Bulletin of Insectology **62** *(1): 35-40, 2009*
ISSN 1721-8861

Crowding affects the life attributes of an aphidophagous ladybird beetle, *Propylea dissecta*

OMKAR, Shuchi PATHAK
Ladybird Research Laboratory, Department of Zoology, University of Lucknow, India

Abstract

The larvae of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant) (Coleoptera Coccinellidae), were reared singly as well as at different densities (4, 8, 16, 25 and 35) under controlled laboratory conditions (25 ± 2 °C, 65 ± 5% R.H. and 14L: 10D) on third instars of the aphid, *Aphis craccivora* Koch. Crowding affects larval development, survival of immature stages and adult size. However, rearing at a density of four larvae per beaker significantly shortened developmental duration, increased immature survival and percentage adult emergence in comparison with single and higher densities of larvae. This suggests that *P. dissecta* may be efficiently mass reared in the laboratory at a density of 4 larvae per beaker rather than other densities.

Key words: Ladybird beetle, *Propylea dissecta*, isolated rearing, group rearing.

Introduction

Increase in population density of insects leads to numerous physiological and morphological changes expressed in colouration, gross morphology and developmental rate (Uvarov, 1966). Most populations are affected in a density- dependent manner by both inter- and intraspecific competitions. Intraspecific competition affects the development of insects (Applebaum and Heifetz, 1999), usually because of variation in the quality and quantity of food available to larvae (Dethier, 1959; Putman, 1977; Melanie *et al.*, 2004).

Insects respond to crowding by rapid changes in their performance with lasting impacts. In polynesian tiger mosquito, *Aedes polynesiensis* Marks (Diptera Culicidae) (Mercer, 1999), autumnal moth, *Epirrita autymnota* (Borkhausen) (Lepidoptera Geometridae) (Tammaru *et al.*, 2000) and velvet bean caterpillar, *Anticarsia gemmatalis* Hubner (Lepidoptera Noctuidae) (Fescemyer and Erlandson, 1993), intraspecific competition, *i.e.* group rearing resulted in longer developmental periods. However, Australian aiolopus, *Aiolopus thalassinus* (F.) (Orthoptera Acrididae), migratory locust, *Locusta migratoria* (L.) (Orthoptera Acrididae) (Staal, 1961), cabbage moth, *Mamestra brassicae* (L.) (Lepidoptera Noctuidae) (Goulson and Cory, 1995), and African armyworm, *Spodoptera exempta* (Walker) (Lepidoptera Noctuidae) (Simmonds and Blaney, 1986) developed faster when reared at higher densities. The differential effects of crowding in grasshoppers differs in different species (Dingle and Haskell, 1967); with *Diabolocatantops axillaris* (Thunberg) (Orthoptera Acrididae) showing limited migration (Reynolds and Riley, 1988), while larvae of *Pyrgodera armata* Fischer de Waldheim (Orthoptera Acrididae) marched together in dense populations (Rubtzov, 1935). Slow rates of development are considered disadvantageous, as they limit the chance of survival by increasing window of exposure to natural enemies (Klok and Chown, 1999) and also decrease reproduction (Gotthard *et al.*, 1994; Fischer and Fiedler, 2000).

Studies also indicate that the effect of varying densities on rates of development differ within the life stages of a species as seen in speckled wood butterfly, *Pararge aegeria* (L.) (Lepidoptera Nymphalidae) where larval development increased with increasing density while pupal mass and size decreased (Gibbs *et al.*, 2004). In Pink stalk borer, *Sesamia nonagrioides* Lefèbvre (Lepidoptera Noctuidae) crowding during larval stages did not significantly increase mortality but resulted in prolonged larval development period with reduced pupal weight (Fantinou *et al.*, 2008).

