36. Pyšek, P., Richardson, D. M., Rejmanek, M., Webster, G. L., Williamson, M. and Kirschner, J., Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, 2004, **53**(1), 131–143.
37. http://theseedsite.co.uk/asteraceae.html
38. Cook, C. D. K., *Aquatic and Wetland Plants of India*, Oxford University Press, Delhi, 1996, pp. 66–74.
39. Hooker, J. D. (ed.), Compositae. In *Flora of British India*, 1881, vol. 3, pp. 219–419.
40. Suthari, S., Biodiversity characterization and aboveground vegetation carbon pool assessment in northern Telangana at landscape level using geospatial technique. Ph D thesis, Department of Botany, Kakatiya University, Warangal, 2013, pp. 113; 114.
41. Suthari, S., Kandagatla, R., Ragan, A. and Raju, V. S., Threat to Eturnagaram and Kinnerasani wildlife sanctuaries in northern Telangana from the invasive Siam weed (*Chromolaena odorata*; Asteraceae). In National Conference on 'Emerging Research Trends in Plant Sciences in 21st Century', Department of Botany, Kakatiya University, 12 and 13 February 2015, pp. 120; 121.
42. Rao, R. S., *Parthenium hysterophorus* L., a new record for India. *J. Bombay Nat. Hist. Soc*., 1956, **54**, 218–220.
43. Roxburgh, W., *Hortus Bengalensis or a Catalogue of the Plants Growing in the Honourable East India Company's Botanic Garden at Calcutta*, The Mission Press, Serampore, 1814, p. 62.
44. Paul, T. K., The earliest record of *Parthenium hysterophorus* L. (Asteraceae) in India. *Curr. Sci*., 2010, **98**(10), 1272.

ACKNOWLEDGEMENTS. S.S. thanks Dr V. K. Dadhwal, Director (NCP-VCP) and Dr Sarnam Singh, Dy. Director (VCP), Indian Institute of Remote Sensing, Dehra Dun for financial support. R.K. thanks UGC, New Delhi, for a fellowship under the Major Research Project. We thank Dr G. V. S. Murthy (Botanical Survey of India, Southern Circle, Coimbatore) for permission to work in the Madras Herbarium, the anonymous reviewers for their constructive suggestions and Dr V. Krishna Reddy, Head, Department of Botany, Kakatiya University, for encouragement and facilities.

Received 2 April 2015; revised accepted 20 October 2015

doi: 10.18520/cs/v110/i7/1337-1343

Food resource exploitation in ladybirds: consequences of prey species and size

Desh Deepak Chaudhary, Bhupendra Kumar, Geetanjali Mishra and Omkar*

Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow 226 007, India

In the present study, preference between larger and smaller instars of *Acyrthosiphon pisum* and *Aphis craccivora* by small and large female variants of ladybirds *Menochilus sexmaculatus* and *Propylea dissecta* has been investigated. Results reveal that both ladybird species consumed smaller prey, *A. craccivora* over larger prey, *A. pisum* when kept individually and/or in combination. Although small and large female variants of both ladybird species consumed smaller and larger instars of *A. craccivora* respectively, they preferred smaller instars of *A. pisum*. Similar results were also recorded within combinations. Thus, food resource exploitation in both ladybirds is due to both prey species and size.

Keywords: Aphids, food resource exploitation, ladybirds, prey species and size resource polymorphism.

IN a biological community, resources are used and exploited both inter- and intra-specifically through resource partitioning and resource polymorphism respectively. While resource partitioning is differential use of resources, such as food and space by different competing species[1,2], resource polymorphism is the occurrence of discrete intraspecific variants that differ in size, colour, behaviour and/or life-history traits and show differential niche use, usually through discrete differences in feeding biology and habitat use[3–5]. Thus, by developing dissimilar resource requirements, resource partitioning allows different species and resource polymorphism allows variants or life stages of the same species to differentially utilize resources[1,6,7].

Although both resource partitioning and resource polymorphism have been widely studied in fish, amphibian and bird predators[4,8,9]; in insect predators, resource partitioning, rather than resource polymorphism has been investigated[10–12]. Within a community, competing insect predators generally partition their prey resources on the basis of their own size and/or size of their prey[10–13]. Amongst insect predators, size-based resource partitioning commonly occurs in ladybirds (Coleoptera: Coccinellidae)[11,12], a group of predatory insects with considerable potential as biocontrol agents of aphids and other pest species[14].

