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CARFAX

REVIEW

Arthropod Natural Enemies of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) in India

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Helicoverpa armigera *(Hübner) (Lepidoptera: Noctuidae) is one of the most serious insect pests in the Old World. In India, it causes substantial losses to legume, fibre, cereal oilseed and vegetable crops. This paper reviews the literature on the biology, ecology, efficacy, rearing and augmentation of endemic parasitoids and predators, as well as exotic parasitoids introduced and released in India. It also provides updated lists of* H. armigera *natural enemies native to India. In addition, reports of augmentative releases of* Trichogramma *spp., the most extensively studied natural enemy of* H. armigera *are summarized.*

Keywords: Helicoverpa armigera, *natural enemies, biological control, India*

INTRODUCTION

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is one of the most serious insect pests in the Old World. It is widely distributed from the Cape Verde Islands in the Atlantic Ocean, through Africa, Asia and Australia to the South Pacific islands and from southern Europe to New Zealand (Reed & Pawar, 1982). In India, *H. armigera* has been recorded on at least 181 plant species from 45 plant families (Manjunath *et al.*, 1989), including major crops such as cotton (*Gossypium* spp.), sorghum (*Sorghum bicolor* Linnaeus), tomato (*Lycopersicon esculentum* Mill.), pigeonpea (*Cajanus cajan* (Linnaeus) Millspaugh) and chickpea (*Cicer arietinum* Linnaeus). Annual losses due to *H. armigera* in pigeonpea and chickpea have recently been estimated to exceed US$600 million (International Crops Research Institute for the Semi-arid Tropics (ICRISAT), 1992). Losses in other crops add substantially to the total damage caused by *H. armigera.*

Life-table studies reveal that *H. armigera* often shows a typical type III survivorship curve (Fitt, 1989) and most mortality, biotic and abiotic, occurs during the egg and early larval stage (e.g. Kyi *et al.*, 1991). However, survivorship may vary between different crops and seasons (e.g. Van den Berg & Cock, 1993a). King *et al.* (1982), King and Coleman (1989) and Fitt (1989) reviewed the potential for biological control of *Heliothis/Helicoverpa* spp., focusing mainly on the New World species *Helicoverpa zea* (Boddie) and *Heliothis virescens* (Fabricius). King *et al.* (1982) listed several examples from the US where, in the absence of insecticides, natural enemies maintain *Heliothis* spp. populations below economic levels.

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This paper reviews research on the natural enemies of *H. armigera* in India. Included are updated lists of endemic parasitoids and predators, replacing earlier lists from Manjunath *et al.* (1989) and Nikam and Gaikwald (1989), as well as a list of exotic parasitoids introduced into India against *H. armigera.* The use of mass releases of *Trichogramma* spp. (native and exotic) for the biological control of *H. armigera* in India is also reviewed. Much of the work reviewed in this paper is unpublished or appears in books and journals not widely available outside India. The primary objectives of this paper are to make these results available to biocontrol workers outside India, and to provide a basis for further research on *H. armigera* natural enemies within India.

The term 'percentage parasitism' is used throughout this review. There are several problems associated with this term (see Van Driesche (1983) for further discussion). In the studies cited here, *H. armigera* eggs and/or larvae were collected in the field and held in the laboratory. The percentage parasitism has been estimated by simply dividing the number of hosts producing parasitoids by the total number of hosts collected. This does not accurately reflect the impact of specific parasitoids on *H. armigera* populations, but is the only measurement given in these studies. In this review, parasitism levels are only cited when both the host stage and the number of hosts collected are reported.

NATIVE EGG AND EGG–LARVAL PARASITOIDS

Six egg parasitoids from two families are recorded from India (Table 1), but only *T. chilonis* Ishii (Hymenoptera: Trichogrammatidae) is found in significant numbers in the eggs of *H. armigera* (Manjunath *et al.*, 1970; Sithanantham *et al.*, 1982a). This species was earlier known as *T. australicum* Girault or *T. confusum* Viggiani, which were synonomized with *T. chilonis* by Nagarkatti and Nagaraja (1979). Of the seven Trichogrammatoidea native to India (Nagaraja, 1978), *T. armigera* Nagaraja, *T. bactrae* Nagaraja and *T. bactrae* sp. *fumata* Nagaraja have been recorded from *H. armigera* eggs. Only a single, unconfirmed report of egg parasitism of *H. armigera* by a *Telenomus* sp. (Hymenoptera: Scelionidae) exists (Manjunath *et al.*, 1970). Four egg–larval parasitoids, all species of *Chelonus* (Hymenoptera: Braconidae), have been recorded parasitizing *H. armigera* eggs (Table 1).