In coccinellids, the presence of too many conspecifics in a limited space is also suggested to decrease growth and development rate, and adult weight (Hodek and Honek, 1996). However, effects of population density and intraspecific competition among coccinellids have been poorly studied, perhaps due to the obvious difficulties of cannibalism. To address this lacuna, the present study has been designed to study the effect of crowding (*i.e.* varying larval density) on larval development, immature survival and adult size in ladybird, *Propylea dissecta* (Mulsant). It is an aphidophagous ladybird of Oriental origin quite common in agricultural and horticultural landscapes and is highly specific for aphids, *viz. Aphis gossypii* Glover, *Aphis craccivora* Koch, *Brevicoryne brassicae* L., *Lipaphis erysimi* (Kaltenbach), *Myzus persicae* (Sulzer), *Rhopalosiphum maidis* (Fitch) and *Uroleucon compositae* (Theobald) (Pervez and Omkar, 2004; Omkar and Mishra, 2005). *P. dissecta* is a better model to investigate the life history attributes owing to marked sexual dimorphism (Omkar and Pervez, 2000), easy availability, higher reproducing ability, shorter life cycle and easy laboratory maintenance (Omkar and Mishra 2005). This study aims to add information to the knowledge on the effects of larval density during rearing on the life attributes; further the data may be helpful in the mass multiplication of a potential bioagent.

Materials and methods

Stock culture

Adults of *P. dissecta*, were collected from fields of bean aphid, *Dolichos lablab* (L.) infested with aphid *A.*

craccivora in areas surrounding Lucknow (26°55'N 80°59'E), were paired in separate Petri dishes (9 x 2 cm) under controlled laboratory conditions (25 ± 2 °C, 65 ± 5% RH and 14L: 10D) in growth chambers providing them with *ad libitum* third instars of *A. craccivora* collected from infestations in our maintained fields of *D. lablab*. Third instars of *A. craccivora* were selected to ensure intermediate size for maximum prey biomass utilization and consumption (Roger *et al*., 2000) and also to standardize the size of prey across all the rearing densities in terms of biomass. The eggs so obtained were collected and incubated under controlled conditions as mentioned above in order to get requisite life stages for use in experiments.

Experimental Protocol

Rearing conditions

(a) Single rearing:

A total of 100 neonates were selected from the above stock and kept singly in beakers (11 x 9 cm; height x diameter) forming 100 replicates. Two hundred aphids were provided every 24h throughout the experiment and the containers cleaned to maintain prey quality and to avoid microbial contamination. The time between moults and number of larvae surviving each moult were recorded every 24h. Pre- pupal and pupal duration along with the number of pupae formed were recorded. The total larval duration (from first instar to pre-pupae), total developmental period (duration from oviposition to adult emergence), percent immature survival [(pre-pupae ÷ eggs) x 100], percent pupation [(number of pupae ÷ total eggs) x 100], percent adult emergence (number of adults emerged ÷ number of pupae x 100) and growth index (1 ÷ total developmental period) were calculated. After emergence, adults were sexed and weighed. Prey and abiotic conditions were the same as in the stock culture.

(b) Group rearing:

For this purpose, the larvae with similar hatching time were grouped at densities of 4, 8, 16, 25 and 35 in plastic beakers with 5 replicates of each combination. The beakers were cleaned and changed every 24 h to prevent microbial contamination. Recordings and calculations done were similar to that of single rearing. Prey and abiotic conditions were maintained similar to the stock. Two hundred third instars were provided per day in each setup. Number of prey provided were kept constant across all the rearing conditions, *viz*. single and group rearing so as to simulate field conditions and to avoid dilution of crowding effect.

Statistical analysis

The data obtained were checked for normal distribution using Bartlett's test, and Levene's test for assumption of approximately equal variances before being subjected to One-way ANOVA using statistical software MINITAB (2003). Comparisons of means were done using *post hoc* Tukey's honest significance test at 5% levels. Total developmental period was also correlated with larval density and weight of adults.

Results

No significant difference was recorded in incubation period of eggs at varying densities. There was however significant effect of larval densities (1, 4, 8, 16, 25 and 35) during rearing on the durations of different immature stages, *viz.* first, second, third, and fourth instars, pre-pupae and pupae (table 1). Significant effect of larval density was also recorded on total larval period, total developmental period, percent adult emergence and weight of adults. Highest immature survival, i.e. minimum mortality was seen at both larval density of 4 and 8 per beaker. Significant effect of higher densities on cannibalism and larval mortality due to unknown factors was observed (table 2). Cannibalism was not found to play an important role in mortality up to the larval density of 8, thereafter at higher densities, an increase in percent cannibalism was seen (table 2). Mortality due to unknown factors was highest at larval density of 1 and 35. Highest percent adult emergence, growth index and heavier individuals were found at the density of 4 instars per beaker (tables 1 and 2). Negative correlation between total developmental period and increasing larval densities ($r = -0.512$; $P < 0.005$) and a positive correlation between weight and different larval densities ($r = 0.125$; $P < 0.05$) was observed.