According to Sloggett's[12] prey size–density and Dixon's[15] hypotheses, when both large and small ladybird species have equal probabilities of catching smaller species of prey, small ladybird species will capture all instars of prey, whereas large ladybird species will capture larger instars. In contrast, when prey is large, small ladybird species will capture smaller instars, whereas large ladybird species will exploit all instars. Thus, large and small competing ladybird species coexist in the same agricultural fields, feeding on the same prey resources, owing to partitioning of prey resources on basis of their size.

However, aphidophagous ladybirds also show natural intraspecific size variations (within the same sex) under laboratory conditions (even when reared on *ad libitum* aphid prey[16]), and both small and large males/females are found within small (e.g. *M. sexmaculatus* and *Propylea dissecta* (Mulsant))[16] and large (e.g. *Coccinella septempunctata* (L.) and *C. transversalis* Fabricius)[17] ladybird species. In agricultural fields, different sized variants of a ladybird species also coexist (pers. obs.). Similarly, aphid

*For correspondence. (e-mail: omkaar55@hotmail.com)

species also show inter- and intraspecific size variations[11,12]. Therefore, in ladybirds, where different sized conspecific variants coexist, it is relevant to question whether these will also differentially exploit resources? Since in ladybirds interspecific variation in the size of predators as well as prey dictates resource partitioning, do size variants also show such differential usage of resources, akin to resource partitioning, but intraspecific not interspecific, or do they show resource polymorphism.

Ecologists have also documented that different sized conspecific individuals differ in their abiotic tolerance[18], microhabitat use[19], prey preferences[20], predation risk[21], parasite resistance/tolerance[22], mutualism[23], dispersal[24], and/or exposure to intraspecific or interspecific competition[7]. Therefore, studying factors that govern size-based resource exploitation in ladybird predators would have wide ecological and agricultural implications.

To answer the above questions, the present study has been undertaken considering two aphidophagous ladybird species, viz. *M. sexmaculatus* and *P. dissecta*. Both are from the oriental region with wide prey range[25,26] and coexist abundantly in aphid-infested agricultural fields of Lucknow, India as well[27]. These were selected for their easy availability in local agroecosystems, and tendency to show natural size variation within field conditions as well as in the laboratory-reared stock. Two prey species selected were pea aphid, *Acyrthosiphon pisum* (Harris) and bean aphid, *Aphis craccivora* Koch. The former is larger than the latter, and both are highly palatable to the selected ladybirds[28]. It is expected that results of the present study would evaluate factors that govern size-based resource polymorphism in ladybirds.

Adults of *M. sexmaculatus* ($n = 40$) and *P. dissecta* ($n = 40$) were collected from fields close to Lucknow (26°50′N, 80°54′E), paired and reared in plastic petri dishes (14.5 × 1.5 sq. cm) under constant abiotic conditions (27° ± 2°C; 65% ± 5% relative humidity; 14 h light: 10 h dark photoperiod) in a BOD incubator (YORCO; York Scientific Industries Pvt Ltd, India). They were provided with *ad libitum* pea aphid on broad bean (*Vicia faba* L., Fabaceae) reared in polyhouse maintained at 22° ± 1°C; 65% ± 5% relative humidity and 14L : 10D photoperiod. Eggs laid were collected every 24 h and observed for hatching. Neonates obtained were reared individually under the above-mentioned abiotic conditions on the same prey species as provided to their parents. Ten-day-old young virgin females were selected randomly from the stock and used for experimentation, as they are more voracious than middle aged[29] and old females. Unmated females were selected because: (i) they do not lay eggs and reduce errors due to variations in reproductive performance of ladybirds[30]; (ii) consumption of their own eggs by mated females may reduce prey consumption, thus providing unrealistic estimates of prey consumed, and (iii) they are more voracious than mated females[31].

From the laboratory stock, 10-day-old virgin females ($n = 100$ per ladybird species) having individuals of different sizes, and naturally developed small (7.00 ± 2.00 mg) and large (14.00 ± 2.00 mg) sized variants of both ladybirds were selected. The difference in biomass was statistically significant (t-value = 9.57; $P < 0.0001$). Variation in size was evaluated using biomass as measure since amount of food required for maintenance scales with body biomass[11,12]. The ladybirds were starved for 12 h and the following experiments were conducted.