The levels of egg parasitism by endemic *Trichogramma* spp. vary widely on different host plants (Table 2). The reasons for low parasitism rates on sunflower (*Helianthus annuus* Linnaeus) have not been investigated; on okra (*Abelmoschus esculentus* (H.) Moench), trichogrammatids are trapped and killed by the sticky exudate on the capsules (Goretzkaya, 1940). Chickpea secretes an acid exudate from all green tissues which is thought to interfere with *Trichogramma* spp. searching behaviour (Yadav *et al.*, 1985; Pawar *et al.*, 1986b). The only record of egg parasitism by native trichogrammatids on chickpea was by Gangaraddi (1987), who found 4% of eggs parasitized by *T. achaeae* Nagaraja and Nagarkatti around Dharwad (Karnataka). No details of sampling procedures or frequency were given, making it difficult to assess. On pigeonpea, parasitoids are repelled on or near the plant surface and walking behaviour has been found to be significantly hindered by trichomes and trichomal exudates on pigeonpea buds and pods (J. Romeis, unpublished).

In traditional pigeonpea–sorghum inter-cropping systems in India, where pigeonpea produces flowers at least 1 month after sorghum anthesis, *Trichogramma* spp. were found to parasitize only low levels of *H. armigera* eggs on the pigeonpea (Bhatnagar & Davies, 1981). When short-duration pigeonpea is inter-cropped with hybrid sorghum, flowering times and the availability of *H. armigera* eggs are more closely synchronized. In this system, Duffield (1994) found that the movement of the parasitoids to pigeonpea was facilitated and egg parasitism levels of up to 69% on different pigeonpea genotypes were recorded. Similar studies have not been able to duplicate these results (J. Romeis, unpublished).

Manjunath (1972) reported an average parasitism level of 4.5% ($n = 1175$) for *T. armigera* in *H. armigera* eggs on tuberose (*Polianthus tuberosa* Linnaeus). There are no reports of field parasitism rates for *T. bactrae* and *T. bactrae* sp. *fumata*. Similary, no levels of parasitism are reported for *Telenomus* sp.

TABLE 1. Parasitoids of *H. armigera* reported from India

Order, family and species[a]	Host stage parasitized[b]	Reference
DIPTERA		
Sarcophagidae		
Sarcophaga sp.	L?	Srinivas & Jayaraj, 1989
Seniorwhitea reciproca (Walker) (as *Sarcophaga orientaloides* White)	Lp	CIBC, 1974
Tachinidae		
Carcelia sp.	L?	Achan *et al.*, 1968
Carcelia S. L. ? *illolacum*[c]	L?	Raodeo, 1971 (in Raodeo & Sarkade, 1979)
Carcelia kockiana Townsend	L?	Achan *et al.*, 1968
[*Carcelia peraequalis* Mesnil]	L?	Achan *et al.*, 1968
Carcelia raoi[c]	L?	Rao, 1968
Compsilura concinnata Meigen	L	CIBC, 1974
Exorista bombycis (Louis)	L	Swamy *et al.*, 1993
Exorista japonica (Townsend)	L	Achan *et al.*, 1968
Exorista xanthaspis (Wiedemann)	L	Bhatnagar *et al.*, 1982
Exorista xanthaspis (Wiedemann) (as *E. fallax* of authors)	L	Achan *et al.*, 1968
Goniophthalmus halli Mesnil	Lp	Achan *et al.*, 1968
Hystricovoria bakeri Townsend (as *Afrovoria indica* (Mesnil)	L	Raodeo *et al.*, 1982
[*Pales coeruleo-nigra* (Mesnil)]	L	CIBC, 1974
Palexorista sp.	L	Mathur, 1970
Palexorista (as *Drino*) sp. nr. *unisetosa*	L	Achan *et al.*, 1968
Palexorista laxa (Curran) (as *Drino imberbis* (Wiedemann))[d]	L	Achan *et al.*, 1968
Palexorista (as *Drino*) *munda* (Wiedemann)	L	Chauthani & Hamm, 1967
Palexorista solennis (Walker)	L	ICRISAT, 1976
Peribaea spp.	L	Tripathi & Sharma, 1985
Peribaea orbata (Wiedemann)	L	Chari *et al.*, 1992
Peribaea orbata (Wiedemann) (as *Strobliomyia aegyptia* (Villeneuve))	L	Achan *et al.*, 1968
Pseudogonia rufifrons (Wiedemann) (as *Isomera cinerascens* (Rondani))	Lp	Achan *et al.*, 1968
Senometopia (as *Eucarcelia*) *illota* (Curran)	L or Lp	Achan *et al.*, 1968
Sisyropa apicata[c]	L	Achan *et al.*, 1968
Sisyropa formosa Mesnil	L	Raodeo *et al.*, 1982
Sturmiopsis inferens Townsend	L	ICRISAT, 1976
Suensonomyia n. sp.	?	Achan *et al.*, 1968
Thecocarcelia acutangulata (Macquart) (as *T. incedens* (Rondani))	L	Achan *et al.*, 1968
Voria ruralis (Fallen)	L	Achan *et al.*, 1968
Voria ruralis (Fallen) (as *V. edentata* Baranov)	L	Achan *et al.*, 1968
Winthemia sp. nr? *diversoides* Baranov	L	Achan *et al.*, 1968
Chloropidae		
Mepachymerus ensifer (Thomson)	L	Verma *et al.*, 1971
HYMENOPTERA		
Bethylidae		
Goniozus sp.	L	Sivagami *et al.*, 1975
Goniozus (as *Parasierola*) sp.	L	Divakar *et al.*, 1983
Odontepyris sp.	L	Rao, 1968
Braconidae		
Agathis fabiae (Nixon)	L	Srinivas & Jayaraj, 1989
Aleiodes (Rogas) sp.[e]	L	Yadav, 1980
Aleiodes sp.? *testaceus* (Spinola)	L	Pawar *et al.*, 1986a
Apanteles sp.	L	Achan *et al.*, 1968