Discussion

The results reveal that larval density during laboratory rearing affected the development, growth index, survival of immature stages and size (in terms of weight) of adults of *P. dissecta*. Larvae reared at the density of four per Petri dish showed faster development, higher developmental rate, growth index, and adult emergence and weight than those reared at the density of 1, 8, 16, 25 and 35 per beaker. Almost similar immature survival was seen at larval densities of 4 and 8, however, based on the other attributes, larval density of 4 seems to be the most suited for rearing of *P. dissecta.*

The poor performance at high larval density may be ascribed to (a) decreased food consumption owing to competition for common food source, (b) increased interference between larvae because of the limited space, leading to the involvement of larvae in prolonged aggressive encounters, ultimately causing heavy mortality, and (c) increased chances of infection due to close contact.

The negative effects of larval crowding due to probable increased competition of food have been observed in a number of insects, *viz*. Pierid butterfly, *Anthocharis scolymus* Butler and yellow meal worm, *Tenebrio molitor* L. which showed lower larval survival on the plants with higher larval density than those of lower density (Masumoto *et al*., 1993; Barnes and Siva-Jothy, 2000). Crowding also resulted in smaller adults because of the probable decreased foraging success (Evans, 1976; Wise, 1975; Evans, 1983).

The increased amounts of waste products (urea), as a result of crowding, have been implicated in the slower development and reduced survivorship of *Drosophila*

Table 1. Effect of different densities on developmental durations (in days) in an aphidophagous ladybird beetle, *P. dissecta* (means ± SE).

Density	IP	L1	L2	L3	L4	PP	P	TLP	TDP	Growth Index	Total weight
1	2.13 ± 0.02a	2.82 ± 0.02d	2.48 ± 0.31d	2.23 ± 0.52c	2.38 ± 0.47c	0.86 ± 0.18b	3.28 ± 0.57b	9.93 ± 1.23e	16.21 ± 1.8sc	0.07 ± 0.017a	7.96 ± 2.13b
4	2.11 ± 0.02a	1.01 ± 0.00a	1.01 ± 0.00a	1.02 ± 0.00a	1.37 ± 0.75a	1.03 ± 0.01b	3.38 ± 0.41b	4.42 ± 0.76a	10.94 ± 0.9sa	0.09 ± 0.007b	11.22 ± 1.51c
8	2.12 ± 0.04a	1.40 ± 0.16c	1.55 ± 0.05c	2.20 ± 0.08c	2.18 ± 0.16c	0.96 ± 0.07bc	3.60 ± 0.24b	7.34 ± 0.28d	13.27 ± 1.7sb	0.07 ± 0.013ab	8.43 ± 1.21b
16	2.10 ± 0.00a	1.25 ± 0.09b	1.50 ± 0.09c	1.87 ± 0.19b	2.18 ± 0.13c	0.94 ± 0.05bc	3.36 ± 0.24b	6.82 ± 0.19c	13.22 ± 0.4sb	0.08 ± 0.007ab	8.11 ± 1.84b
25	2.10± 0.00a	1.24 ± 0.09b	1.22 ± 0.09b	1.76 ± 0.08b	1.90 ± 0.08b	0.89 ± 0.02bc	3.21 ± 0.11b	6.66 ± 0.23c	12.87 ± 0.2sb	0.08 ± 0.005ab	6.21 ± 1.29a
35	2.10± 0.00a	1.20 ± 0.08b	1.22 ± 0.04b	1.77 ± 0.17b	1.55 ± 0.19ab	0.61 ± 0.05a	2.20 ± 0.21a	5.75 ± 0.34b	10.67 ± 0.50a	0.08 ± 0.005c	5.34 ± 1.68a
F-values	1.93 NS	261.7**	67.45**	16.28**	5.31*	13.25**	10.68**	42.08**	15.31**	8.12**	7.66**

IP incubation period; L1 first instar; L2 second instar; L3 third instar; L4 fourth instar; PP pre-pupal; P pupal; TLP total larval period; TDP total developmental period.
Means followed by the same letter are not statistically significant.
* significant at $P < 0.01$; ** significant at $P < 0.001$; NS non significant at $P>0.05$; df 5, 24; Tukey's critical value 4.37.