Different-sized prey species – singly: A single small-sized female of *M. sexmaculatus* was placed in a petri dish (size as mentioned earlier) containing any one of the following diets: (i) a mixed diet of 10 sec instars (small ~0.61 ± 0.05 mg) of *A. pisum* (reared on *V. faba*) and 10 sec instars (small ~0.11 ± 0.01 mg) of *A. craccivora* (reared on bean, *Dolichos lablab* L., Fabaceae), and (ii) a mixed diet of 10 fourth instars (large ~1.41 ± 0.07 mg) of *A. pisum* and 10 fourth instars (large ~0.90 ± 0.01 mg) of *A. craccivora*. The arena was sealed for the next 6 h. Thereafter, the numbers of unconsumed aphids of each species in each arena were counted and recorded. The arena was devoid of host plant twigs so that aphid instars may not grow and reproduce, and their numbers remain constant. Similar experiments were conducted using large females of *M. sexmaculatus*, and small and large females of *P. dissecta*. Abiotic conditions for the duration of experiments were maintained at stock culture levels. Each experiment was done, considering 10 replicates per diet per size variant in each ladybird species, totalling 40 large and 40 small females per ladybird species.

A preliminary study ($n = 20$ per variant per ladybird species) was undertaken prior to the start of experiments to ensure that (i) 20 aphids were sufficient (*ad libitum*) for large and small variants of both ladybird species, and (ii) 6 h was sufficient for aphids to remain alive in the absence of host plant and not moult to advanced stages.

In combination: Three conspecific two-predator combinations, L + L, S + S and L + S (L = large and S = small) were formed using small and large females of *M. sexmaculatus* and *P. dissecta* in plastic petri dishes (size as above). Each two-predator combination was provided with one of the following diets: (i) a mixed diet of 20 sec instars (small) of *A. pisum*, and 20 sec instars (small) of *A. craccivora*, and (ii) a mixed diet of 20 fourth instars (large) of *A. pisum* and 20 fourth instars (large) of *A. craccivora*. Petri dishes were kept under the above-mentioned abiotic conditions for 6 h. Thereafter, unconsumed aphids of each species were counted and recorded within each two-predator combination. Each treatment was conducted in 10 replicates, totalling 120 conspecific two-predator combinations.

Different-sized instars per prey species – singly: A small-sized female of *M. sexmaculatus* was kept singly in a petri dish (size as above), containing one of the following diets: (i) a mixed diet of 10 sec and 10 fourth instars of *A. pisum*, and (ii) a mixed diet of 10 sec and 10 fourth instars of *A. craccivora*, and the arena was sealed for the next 6 h. The number of unconsumed aphids in each arena was counted after 6 h and recorded. Similar experiments were conducted with large female of *M. sexmaculatus*, and large and small females of *P. dissecta*. Abiotic conditions for the duration of experiments were maintained at stock culture levels. Each experiment was conducted in 10 replicates per diet per variant and per ladybird species, totalling 40 large and 40 small females per ladybird species.

In combination: Three conspecific two-predator combinations, L + L, S + S and L + S, were formed using small and large females of *M. sexmaculatus* and *P. dissecta* in plastic petri dishes (size as above). They were provided with one of the following diets: (i) a mixed diet of 20 sec and 20 fourth instars of *A. pisum*, and (ii) a mixed diet of 20 sec and 20 fourth instars of *A. craccivora*. Petri dishes were kept under the above-mentioned abiotic conditions for 6 h. Unconsumed aphids of each size were counted after 6 h and recorded within each two-predator combination. Each experiment was conducted in 10 replicates, totalling 120 conspecific two-predator combinations.

Data were checked for normal distribution using Kolmogorov–Smirnov test for normality and Bartlett's test for homogeneity of variances prior to further analysis as described below. Percentage of prey consumption was calculated as follows: [(Number of prey consumed × 100)/total number of prey].

For different-sized prey species, percentage of prey consumption (dependent factor), singly and in combination, was subjected to multivariate analysis of variance (MANOVA) followed by Tukey's post-hoc comparison of means with: (i) ladybird species (*M. sexmaculatus* and *P. dissecta*), (ii) ladybird size (large/small)/two-predator combination size (size of predators within combinations L + L, S + S and L + S), (iii) aphid species (*A. craccivora*/*A. pisum*), and (iv) aphid species size (large/small) as independent factors, and percentage of prey consumption as the dependent factor. Prior to MANOVA, all percentage of data were subjected to arcsine square root transformation.