TABLE 1. *Continued*

Order, family and species[a]	Host stage parasitized[b]	Reference
Apanteles sp. nr. *taprobanae* Cameron	L	Yadav, 1980
Apanteles sp. (*vitripennis* group)	L	Kushwaha, 1995
Apanteles angaleti Muesebeck	L	Patil *et al.*, 1991
Bracon sp.	L	Achan *et al.*, 1968
Bracon cushmani Muesebeck	L	CIBC, 1974
Bracon gelechiae Ashmead	L	Achan *et al.*, 1968
Bracon greeni (Ashmead)	L	Achan *et al.*, 1968
Bracon lefroyi (Dudgeon & Gough)	L	Seshu Reddy, 1973 (in Jayaramaiah & Jagadeesh Babu, 1992)
Chelonus sp.	El	Bhatnagar *et al.*, 1982
Chelonus curvimaculatus (Cameron)	El	Bhatnagar *et al.*, 1982
Chelonus formosanus Sonan	El	Yadav, 1980
Chelonus heliopae Gupta	El	Achan *et al.*, 1968
Chelonus narayani Subba Rao	El	Subba Rao, 1955
Cotesia (as *Apanteles*) sp. nr. *glomeratus* (Linnaeus)	L	Achan *et al.*, 1968
Cotesia (as *Apanteles*) sp. (*glomeratus* group)	L	Achan *et al.*, 1968
Cotesia (as *Apanteles*) *ruficrus* (Haliday)	L	Achan *et al.*, 1968
Cryptosalius sp.	L?	Srinivas & Jayaraj, 1989
Glyptapanteles (as *Apanteles*) sp. nr. *phytometrae* (Wilkinson)	L	Yadav, 1980
Habrobracon (as *Bracon*) *brevicornis* (Wesmael)	L	Achan *et al.*, 1968
Habrobracon (as *Bracon*) *hebetor* (Say)	L	CIBC, 1974
Microplitis sp.	L	Hussain & Mathur, 1924
Microplitis flaviventris Ivanov	L	Yadav, 1980
Snellenius (as *Microplitis*) *maculipennis* (Szepligeti)	L	Krishnamurti & Usman, 1954
Chalcididae		
Brachymeria albicrus (Klug) (as *B. responsator* (Walker))	P	Achan *et al.*, 1968
Brachymeria marmonti (Girault) (as *B. wittei* (Schmitz))[f]	—	Singh *et al.*, 1990
Eulophidae		
Euplectrus sp.	L	Mathur, 1970
Euplectrus euplexiae Rohwer	L	Singh & Balan, 1986
Stenomesius japonicus (Ashmead) (as *S. impressus* Masi)	L	Yadav, 1980
Tetrastichus howardi (Olliff) (as *T. ayyari* Rohwer)	P	Cherian & Subramaniam, 1940
Ichneumonidae		
Agrypon nox Morley	Lp	Mathur, 1970
Attractodes sp.	L	Hussain & Mathur, 1924
Banchopsis ruficornis (Cameron)	L	Mathur, 1967
Barichneumon sp.	Lp	Mathur, 1967
Briborus sp.	L?	Yadav, 1980
Campoletis sp.	L	CIBC, 1974
Campoletis chlorideae Uchida	L	ICRISAT, 1976
Campoletis multicinctus Gravenhorst	L	Dutt, 1923
Campoplex collinus (Morley)	L	Kakar & Dogra, 1989
Charops aditya Gupta & Maheshwary	L	Nanthagopal & Uthamasamy, 1989
Charops bicolor (Szepligeti)	L	Singh *et al.*, 1990
Disophrys sp.	L	Pawar *et al.*, 1986b
Ecthromorpha sp.	P	Raodeo *et al.*, 1982
Enicospilus sp.	L	Achan *et al.*, 1968
Enicospilus sp. nr. *shinkanus* Uchida	L	Pawar *et al.*, 1986b
Enicospilus sp. nr. *insinuator* (Smith) (as nr. *zyzzus* Chiu)	L	ICRISAT, 1976
Enicospilus capensis (Thunberg)	L	Gauld & Mitchell, 1981
Enicospilus heliothidis Viereck	L	Gauld & Mitchell, 1981
Enicospilus heliothidis Viereck (as *E. biconatus* Townes, Townes & Gupta)	L	Bilapate, 1981a