Table 2. Mortality in *P. dissecta* at different larval densities (means ± SE).

Rearing density	Percent Mortality		Percent immature survival	Percent adult emergence
	Due to cannibalism	Due to unknown factors		
1	0.00 ± 0.00a	16.00 ± 3.68c	84.00 ± 16.73b	76.00 ± 16.73a
4	0.00 ± 0.00a	5.00 ± 5.00b	95.00 ± 4.18c	100.00 ± 0.00b
8	0.00 ± 0.00a	5.00 ± 3.06b	95.00 ± 4.11c	91.78 ± 7.54c
16	6.25 ± 1.98b	1.25 ± 1.25a	92.50 ± 5.23bc	87.62 ± 17.04d
25	9.60 ± 2.99c	2.40 ± 1.60a	88.00 ± 4.90b	88.92 ± 2.34d
35	25.71 ± 3.00d	14.29 ± 4.87c	60.00 ± 5.71a	72.69 ± 5.66a
F-value	15.58**	2.76*	9.94**	4.67*

Means followed by the same letter are not statistically significant.
* significant at $P < 0.01$; ** significant at $P < 0.001$; df 5, 24; Tukey's critical value 4.37.

melanogaster Meigen (Botella *et al*., 1985). The increased number of direct contacts between insects as a result of crowding may increase the rate of transmission of certain infectious agents In lepidopteran larvae of *Junonia coenia* Hubner and *Colias philodice eurytheme* Boisduval, crowding induces disease by viruses, bacteria and occasionally protozoan (Microsporidia) (Steinhaus, 1958). Also the increased concentration of infectious material released by infected insects due to crowding, increases the risk of healthy insects encountering contaminated food or other objects in surrounding (Steinhaus, 1958).

In predaceous organisms, like the ladybird under study, cannibalism is invariably observed at high larval densities (Tschinkel *et al*., 1967; Savridou and Bell, 1994) and has been suggested to increase the risk of pathogenesis (Pfenning *et al*., 1998) as a result of consumption of con- as well as heterospecifics diseased organisms (Tschinkel *et al*., 1967; Savridou and Bell, 1994; Pfenning *et al*., 1998).

But crowding doesn't always produce harmful effects, and under many conditions there are also some beneficial results, *viz*. increase in body mass (Wiklund and Forsberg, 1991) due to increased food consumption (Rahman, 1969), increase in social feeding, to mate search, and reduced predation risk (Alee, 1931; Stamp, 1980; Thornhill and Alcock, 1983; Nahrung *et al*., 2001).

The costs of crowding appears to be higher in females as compared to males because smaller body size more strongly affects fitness attributes, such as life span, fecundity, *etc*. (Ellers *et al*., 1998; Hardy *et al*., 1992). Fecundity is known to be largely dependent on the resources accumulated during larval stages (Kaddou, 1960; Smith, 1965; Kawauchi, 1990; Ng, 1991; Masumoto *et al*., 1993; Wiklund *et al*., 2001; Bergström *et al*., 2002).

Thus, based on the above account of negative influence of crowding on life attributes, it is expected that the singly reared larvae should perform better. However, our results show otherwise. Singly reared larvae were found to have increased larval and total developmental periods, lower immature survival and relatively smaller adults despite prey being provided in equal numbers across all experimental sets. This corroborates well with the findings on *A. thalassinus* (Heifetz and Applebaum, 1995).

However, in the present study, the larvae reared at density of four have developed faster, with lesser mortality, into healthier adults than those reared at larval density of 1 despite there being reduced competition for food as well as no interferences in the latter. This could be attributed to (a) poor predation due to relatively larger size of aphid, (b) lack of social feeding, and (c) probable lack of some fitness increasing social behaviours. Larger size aphids have been known to kick away smaller sized ladybird instars or employ other defensive means (Dixon, 1958; Lucas and Brodeur, 2001), thereby causing them injury or even mortality. The large size of aphids in comparison to that of first instar could be responsible for poor consumption. Also, the walking speed of first instar is also probably lower than that of an aphid third instar, thereby, making predation a doubly difficult proposition. It has been previously reported that first instars of ladybirds exhibit social feeding (Hemptinne *et al*., 2000), which increases the chance of capture of the first prey by the first instar which is critical determinant of its survival to the second instar. The above outlined difficulties in prey capture and the absence of a chance to indulge in social feeding may together be responsible for the relatively poor biological attributes displayed at single rearing. Other than social feeding, there might also exist certain social behaviours which increase fitness. The nature of these social influences is largely unclear but it might lead to social stimulation of feeding (Nahrung *et al*., 2001; Stamp, 1980) and faster development under influence of pheromones.

