of coccinellid fauna of the Oriental region and available almost throughout the year both in the presence or absence of prey (Bind, 1998). Its regular occurrence in varied prey habitats (Agarwala & Yasuda, 2000; Omkar & Pervez, 2004) further corroborates our finding that it is benefited intrinsically. This possibly counterbalances its disadvantages, like relatively lower size and weight, compared to other coexisting ladybird species, thereby allowing a competitive coexistence with bigger species in nature. Similarly, it was supposed that the invasive establishment of aphidophagous ladybird, *Harmonia axyridis* (Pallas) in the US and Europe might be due to certain intrinsic advantages (Michaud, 2002). However, laboratory studies denied such advantages for *H. axyridis* after comparing its life attributes with two other coexisting ladybirds (Lanzoni *et al*., 2004).

The developmental rate of three ladybird species tested has a negative correlation with body size. *C. sexmaculata* developed faster than the bigger *Coccinella* species possibly indicating a trade-off between developmental rate and body size. This supports evolutionary theory predicting decreased biological rates including development with increase in body mass (Lindstedt & Calder, 1981; Gillooly *et al*., 2002). However, bigger individuals within a species could develop faster than the smaller ones (Dixon, 2000). Delayed development has a cost in terms of vulnerability of immature life stages to natural enemies (Brooks & Dodson, 1965; Allan, 1978; Lynch, 1980; Reznick, 1982; Wellborn, 1994). The developmental rate of immature stages seems to be the apt result of a trade-off between maximizing body size in direct relation to the parents' initial investment and completing development faster to avoid predation (Werner & Anholt, 1993; Abrams *et al*., 1996).

Immature survival of *C. sexmaculata* was higher than the other two species. It is likely that the hairs and tuft on the body of its larvae give a horny armature, which may possibly reduce their vulnerability against natural enemies and unsuitable abiotic conditions. Decreased immature survival of *C. transversalis* might possibly be due to the presence of male-killing bacteria (Majerus & Hurst, 1997; Hurst *et al*., 1999).

Females of bigger species normally lay bigger egg batches than the smaller ones (Omkar *et al*., unpublished data) as the egg batch size is positively correlated to the body size (Dixon & Guo, 1993). Owing to the larger size of egg batches, it was expected that bigger *Coccinella* species would be more fecund. However, it was not the case in the present study, possibly due to the shorter inter-oviposition period of *C. sexmaculata* enabling it to reproduce faster, thereby overcoming its disadvantage of laying relatively smaller egg batches (Omkar *et al*., unpublished data). This was supplemented by its higher efficiency of conversion of ingested food, tending it to convert its prey biomass maximally into its progeny. This significantly higher bio-conversion efficiency might be of adaptive significance to the constraints of its small size and may possibly make it more competitive with larger ladybird species in field conditions.

Single mating resulted in exceptionally high fecundity in *C. sexmaculata*. Its egg viability was, however, significantly lower than those of bigger ones. We found a trade-off between egg viability and fecundity after single mating, which indicates maternal investments are more than the paternal ones. It is hypothesized that the sperm from single mating are not sufficient to fertilize all ova. It has been noticed that some of the later egg batches of *C. sexmaculata* were unviable, indicating a probable sperm deficiency (Omkar *et al*., unpublished data). Furthermore, in bigger species, fecundity decreased significantly, which indicates that there were fewer ova and consequently lesser amount of sperm was required for fertilization. This could be a probable explanation for high egg viability in bigger species of ladybirds. However, this needs to be further investigated by making anatomical studies of gonads in ladybirds. The comparatively low percent egg viability in *C. sexmaculata* warrants the need for more mating stimulus for high progeny output. Similar decrease in egg viability was also observed in the ladybird, *Propylea dissecta* (Mulsant) (Pervez *et al*., 2004).

Thus, it may be concluded that: (i) *C. sexmaculata* had better performance than two relatively bigger *Coccinella* species; (ii) developmental rate has a trade-off with size and smaller species develop faster supporting the evolutionary theory of biological rates; (iii) there is a trade-off between fecundity and egg viability in relation to single mating, indicating greater maternal investments than paternal ones; and (iv) if smaller species coexists with bigger ones sharing a common prey resource, it is likely that it possesses certain intrinsic advantages to maintain its stable coexistence.

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