TABLE 1. *Continued*

Order, family and species[a]	Host stage parasitized[b]	Reference
Enicospilus melanocarpus Cameron	L	Gauld & Mitchell, 1981
Enicospilus shinkanus (Uchida)	Lp	Bhatnagar *et al.*, 1982
Enicospilus signativentris (Tosquinet)	L	Nikam, 1980
Enicospilus signativentris (Tosquinet) (as *E. pectiniclavae* Rao & Nikam)	L	Nikam, 1980
Eriborus sp.	L	Achan *et al.*, 1968
Eriborus argenteopilosus (Cameron)	L	Achan *et al.*, 1968
Eriborus pilosellus (Cameron)	L	Achan *et al.*, 1968
Eriborus trochanteratus (Morley)	L	Bhatnagar *et al.*, 1982
Eutanyacra (as Amblyteles) *albuannulatus* Cameron	P	CIBC, 1974
Gelis sp.	L?	Singh, 1994
Ichneumon sp.	L	ICRISAT, 1976
Leptobatopsis indica (Cameron)	L?	Srinivas & Jayaraj, 1989
Metopius rufus Cameron	L?	ICRISAT, 1976
Netelia sp.	L	Mathur, 1970
Temelucha sp.	L	Bhatnagar *et al.*, 1982
Xanthopimpla sp.	L?	Srinivas & Jayaraj, 1989
Xanthopimpla punctata (Fabricius)	P	CIBC, 1974
Xanthopimpla scutellare[c] (Fabricius)	P	CIBC, 1974
Xanthopimpla stemmator (Thunberg)	Lp	ICRISAT, 1976
Scelionidae		
Telenomus sp.	E	Manjunath *et al.*, 1970
Trichogrammatidae		
Trichogramma sp.	E	Bhatnagar *et al.*, 1982
Trichogramma achaeae Nagaraja & Nagarkatti	E	Nagaraja & Nagarkatti, 1969
Trichogramma chilonis Ishii (as *T. australicum* Girault, *T. confusum* Viggiani[g])	E	Manjunath *et al.*, 1970
Trichogrammatoidea sp.	E	Bhatnagar *et al.*, 1982
Trichogrammatoidea armigera Viggiani	E	Manjunath, 1972
Trichogrammatoidea bactrae Nagaraja	E	Jai Rao *et al.*, 1980
Trichogrammatoidea bactrae sp. *fumata* Nagaraja	E	Bhatnagar *et al.*, 1982

[a]Species in [square brackets] are African (N. P Wyatt, personal communication, 1996).
[b]E = egg; El = egg–larval; L = larval; Lp = larval–pupal; P = pupal parasitoid; L? = larvae were attacked, hos stage of emergence is unknown; ? = unknown.
[c]These species names are probably not valid (N. P. Wyatt, personal communication, 1996).
[d]Misidentification recognized by CIBC (1978).
[e]The genus *Rogas* was transferred to *Aleiodes* (see Van den Berg *et al.*, 1988).
[f]Hyper-parasitoid of Braconidae and Ichneumonidae (Bouček, 1988).
[g]Synonomized by Nagarkatti and Nagaraja (1979).

Little is known about the ecology of *Chelonus* spp. egg–larval parasitoids. Parasitism levels caused by *C. heliopae* Gupta and *C. narayani* Subba Rao were found to be 'negligible' in Rajasthan (Achan *et al.*, 1968). For *C. curvimaculatus* (Cameron), parasitism levels (based on samples of first to third instar larvae) were found to be below 2% on different crops, with 7.5% recorded on pearl millet by Pawar *et al.* (1986a) (Table 3). In addition, Duffield (1993) found that up to 5% of the first and second instar larvae collected ($n = 784$) on different pigeonpea varieties were parasitized by this parasitoid. Similar low levels of parasitism were reported by Kushwaha (1995) from first to sixth instar larvae collected on chickpea ($n = 1495$), pigeonpea ($n = 965$) ($< 1\%$) and lucerne (*Medicago sativa* Linnaeus) (2%, $n = 280$). The levels of parasitism caused by this group of parasitoids are likely to have been underestimated in many studies; the first two larval instars, which are difficult to find in the field and are often overlooked, are the optimal host stages from which to sample *Chelonus* spp.