Social feeding, should theoretically lead to attainment of better biological attributes at higher densities, but the absence of such a scenario at the higher densities of 16, 25 and 35 can be probably explained through the interplay of multitude of factors, *viz*. (a) benefits of social feeding vs. costs of increased aggressive encounters, (b) increased competition for food, and (c) increased probability of infection. Social feeding is probably required at the first instar stage, which are poor foragers, to increase their chances of obtaining food. However, later in larval life, it probably becomes redundant due to sharp increase in predatory efficiencies of the later instars. So in the group rearing setups, social feeding allows the advancement of the first instar to the next stage. Whereas in single rearing, the lack of social feeding may probably reduce the chance of the survival of the first instar due to insufficient food, thereby explaining the poor developmental attributes.

The increased mortality due to cannibalism at higher densities is clearly due to increased aggression and limitation of food resources due to increased competition for food. The high mortality due to unknown reasons at group rearing of 16 and above could be due to increased infections.

It is thus apparent from the present findings that group rearing at the rate of four larvae per beaker helps in obtaining increased number of fitter individuals of *P. dissecta*, thereby having implications in mass rearing and the augmentative field releases for the biocontrol of insects pests, especially the aphids. Of course, these results are subject to multiple number of factors, such as change in prey density and size of experimental arena. It is however, our opinion that though prey density is definitely a confounding factor, size of experimental arena is unlikely to change the result and interactions obtained in the case of this ladybird if prey and predator density is maintained.

References

ALEE W. C., 1931.- *Animal Aggregations. A study in General Sociology*.- University of Chicago Press, Chicago, USA.

APPLEBAUM S. W., HEIFETZ Y., 1999.- Density-dependent physiological phase in insects.- *Annual Review of Entomology*, 44: 317-341.

BARNES A. I., SIVA-JOTHY M. T., 2000.- Density- dependent propylaxis in the mealworm beetle *Tenebrio molitor* L. (Coleoptera: Tenebriodae): Cuticular melanization in an indicator of investment in immunity.- *Proceedings of Royal Society: Biological Sciences*, 267 (1439): 177-182.

BERGSTRÖM J., WIKLUND C., KAITALA A., 2002.- Natural variation in female mating frequency in a polyandrous butterfly: effects of size and age.- *Animal Behaviour*, 64: 49-54.

BOTELLA L. M., MOYA A., GONZALEZ M. C., MENSUA J. L., 1985.- Larval stop, delayed development and survival in overcrowded cultures of *Drosophila melanogaster*; effect of urea and uric acid.- *Journal of Insect Physiology*, 31: 179-185.

DETHIER V. G., 1959.- Food-plant distribution and larval dispersal as factors affecting insect populations.- *Canadian Entomology*, 88: 581-596.

DINGLE H., HASKELL J. B., 1967.- Phase polymorphism in the grasshopper *Melanoplus differentialis*.- *Science*, 155: 590-592.

DIXON A. F. G., 1958.- The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.).- *Transactions of the Royal Entomological Society of London*, 110: 319-334.

ELLERS J., VAN ALPHEN J. J. M., SEVENSTER J. G., 1998.- A field study of size fitness relationships in the parasitoid *Asobara tabida*.- *Journal of Animal Ecology*, 67: 318-324.

EVANS H. F., 1976.- Mutual interference between predatory anthocorids.- *Ecological Entomology*, 1: 283-286.

EVANS E. W., 1983.- Niche relations of predatory stinkbugs (*Podius* spp., Pentatomidae) attacking tent caterpillars (*Malacosoma americanum*, Lasiocampidae).- *American Midland Naturalist*, 109: 316-323.

FANTINOU A. A, PERDIKIS D. C., STAMOGIANNIS N., 2008.- Effect of larval crowding on the life history traits of *Sesamia nonagrioides* (Lepidoptera: Noctuidae).- *European Journal of Entomology*, 105: 625-630.