For different-sized instars per prey species, data on percentage of prey consumption, singly and in combination, were subjected to MANOVA, considering: (i) ladybird species, (ii) ladybird size/two-predator combination size, (iii) aphid species, and (iv) aphid instars size (second instar ~ small/fourth instar ~ large) per aphid species as independent factors, and percentage of prey consumption as the dependent factor, followed by Tukey's post hoc comparison of means. All percentage of data were subjected to arcsine square root transformation prior to MANOVA. All analyses were conducted using statistical software SAS (version 9.0). The results are given below.

Different-sized prey species – singly: MANOVA revealed significant influence of ladybird species, ladybird size, aphid species and aphid size on percentage of prey consumption. Except for interactions between ladybird size and aphid species, ladybird size and aphid species size, and aphid species and aphid species size, which significantly affected percentage of prey consumption, other interactions were not statistically significant (Table 1). Comparison of means exemplified that both large and small females of *M. sexmaculatus* and *P. dissecta* consumed smaller aphid species, *A. craccivora* more than larger aphid species, *A. pisum*, though prey consumption of *M. sexmaculatus* was higher than *P. dissecta* (Table 2).

In combination MANOVA further revealed significant influence of ladybird species, two-predator combination size, aphid species and aphid species size on percentage of prey consumption. Percentage of prey consumption was also significantly affected by interactions between ladybird species and aphid species size, between two-predator combination size and aphid species, and between ladybird species, two-predator combination size and aphid species size. However, percentage of prey consumption did not vary significantly with interactions between other independent factors (Table 1). Comparison of means revealed that smaller aphid species, *A. craccivora* was consumed more than larger aphid species, *A. pisum* by predators within combinations. Combinations having two-small females consumed lower prey biomass than combinations having two-large females. Moreover, percentage of prey consumption was relatively higher in *M. sexmaculatus* than *P. dissecta* combinations (Table 3).

Different-sized instars per prey species – singly: MANOVA revealed significant influence of ladybird species, ladybird size, aphid species and aphid instar size on percentage of prey consumption. Percentage of prey consumption was also significantly influenced by interactions between ladybird size and aphid instar size, and between ladybird size, aphid species and aphid instar size (Table 4). Small and large females of both ladybirds consumed smaller and larger instars of *A. craccivora* respectively. However, small and large females of *M. sexmaculatus* and *P. dissecta* consumed smaller instars of *A. pisum* more in number than its larger instars (Table 2).

In combination MANOVA further revealed significant influence of ladybird species, two-predator combination size, aphid species and aphid instar size on percentage of prey consumption. However, except interactions between two-predator combination size and aphid instar size, between aphid species and aphid instar size, and between two-predator combination size, aphid species and aphid instar size, percentage of prey consumption did not vary significantly with interactions between other factors

Table 1. MANOVA table showing the effect of different-sized prey species on percentage of prey consumption by large and small females of *Menochilus sexmaculatus* and *Propylea dissecta*, when kept singly and in combination (*F*-values significant at $P < 0.05$)

	Prey consumption (%)		
Tested variables	*F*-value	*P*-value	*d.f.*
Singly			
Ladybird species	5.16	0.0246	1159
Ladybird size	3.30	0.0412	1159
Aphid species	112.44	<0.0001	1159
Aphid species size	50.69	<0.0001	1159
Ladybird species × ladybird size	1.13	0.289	1159
Ladybird species × aphid species	0.58	0.448	1159
Ladybird species × aphid species size	0.83	0.363	1159
Ladybird size × aphid species	4.53	0.035	1159
Ladybird size × aphid species size	46.82	<0.0001	1159
Aphid species × aphid species size	28.32	<0.0001	1159
Ladybird species × ladybird size × aphid species	1.87	0.173	1159
Ladybird species × ladybird size × aphid species size	0.83	0.363	1159
Ladybird size × aphid species × aphid species size	2.80	0.097	1159
Ladybird species × ladybird size × aphid species × aphid species size	0.83	0.365	1159
In combinations			
Ladybird species	40.32	<0.0001	1239
Two-predator combination size	49.21	<0.0001	2239
Aphid species	377.12	<0.0001	1239
Aphid species size	4.93	0.0275	1239
Ladybird species × two-predator combination size	0.77	0.463	2239
Ladybird species × aphid species	0.02	0.902	1239
Ladybird species × aphid species size	10.71	0.001	1239
Two-predator combination size × aphid species	16.64	<0.0001	2239
Two-predator combination size × aphid species size	1.60	0.204	2239
Aphid species × aphid species size	2.38	0.124	1239
Ladybird species × two-predator combination size × aphid species	0.31	0.734	2239
Ladybird species × two-predator combination size × aphid species size	4.79	0.009	2239
Two-predator combination size × aphid species × aphid species size	2.55	0.081	2239
Ladybird species × two-predator combination size × aphid species × aphid species size	0.91	0.403	2239