The mass rearing of *Trichogramma* spp. has been widely studied. In India, they are usually reared on eggs of the factitious host *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae)

TABLE 2. Mean parasitism levels of *H. armigera* eggs caused by naturally occurring populations of *Trichogramma* spp. on different crops and weeds

Host plant	No. of eggs collected	Parasitism level (%)	Reference
Chickpea	4 084	0.0	Pawar *et al.*, 1986a[a]
	1 022	0.0	Sithanantham *et al.*, 1982a
	865	0.0	Yadav & Patel, 1981
	650	0.0	Yadav *et al.*, 1985
Cotton	158	60.1	Patel, 1980
	86	51.0	Naganagoud & Thontadarya, 198‹
	40	50.0	Yadav *et al.*, 1985
	150	38.0	Sithanantham *et al.*, 1982a
	245	29.8	Pawar *et al.*, 1986a
	150	3.0	Dhandapani *et al.*, 1992
Cowpea	887	37.0	Sithanantham *et al.*, 1982a
	1 048	35.8	Pawar *et al.*, 1986a
Green gram	23	17.4	Pawar *et al.*, 1986a
Groundnut	709	32.3	Sithanantham *et al.*, 1982a
	2 805	14.8	Pawar *et al.*, 1986a
Lucerne	122	29.5	Yadav *et al.*, 1985
Maize	392	47.2	Sithanantham *et al.*, 1982a
	3 150	32.9	Pawar *et al.*, 1986a
Okra	150	8.0	Thontadarya *et al.*, 1978
	124	5.0	Naganagoud & Thontadarya, 198‹
	680	0.1	Pawar *et al.*, 1986a
	676	0.1	Sithanantham *et al.*, 1982a
Pearl millet	255	15.3	Sithanantham *et al.*, 1982a
	3 281	12.5	Pawar *et al.*, 1986a
Pigeonpea	26 756	0.2	Pawar *et al.*, 1986a
	6 887	0.2	Sithanantham *et al.*, 1982a
Potato	407	56.0	Yadav *et al.*, 1985
Safflower	612	17.5	Pawar *et al.*, 1986a
Sorghum	9 466	40.6	Sithanantham *et al.*, 1982a
	35 408	33.6	Pawar *et al.*, 1986a
Sunflower	287	0.3	Pawar *et al.*, 1986a
Tomato	585	14.9	Yadav *et al.*, 1985
	440	2.3	Sithanantham *et al.*, 1982a
	447	2.2	Pawar *et al.*, 1986a
Tuberose	1 175	35.7	Manjunath, 1972
Acanthospermum hispidum	173	4.0	Pawar *et al.*, 1986a
Cleome gynandra	160	0.0	Pawar *et al.*, 1986a
Cocculus hirsutus	50	6.0	Pawar *et al.*, 1986a
Commelina benghalensis	115	9.6	Pawar *et al.*, 1986a
Corchorus trilocularis	108	1.0	Pawar *et al.*, 1986a
Datura metel	2 688	0.4	Pawar *et al.*, 1986a
Emilia sonchifolia	50	6.0	Pawar *et al.*, 1986a

TABLE 2. *Continued*

Host plant	No. of eggs collected	Parasitism level (%)	Reference
Lagascea mollis[b]	1 935	0.5	Pawar *et al.*, 1986a
	4 204	5.9	Romeis, unpublished
Sesbania bispinosa	50	16.0	Pawar *et al.*, 1986a
Sonchus oleraceus	295	9.1	Pawar *et al.*, 1986a

[a]Parts of the data in Pawar *et al.* (1986a) have been reported in Bhatnagar *et al.* (1982, 1983) and Pawar *et al.* (1986b, 1989a).
[b]Earlier misidentified as *Gomphrena celosioides* (N. J. Armes, personal communication, 1996).

TABLE 3. Parasitism levels of *H. armigera* larvae by common parasitoids on different crops and weeds in Andhra Pradesh, Maharashtra and Karnataka (after Pawar *et al.*, 1986a)[a]

	No. of larvae collected[b]		Parasitism level (%) caused by			
Crop	L1–L3	L4–L6	*Chelonus curvimaculatus*[c]	*Eriborus* spp.[c]	*Senometopia illota*[d]	*Goniophtalmus halli*[d]
Bean	9	116	0.0	0.0	0.9	1.7
Chickpea	33 960	30 398	<0.1	<0.1	7.0	0.4
Cotton	86	115	0.0	0.0	0.0	0.0
Cowpea	1 949	4 256	0.2	0.1	0.8	3.3
Green gram	58	738	1.7	0.0	3.1	0.4
Groundnut	3 627	3 308	<0.1	0.2	1.5	1.9
Linseed	1 040	1 020	0.5	12.1	8.1	15.2
Maize	556	1 669	0.0	0.5	0.3	0.2
Onion	21	80	0.0	0.0	3.8	1.2
Pearl millet	784	365	7.5	1.3	6.3	0.5
Pigeonpea	21 294	68 394	<0.1	5.6	8.2	7.4
Safflower	2 831	2 509	1.0	6.5	7.5	1.6
Sorghum	19 104	18 627	1.3	1.4	3.4	0.4
Sunflower	224	127	0.0	0.0	0.0	4.7
Tomato	973	2 076	0.0	0.1	0.3	0.3
Acanthospermum hispidum	485	1 566	3.7	0.2	0.0	0.1
Cleome gynandra	1 546	480	7.1	0.8	0.0	0.0
Datura metel	2 227	2 891	0.0	0.0	0.9	0.2
Lagascea mollis[e]	3 943	1 800	3.0	0.4	0.5	1.0
Sesbania bispinosa	101	592	0.0	13.9	4.6	20.1