FESCEMYER H. W., ERLANDSON C. M., 1993.- Influence of diet on the density- dependent phase polymorphism of velvet bean caterpillars (Lepidoptera: Noctuidae).- *Environmental Entomology*, 22: 933-941.

FISCHER K., FIEDLER K., 2000.- Sex-related differences in reaction norms in the, butterfly *Lycaena tityus* (Lepidoptera: Lycaenidae).- *Oikos*, 90: 372-380.

GIBBS M., LACE L. A., JONES M. J., MOORE A. J., 2004- Intraspecific competition in the speckled wood butterfly *Pararge aegeria*: Effect of rearing density and gender on larval life history.- *Journal of Insect Science*, 4 (16): 1-6. [online] URL: http://www.insectscience.org/4.16

GOTTHARD K., NYLIN S, WIKLUND C., 1994.- Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*.- *Oecologia*, 99: 281-289.

GOULSON D., CORY J. S., 1995.- Responses of *Mamestra brassicae* (Lepidoptera: Noctuidae) to crowding: interactions with disease resistance, colour phase and growth.- *Oecologia*, 104: 416-423.

HARDY I. C. W., GRIFFITHS N. T., GODFRAY H. C. T., 1992.- Clutch size in a parasitoid wasp: a manipulation experiment.- *Journal of Animal Ecology*, 61: 121-129.

HEIFETZ Y., APPLEBAUM S. W., 1995.- Density dependent physiological phase in non migratory locust, *Locusta migratoria* (L.) (Orthoptera: Acrididae).- *Journal of Orthoptera Research*, 2: 15-20.

HEMPTINNE J. L., GAUDIN M., DIXON A. F. G., LOGNAY G., 2000.- Social feeding in ladybirds: adaptive significance and mechanism.- *Chemoecology*, 10 (3): 149-152.

HODEK I., HONEK A., 1996.- *Ecology of Coccinellidae*.- Kluwer Academic Publishers, Dordrecht, The Netherlands.

KADDOU I. K., 1960.- The feeding behaviour of *Hippodamia quinquesignata* (Kirby) larvae.- *University of California Publications in Entomology*, 16: 181- 228.

KAWAUCHI S., 1990.- Studies on the comparative ecology of three aphidophagous coccinellids.- *Kurume University Journal*, 39: 239-305.

KLOK C. J., CHOWN S. L., 1999.- Assessing the benefits of aggregation: thermal biology and water relations of anomalous Emperor Moth caterpillars.- *Functional Ecology*, 13: 417-427.

LUCAS E., BRODEUR J., 2001.- A fox in sheep's clothing: furtive predators benefit from the communal defense of their prey.- *Ecology*, 82: 3246-3250.

MASUMOTO T., NOMAKUCHI S., SAWADA K., 1993.- Host plant conspicuousness and the distribution of eggs and larvae in the butterfly, *Anthochais scolymus* (Lepidoptera: Pieridae).- *Researches on Population Ecology*, 35: 241-250.

MELANIE G., LESELY A. L., MARTIN J. J., ALLEN J. M., 2004.- Intra-specific competition in the speckle wood butterfly *Pararge aegeria*: Effect of rearing density and gender on larval life history.- *Journal of Insect Science*, 4: 1-6.

MERCER D. R., 1999.- Effects of larval density on the size of *Aedes polynesiensis* adults (Diptera: Culicidae).- *Journal of Medical Entomology*, 36: 702-708.

MINITAB, 2003.- *Minitab 13.0*.- Minitab Inc., Philadelphia, USA.

NAHRUNG H. F., DUNSTAN P. K., ALLEN G. R., 2001.- Larval gregariousness and neonate establishment of the eucalypt-feeding beetle *Chrysophtharta agricola* (Coleoptera: Chrysomelidae: Paropsini).- *Oikos*, 94: 358-364.

NG S. M., 1991.- Voracity, development and growth of larvae of *Menochilus sexmaculatua* (Coleoptera: Coccinellidae) fed on *Aphis spiraecola*, pp. 199-206. In: *Behavior and impact of aphidophaga* (POLGAR L., CHAMBERS R. J., DIXON A. F. G., HODEK I., Eds).- SPB Academic, The Hague, The Netherlands.

OMKAR, MISHRA G., 2005.- Preference- performance of a generalist predatory ladybird: a laboratory study.- *Biological Control*, 34 (2): 187-195.