Table 2. Percentage of prey consumption by large and small females of *M. sexmaculatus* and *P. dissecta*, when kept singly and given a choice of either (i) large (*A. pisum*, *Ap*) and small (*A. craccivora*, *Ac*) aphid species; or (ii) large (fourth instar) and small (second instar) instars of *A. craccivora* and *A. pisum* (values are means ± SE; large and small letters represent comparison of means between aphid species and between sizes of aphid instars respectively)

Ladybird species	Ladybird size	Aphid species	Aphid species size	Aphid instar size	Prey consumption (%)
M. sexmaculatus	Large	*Ac*	Small	Small instar	88.00 ± 2.73^{Ba}
				Large instar	93.00 ± 2.97^{Bb}
		Ap	Large	Small instar	68.00 ± 3.59^{Ab}
				Large instar	59.00 ± 3.35^{Aa}
	Small	*Ac*	Small	Small instar	83.00 ± 4.48^{Bb}
				Large instar	60.00 ± 5.96^{Ba}
		Ap	Large	Small instar	60.00 ± 3.20^{Ab}
				Large instar	40.00 ± 1.80^{Aa}
P. dissecta	Large	*Ac*	Small	Small instar	82.00 ± 2.48^{Ba}
				Large instar	89.00 ± 3.35^{Bb}
		Ap	Large	Small instar	63.00 ± 6.33^{Ab}
				Large instar	54.00 ± 2.67^{Aa}
	Small	*Ac*	Small	Small instar	77.00 ± 3.40^{Bb}
				Large instar	60.00 ± 5.96^{Ba}
		Ap	Large	Small instar	48.00 ± 2.40^{Ab}
				Large instar	40.00 ± 1.80^{Aa}

Table 3. Percentage of prey consumption by large (L) and small (S) females of either *M. sexmaculatus* or *P. dissecta* within two-predator combinations, when given a choice of either (i) large (*Ap*) and small (*Ac*) aphid species; or (ii) large (fourth instar) and small (second instar) instars of *A. craccivora* and *A. pisum* (values are means ± SE; large and small letters represent comparison of means between aphid species and between sizes of aphid instars, respectively)

Ladybird species	Ladybird size	Aphid species	Aphid species size	Aphid instar size	Prey consumption (%)
M. sexmaculatus	(L + L)	*Ac*	Small	Small instar	65.00 ± 2.50[Ba]
				Large instar	87.00 ± 3.00[Bb]
		Ap	Large	Small instar	58.00 ± 2.10[Ab]
				Large instar	53.00 ± 3.30[Aa]
	(S + S)	*Ac*	Small	Small instar	75.00 ± 3.40[Bb]
				Large instar	52.00 ± 2.80[Ba]
		Ap	Large	Small instar	49.00 ± 2.40[Ab]
				Large instar	43.00 ± 2.30[Aa]
	(L + S)	*Ac*	Small	Small instar	75.00 ± 3.40[Ba]
				Large instar	79.00 ± 3.10[Ba]
		Ap	Large	Small instar	52.00 ± 3.80[Ab]
				Large instar	46.00 ± 3.70[Aa]
P. dissecta	(L + L)	*Ac*	Small	Small instar	53.00 ± 2.10[Ba]
				Large instar	87.00 ± 2.00[Bb]
		Ap	Large	Small instar	48.00 ± 1.90[Ab]
				Large instar	42.00 ± 2.70[Aa]
	(S + S)	*Ac*	Small	Small instar	71.00 ± 3.50[Bb]
				Large instar	49.00 ± 2.70[Ba]
		Ap	Large	Small instar	49.40 ± 2.20[Aa]
				Large instar	40.00 ± 3.00[Aa]
	(L + S)	*Ac*	Small	Small instar	68.00 ± 1.50[Ba]
				Large instar	70.00 ± 2.70[Ba]
		Ap	Large	Small instar	46.00 ± 2.90[Ab]
				Large instar	40.00 ± 2.40[Aa]

(Table 4). Comparison of means revealed higher consumption of larger and smaller instars of *A. craccivora* by ladybirds within L + L and S + S combinations respectively; but equal number of larger and smaller instars of *A. craccivora* within L + S combination. However, smaller instars of *A. pisum* were consumed more in number over their larger instars within the three conspecific combinations. Moreover, percentage of consumption of aphid instars per aphid species was relatively higher in *M. sexmaculatus* than *P. dissecta*, both individually and in combination (Tables 2 and 3).