[a]Parts of the data in Pawar *et al.* (1986a) have been reported in Bhatnagar *et al.* (1983) and Pawar *et al.* (1985a, 1986b, 1989a).
[b]L1–L3 = first to third instar larvae; L4–L6 = fourth to sixth instar larvae.
[c]Parasitism levels are based on collected first to third instar larvae.
[d]Parasitism levels are based on collected fourth to sixth instar larvae.
[e]Earlier misidentified as *Gomphrena celosioides* (N. J. Armes, personal communication, 1996).

(Singh *et al.*, 1994a). Navarajan Paul *et al.* (1981) have shown this to be a suitable alternative to *H. armigera*. Before exposure to the parasitoids, *C. cephalonica* eggs should be killed because the larvae are cannibalistic. Eggs are usually killed by ultraviolet (UV) irradiation (Maninder & Varma, 1980; Singh *et al.*, 1994a). The recommended exposure time varies according to the intensity of the UV source. Hugar *et al.* (1990) showed that eggs could be killed by chilling at −5°C for 48 h, but these eggs were significantly less acceptable to *T. chilonis* than were untreated eggs. Parasitized eggs can be stored at 10°C for as long as 49 days without affecting parasitoid survival (Jalali & Singh, 1992). Patil *et al.* (1978) reported that eggs parasitized by the exotic *T. brasiliensie* Ashmead could be stored at 8°C for up to 1 week without affecting parasitoid fecundity. Several potentially serious constraints to mass rearing *T. chilonis* have been reported. Laboratory-reared females have shown a significantly higher degree of sterility than wild-type females (Nagarkatti & Nagaraja, 1978), and laboratory-reared populations were more sensitive to both high and low temperatures than wild types (Nagarkatti, 1979).

In searching for strains of *T. chilonis* better adapted to certain field conditions, Mandal and Somchoudhury (1991), as well as Jalali and Singh (1993), compared parasitoid populations collected from different habitats and localities. They found variations in morphometric and biological attributes, such as the number of host eggs parasitized per female and adult longevity. Abraham and Pradhan (1976) attempted to select a *T. chilonis* strain adapted to high temperatures and low humidity, but without success.

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Another egg parasitoid, *T. bactrae*, was successfully reared on *C. cephalonica* eggs (Jai Rao *et al.*, 1980). Neither species of Trichogrammatoidae has been mass reared.

The potential for mass rearing the egg–larval parasitoid *C. heliopae* has been studied by Patel *et al.* (1973). One-day-old eggs of *Spodoptera litura* Fabricius (Lepodoptera: Noctuidae) were the most suitable factitious hosts. Super-parasitism was common in laboratory cultures and was suspected to be the reason why large numbers of parasitized eggs failed to hatch. Subba Rao (1955) successfully reared *C. narayani* on *C. cephalonica*.

Patel (1975) attempted weekly field releases of *C. heliopae* in 0.4-ha plots of tomato and chickpea. In tomato, the highest parasitism rate (6–7%) was reached after two releases of 150 000 parasitoids per hectare per week or after five releases of 100 000 parasitoids per hectare per week. In chickpea, the maximum parasitism rate was higher (up to 21%) after four releases of 100 000 parasitoids per hectare per week. 'Young' post larvae were collected to evaluate the parasitism level. This parasitoid was not successful in regulating *H. armigera* populations in either crop.

NATIVE LARVAL AND LARVAL–PUPAL PARASITOIDS

The largest group of *H. armigera* natural enemies reported from India are the larval and larval–pupal parasitoids with more than 60 identified species (Table 1).

The most important and well-studied larval parasitoid, *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae), is reported to be an important mortality factor for *H. armigera* on several crops and weeds (Table 5). It preferentially attacks second instar larvae (Nikam & Gaikwald, 1989) and is therefore potentially effective in suppressing larval populations before significant damage is caused (Nikam & Gaikwald, 1991; Kushwaha, 1995). Parasitoid larvae emerge from third and fourth instar host larvae to pupate and spin a cocoon, and thus sampling the first three instars of *H. armigera* larvae would be necessary to evaluate accurately the impact of this parasitoid. Unfortunately, very few authors have collected only the small (first to third instar) larvae. Therefore, as a comparison, parasitism levels measured on collections of first to sixth instar larvae are also listed in Table 5. As the table shows, collecting all larval instars underestimates the actual parasitoid impact.