OMKAR, PERVEZ A., 2000.- Sexual dimorphism in *Propylea dissecta* (Mulsant), (Coleoptera: Coccinellidae).- *Journal of Aphidology*, 14: 139-140.

PERVEZ A., OMKAR, 2004.- Prey-dependent life attributes of an aphidophagous ladybird beetle, *Propylea dissecta* (Coleoptera: Coccinellidae).- *Biocontrol Science and Technology*, 14 (4): 385-396.

PFENNING D. W., HO S. G., HOFFMAN E. A., 1998.- Pathogen transmission as a selective force against cannibalism.- *Animal Behaviour*, 55: 1255-1261.

PUTMAN R. J., 1977.- The dynamics of the blowfly *Calliphora erythrocephala* within carrion.- *Journal of Animal Ecology*, 46: 853-866.

RAHMAN M., 1969.- Effects of different foods on the development of *Pieris rapae* L. larvae (Lep: Pieridae).- *Pakistan Journal of Zoology*, 1: 35-40.

REYNOLDS D. R., RILEY J. R., 1988.- A migration of grasshoppers, particularly *Diabolocatantops axillaris* (Thunberg) (Orthoptera: Acrididae) in the West African Sahel.- *Bulletin of Entomological Research*, 78:251:271.

ROGER C., CODERRE D., BOVIN G., 2000.- Differential prey utilization by Generalist predator *Coleomegilla maculata lengi* according to prey size and species.- *Entomologia Experimentalis et Applicata*, 94: 3-13.

RUBTZOV I. A., 1935.- Phase-variation in non swarming grasshoppers.- *Bulletin of Entomological Research*, 26: 499-524.

SAVRIDOU N., BELL C. H., 1994.- The effect of larval density, photoperiod and food change on the development of *Gnatocercus cornutus.* (F.) (Coleoptera: Tenebrionidae).- *Journal of Stored Products Research*, 30: 17-21.

SIMMONDS M. S. J., BLANEY W. M., 1986.- Effects of rearing density on development and feeding behaviour in larvae of *Spodoptera exempta*.- *Journal of Insect Physiology*, 32: 1043-1053.

SMITH B .C., 1965.- Effect of the food on the longevity, fecundity and development of adult coccinellids.- *Canadian Entomologist*, 7: 7-10.

STAAL G. B., 1961.- Studies on the physiology of phase induction in *Locusta migratoria migratorioides* R. and F.- *Doctoral thesis*, Publikatie Fonds Landbouw Export Bureau 1916-1918, 40: 1-125.

STAMP N. E., 1980.- Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly?- *The American Naturalist*, 115: 367-380.

STEINHAUS E. A., 1958.- Crowding as a possible stress factor in insect disease.- *Ecology*, 39: 503-514.

TAMMARU T., RUOHOMAKI K., MONTOLA M., 2000.- Crowding induced plasticity in *Epirrita autumnata* (Lepidoptera: Geometridae): weak evidence of specific modifications in reaction.- *Oikos*, 90: 171-181.

THORNHILL R. J., ALCOCK J., 1983. - *The evolution of insect mating systems*.- Harvard University Press, Cambridge, Massachusetts, USA.

TSCHINKEL W., WILLSON C., BERN H. A., 1967.- Sex pheromone of the mealworm beetle (*Tenebrio molitor*).- *Journal of Experimental Biology*, 164: 81-86.

UVAROV V. B., 1966.- *Grasshoppers and Locusts, Vol. 1*.- Cambridge University Press, UK.

WIKLUND C., FORSBERG J., 1991.- Sexual size dimorphism in relation to female polygamy and protandry in butterflies: a comparative study of Swedish Pieridae and Satyridae.- *Oikos*, 60: 373-381.

WIKLUND C., KARLSSON B., LEIMAR O., 2001.- Sexual Cupertino in butterfly reproduction: a comparative study of polyandry and female fitness.- *Proceedings of the Royal Society of London B*, 268: 1661-1667.

WISE D. H., 1975.- Food limitation of the spider *Linyphia marginata* experimental field studies.- *Ecology*, 56: 637-646.

Authors' addresses: OMKAR (corresponding author, e-mail: omkaar55@hotmail.com), Shuchi PATHAK, Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow 226 007, India.

Received August 19, 2008. Accepted January 26, 2009.