Results reveal that large and small female variants of both ladybird species, individually and in combination, consume *A. craccivora* more than *A. pisum*. Higher consumption of *A. craccivora* by all size variants of both ladybird species may be owing to its relatively smaller size, making it easy to attack and consume. On the other hand, large size and long legs of *A. pisum* instars probably help this species to actively evade capture and even fight-off small ladybirds[32,33]. Thus, small ladybird species consume smaller prey species when given a choice of both larger and smaller prey species; their small size probably being a constraint to their prey preference. Findings of the present study are also in agreement with other studies on ladybirds[34,35].

Within conspecific combinations (L + L, S + S and L + S), higher consumption of *A. craccivora* over *A. pisum* by size variants of both ladybird species also confirms that it is the most suitable prey for small-sized ladybirds. Contrary to these findings, prey consumption by large and small female variants of *C. septempunctata* and *C. transversalis* is not influenced by size of prey species; and regardless of their size, the former consumed *A. pisum* more than *A. craccivora*, whereas the latter consumed *A. craccivora* more than *A. pisum*[17].

Amongst aphid instars, large females of both ladybird species consumed larger instars of *A. craccivora* more frequently than smaller instars; whereas small variants consumed smaller instars of *A. craccivora* more than larger instars. However, both large and small female

Table 4. MANOVA table showing the effect of different sized instars per prey species on percentage of prey consumption by large and small females of *M. sexmaculatus* and *P. dissecta*, when kept singly and in combination (*F*-values significant at $P < 0.05$)

Tested variables	Prey consumption (%)		
	F-value	*P*-value	*d.f.*
Singly			
Ladybird species	7.73	0.006	1159
Ladybird size	76.74	< 0.0001	1159
Aphid species	189.49	< 0.0001	1159
Aphid instar size	27.92	< 0.0001	1159
Ladybird species × ladybird size	0.08	0.780	1159
Ladybird species × aphid species	0.08	0.780	1159
Ladybird species × aphid instar size	1.58	0.210	1159
Ladybird size × aphid species	0.96	0.329	1159
Ladybird size × aphid instar size	17.60	< 0.0001	1159
Aphid species × aphid instar size	1.25	0.265	1159
Ladybird species × ladybird size × aphid species	0.31	0.577	1159
Ladybird species × ladybird size × aphid instar size	1.58	0.210	1159
Ladybird size × aphid species × aphid instar size	7.82	0.006	1159
Ladybird species × ladybird size × aphid species × aphid instar size	0.17	0.677	1159
In combinations			
Ladybird species	29.76	< 0.0001	1239
Two-predator combination size	19.08	< 0.0001	2239
Aphid species	296.01	< 0.0001	1239
Aphid instar size	4.02	0.048	1239
Ladybird species × two-predator combination size	0.81	0.445	2239
Ladybird species × aphid species	0.44	0.507	1239
Ladybird species × aphid instar size	2.90	0.90	1239
Two-predator combination size × aphid species	2.70	0.70	2239
Two-predator combination size × aphid instar size	29.04	< 0.0001	2239
Aphid species × aphid instar size	17.22	< 0.0001	1239
Ladybird species × two-predator combination size × aphid species	1.81	0.167	2239
Ladybird species × two-predator combination size × aphid instar size	0.02	0.985	2239
Two-predator combination size × aphid species × aphid instar size	41.97	< 0.0001	2239
Ladybird species × two-predator combination size × aphid species × aphid instar size	0.81	0.446	2239

variants of both ladybird species consumed smaller instars of *A. pisum* more frequently than their larger instars. Similar preferences for smaller and larger instars of *A. craccivora* and smaller instars of *A. pisum* were recorded within conspecific combinations.