Pimbert and Srivastava (1989) found significantly higher levels of *H. armigera* larvae parasitized by *C. chlorideae* on chickpea inter-cropped with coriander (*Coriandrum sativum*

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	10	7	250 000	*T. chilonis*	0.2	27–96	15–52	65% Reduction in fruit damage	Yadav *et al.*, 1985
	8	10	125 000	*T. chilonis*	0.2	20–50	0–11	No record	Yadav *et al.*, 1985
	6	7	50 000	*T. brasiliense*	1.0	78	12	55% Reduction in fruit damage	Singh *et al.*, 1994b
	?[c]	7	250 000	*T. chilotraeae*	?	92	?	50–75% Reduction in fruit damage	Patel (in Stinner, 1977)
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[c]Unknown.

TABLE 5. Mean parasitism levels of *H. armigera* larvae caused by *C. chlorideae* on different crops and weeds

	No. of larvae collected[a]		Parasitism level (%)[a]		
Crop	L1–L3	L1–L6	L1–L3	L1–L6	Reference
Chickpea		78		35.9	Prasad & Chand, 1986
		14 950		18.5	Kushwaha, 1995
	33 960	64 358	29.2	15.4	Pawar *et al.*, 1986a[b]
		666		12.2	Bilapate, 1981b
	18 111	30 222	14.7	8.8	Bilapate *et al.*, 1988
Cotton		405		10.4	Bilapate, 1981b
		135		9.6	Patel, 1980
	86	201	8.1	3.5	Pawar *et al.*, 1986a
		119		2.5	Kushwaha, 1995
Cowpea	1 949	6 205	6.9	2.2	Pawar *et al.*, 1986a
Green gram	58	796	13.8	1.0	Pawar *et al.*, 1986a
Groundnut	3 627	6 935	6.8	3.6	Pawar *et al.*, 1986a
Linseed	1 040	2 060	13.6	6.8	Pawar *et al.*, 1986a
Lucerne		566		3.9	Kushwaha, 1995
Maize	556	2 225	17.8	4.4	Pawar *et al.*, 1986a
		52		3.8	Kushwaha, 1995
Pea		86		24.4	Kushwaha, 1995
Pearl millet	784	1 149	49.0	33.4	Pawar *et al.*, 1986a
Pigeonpea		965		10.2	Kushwaha, 1995
		202		1.5	Bilapate, 1981b
	(1 256)[c]	1 393	(1.6)	1.4	Duffield, 1993
	21 294	89 688	3.6	0.9	Pawar *et al.*, 1986a
	13 625	26 437	1.4	0.7	Bilapate *et al.*, 1988
Safflower		738		36.2	Pawar *et al.*, 1985a
	2 831	5 340	41.6	22.1	Pawar *et al.*, 1986a
		49		12.2	Bilapate, 1981b
		481		11.8	Kushwaha, 1995
Sorghum	19 104	37 731	49.2	24.9	Pawar *et al.*, 1986a
	(402)		(17.2)		Duffield, 1993[c]
Sunflower	224	351	6.3	4.0	Pawar *et al.*, 1986a
Tomato		3 311		4.2	Kushwaha, 1995
	973	3 049	5.3	1.7	
Acanthospermum hispidum	485	2 051	2.1	0.5	Pawar *et al.*, 1986a
Cleome gynandra	1 546	2 026	6.6	5.0	Pawar *et al.*, 1986a
Datura metel	2 227	5 118	7.6	3.2	Pawar *et al.*, 1986a
Lagascea mollis[d]	3 943	5 743	21.4	14.7	Pawar *et al.*, 1986a
Sesbania bispinosa	101	693	23.8	3.5	Pawar *et al.*, 1986a
Aeschynomene indica	65	230	24.6	7.0	Pawar *et al.*, 1986a

[a]L1–L3 = first to third instar larvae; L1–L6 = first to sixth instar larvae.
[b]Parts of the data in Pawar *et al.* (1986a) have been reported in Bhatnagar *et al.* (1983) and Pawar *et al.* (1985a, 1986b, 1989a,b).
[c]Data in parentheses are based on collected first to fourth instar larvae.
[d]Earlier misidentified as *Gomphrena celoisoides* (N. J. Armes, personal communication, 1996).

TABLE 6. Parasitism levels of first to sixth instar *H. armigera* larvae by the tachinids *Carcelia* spp. (most probably including *S. illota*) in Maharashtra (after Bilapate, 1981b)

Crop	No. of larvae (first to sixth instar) collected	Parasitism level (%) caused by	
		Carcelia spp.	*G. halli*
Chickpea	666	0.0	6.5
Cotton	405	0.5	1.2
Pigeonpea	202	4.0	5.9
Safflower	49	0.0	10.2
Sorghum	25	52.0	8.3

Linnaeus) than on sole cropped chickpea plants. They suggested that nectar-rich coriander plants were used as an adult food source and attracted parasitoids to the chickpea crop.