Higher consumption of larger and smaller instars of *A. craccivora* by large and small female variants respectively, further suggests that when aphid species is small, variants exhibit behaviour similar to resource partitioning. Even in the presence of both size variants of aphid instars, large females selectively consume larger instars to bear their high metabolic costs. In contrast, size of small females is a constraint in capturing and consuming larger aphid instars. They, therefore, fulfil their energy requirements mainly by consuming higher number of smaller aphid instars. Thus, both large and small variants of a small ladybird species possibly coexist in an agricultural field if crops are infested with different sized instars of a small aphid species.

However, if the prey species is large, as in *A. pisum*, both sized variants of small ladybird species may prefer to consume smaller instars, because these are comparable to larger instars of the small aphid species, and thus easier to capture. Probably small size of ladybird species is a constraint to their prey preference. Hence, large individuals would possibly compete with small ones if an agriculture field is infested with different sized instars of a large aphid species.

In comparison to *P. dissecta*, higher prey consumption by *M. sexmaculatus*, both individually and in combination, may be owing to its higher voracity and prey utilization abilities[28,29].

The results of the present study suggest that in case of small ladybird species: (i) when aphid species is small, the variants exhibit behaviour akin to interspecific resource partitioning, and (ii) if prey species is large, there is absence of resource partitioning and variants of all sizes prefer to consume smaller instars owing to size constraint. Thus, both resource partitioning, and size based resource polymorphism may be present in ladybirds due to existence of size polymorphism within the same sex. This resource polymorphism not only facilitates large and small variants of a ladybird species to exploit different prey, but also helps them to exploit instars of suitable size and coexist within the same community. However, further field-based studies are needed to strengthen the present findings.

1. Schoener, T. W., Resource partitioning in ecological communities. *Science*, 1974, **185**, 27–39.
2. Roughgarden, J., Resource partitioning among competing species – a coevolutionary approach. *Theor. Popul. Boil.*, 1976, **9**(3), 388–424.
3. Skúlason, S. and Smith, T. B., Resource polymorphisms in vertebrates. *Trends Ecol. Evol.*, 1995, **10**(9), 366–370.
4. Smith, T. B. and Skúlason, S., Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.*, 1996, **27**, 111–133.
5. Sol, D., Elie, M., Marcoux, M., Chrostovsky, E., Porcher, C. and Lefebvre, L., Ecological mechanisms of a resource polymorphism in Zenaida Doves of Barbados. *Ecology*, 2005, **86**(9), 2397–2407.
6. Dixon, A. F. G., *Insect Predator–Prey Dynamics: Ladybird Beetles and Biological Control*, Cambridge University Press, Cambridge, UK, 2000, p. 268.
7. Svanbäck, R. and Bolnick, D. I., Intraspecific competition drives increased resource use diversity within a natural population. *Proc. R. Soc. Biol. Sci.*, 2007, **274**, 839–844.
8. Svanbäck, R. and Eklöv, P., Effect of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia*, 2002, **131**, 61–70.
9. Svanbäck, R. and Eklöv, P., Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos*, 2003, **102**, 273–284.
10. Stephens, D. W. and Krebs, J. R., *Foraging Theory*. Princeton University Press, Princeton, NJ, 1986.
11. Sloggett, J. J., Weighty matters: body size, diet and specialization in aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *Eur. J. Entomol.*, 2008, **105**, 381–389.
12. Sloggett, J. J., Habitat and dietary specificity in aphidophagous ladybirds (Coleoptera: Coccinellidae): explaining specialization. In Proceedings of the Netherlands Entomological Society Meeting, Amsterdam, 2008, vol. 19, pp. 95–113.
13. Costa, G. C., Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, 2009, **90**, 2014–2019.
14. Michaud, J. P., Coccinellids in biological control. In *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae)* (eds Hodek, I., van Emden, H. F. and Honek, A.), John Wiley, Chichester, UK, 2012, pp. 488–519.
15. Dixon, A. F. G., Body size and resource partitioning in ladybirds. *Popul. Ecol.*, 2007, **49**, 45–50.
16. Chaudhary, D. D., Kumar, B., Mishra, G. and Omkar, Resource partitioning in a ladybird, *Menochilus sexmaculatus*: function of body size and prey density. *Bull. Entomol. Res.*, 2015, **105**, 121–128.
17. Bista, M. and Omkar, Effects of body size and prey quality on reproductive attributes of two aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *Can. Entomol.*, 2013, **145**, 566–576.
18. Meyer, E., Davies, S., Wang, S., Willis, B. L., Abrego, D., Juenger, T. E. and Matz, M. V., Genetic variation in responses to a settlement cue and elevated temperature in the reef-building coral *Acropora millepora*. *Mar. Ecol. Prog. Ser.*, 2009, **392**, 81–92.
19. Bolnick, D. I., Snowberg, L. K., Patenia, C., Stutz, W. E., Ingram, T. and Lau, O. L., Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution*, 2009, **63**, 2004–2016.
20. Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T. and Lyon, B. E., Individual variation in prey selection by sea otters: patterns, causes and implications. *J. Anim. Ecol.*, 2003, **72**, 144–155.
21. Eklöv, P. and Svanbäck, R., Predation risk influences adaptive morphological variation in fish populations. *Am. Nat.*, 2006, **167**, 440–452.
22. Ganz, H. H. and Ebert, D., Benefits of host genetic diversity for resistance to infection depend on parasite diversity. *Ecology*, 2010, **91**, 1263–1268.
23. Heinrich, B., Majoring and minoring by foraging bumblebees, *Bombus vagans* – experimental analysis. *Ecology*, 1979, **60**, 245–255.
24. Chapman, B. B., Bronmark, C., Nilsson, J. A. and Hansson, L. A., The ecology and evolution of partial migration. *Oikos*, 2011, **120**, 1764–1775.
25. Omkar and Pervez, A., Biodiversity of predaceous coccinellids (Coleoptera: Coccinellidae) in India: a review. *J. Aphidol.*, 2000, **14**, 41–67.
26. Agarwala, B. K. and Yasuda, H., Competitive ability of ladybird predators of aphids: a review of *Cheilomenes sexmaculata* (Fabr.) (Coleoptera: Coccinellidae) with a worldwide checklist of prey. *J. Aphidol.*, 2000, **14**, 1–20.
27. Pervez, A. and Omkar, Functional responses of coccinellids predators: an illustration of a logistic approach. *J. Insect Sci.*, 2005, **5**(5), 6.
28. Kumar, B., Pandey, G., Mishra, G. and Omkar, Predatory performance of four aphidophagous ladybirds: a measure of prey suitability. *Int. J. Trop. Insect Sci.*, 2013, **33**(2), 120–126.
29. Mishra, G., Omkar, Kumar, B. and Pandey, G., Stage and age specific predation in four aphidophagous ladybird beetles. *Biocontrol. Sci. Technol.*, 2013, **22**, 463–476.
30. Omkar, Mishra, G., Kumar, B., Singh, N. and Pandey, G., Risks associated with tandem release of large and small ladybirds (Coleoptera: Coccinellidae) in heterospecific aphidophagous guilds. *Can. Entomol.*, 2014, **146**, 52–66.
31. Rhamahalinghan, M., Feeding behaviour of *Coccinella septempunctata* L. var. *confusa* Wiedemann (Coleoptera: Coccinellidae) in relation to temperature – I. Pre-oviposition period. *J. Entomol. Res.*, 2012, **11**, 178–183.
32. Tokunaga, E. and Suzuki, N., Colony growth and dispersal in the ant-tended aphid, *Aphis craccivora* Koch, and the non-ant-tended aphid, *Acyrthosiphon pisum* Harris, under the absence of predators and ants. *Popul. Ecol.*, 2008, **50**, 45–52.
33. Bista, M., Mishra, G. and Omkar, Influence of crowding and diet on the development and survival of the ladybird *Brumoides suturalis* (Coleoptera: Coccinellidae) reared on two aphid species. Inter. *J. Trop. Insect Sci.*, 2012, **32**(1), 64–68.
34. Agarwala, B. K. and Bardhanroy, P., Numerical response of ladybird beetles (Col., Coccinellidae) to aphid prey (Hom., Aphididae) in a field bean in north-east India. *J. Appl. Entomol.*, 1999, **123**, 401–405.
35. Mignault, M. P. and Brodeur, J., Soybean aphid predators in Québec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *BioControl*, 2006, **51**, 89–106.

ACKNOWLEDGEMENTS. We thank the Department of Science and Technology, New Delhi and Centre of Excellence, Department of Higher Education, Government of Uttar Pradesh for financial assistance.

Received 4 September 2014; revised accepted 20 November 2015

doi: 10.18520/cs/v110/i7/1343-1349