There was much confusion about the taxonomic status of *C. chlorideae*. It was earlier misidentified as *Diadegma* (*Horogenes*) *fenestrale* (Holmgren) (Tikar & Thakare, 1961; see Mathur & Dharmadhikari, 1970) or as *C. flavicincta* (Ashmead) (*C. perdistinctus* (Viereck)) (Gangrade, 1964; Achan *et al.*, 1968; Vaishampayan & Veda, 1980). The latter is known as a parasitoid of *Heliothis* spp. from the Americas (Kogan *et al.*, 1989) and does not occur in India. This misidentification was discussed by Gupta (1974). However, Singh *et al.* (1991) still listed *D. fenestrale* as a parasitoid of *H. armigera.*

One other genus of hymenopteran larval parasitoids, *Eriborus* spp. (Hymenoptera: Braconidae), can cause significant mortality in the first to third instar larvae on some crops and weeds (Table 3). Kushwaha (1995) collected first to sixth instar larvae on different crops and reported 23% parasitism from pigeonpea ($n = 90$) and less than 1% from chickpea ($n = 14\,950$) and lucerne ($n = 112$). Duffield (1993) collected over 400 first to fourth instar larvae sorghum and reported less than 1% parasitism by *Eriborus* spp. They preferentially parasitize second instar larvae (Nikam *et al.*, 1990).

Tachinids are the most important group of dipteran parasitoids. They parasitize older instars and emerge from sixth instar larvae or pupae (Bilapate, 1981a,c; Nikam & Gaikwald, 1989). Achan *et al.* (1968) and Rao (1968) found 16–20% of *H. armigera* larvae (based on collections of first to sixth instar larvae) to be parasitized by each of three species: *Palexorista laxa* (*Curran*) (earlier misidentified as *Drino imberbis* (Wiedemann), as recognized by the Commonwealth Institute of Biological Control (CIBC), 1978) and the larval–pupal parasitoids *Senometopia* (as *Eucarcelia*) *illota* (Curran) and *Goniophthalmus halli* Mesnil. *S. illota*, emerges from host larvae (as a larval parasitoid) when early instars have been parasitized (Patel *et al.*, 1970). Collecting fourth to six or first to sixth instar host larvae, Pawar *et al.* (1986a) and Bilapate (1981b) respectively observed differences in the level of parasitism caused by tachinids among different crops and weeds (Tables 3 and 6). One difficulty with the study by Bilapate (1981b) is that all larval instars (first to sixth) were collected. As mentioned earlier, this will underestimate the level of parasitism and may also bias the comparison between host plants. For example, small larvae are easier to find on chickpea than on pigeonpea (Reed *et al.*, 1987; Reed & Lateef, 1990), and the proportion of large larvae collected will be relatively higher on pigeonpea, resulting in an overestimate of the level of parasitism caused by tachinids. Patel *et al.* (1970) reported a mean parasitism level of 9.9% caused by *S. illota* on fourth to sixth instar host larvae ($n = 3982$) collected on different crops. Duffield (1993) sampled third to sixth instar larvae ($n = 747$) on piegeonpea and reported a parasitism level of 6.3% caused by tachinids.

The host plant on which *H. armigera* is found has an important effect on the distribution and abundance of larval parasitoids. Some authors (e.g. Bhatnagar *et al.*, 1982; Sithanantham, 1985) have generalized that larvae of *H. armigera* on pigeonpea suffer greater parasitism by dipteran than by hymenopteran parasitoids, while on chickpea the latter are more common. This may be true for some techinids (Tables 3 and 6; Sithanantham, 1981) and *C. chlorideae* (Table 5) but should not be extrapolated to all dipteran and hymenopteran larval parasitoids. Sithanantham *et al.* (1982b, 1983) observed that the choice of cultivar could affect the efficacy of larval parasitoids. They reported lower parasitization rates on resistant, compared with susceptible, cultivars of chickpea and pigeonpea.

The development of techniques used to rear larval parasitoids has largely focused on *C. chlorideae.* The optimal developmental temperature for *C. chloridae* was 31°C (Nikam & Basarkar, 1978); at this temperature, egg-to-adult development was completed in 17 days, and adult longevity was 9 days when insects were provided with 20% honey solution. Patel *et al.* (1988a) observed 100% emergence in *C. chlorideae* pupae stored at 8.2°C for 10 days, but after 15 days emergence declined to 75%. The adult life span, however, was not adversely affected. Although this preliminary work has been carried out, a technique for mass producing *C. chlorideae* is still not available (Manjunath, 1992). Two factors limiting *C. chlorideae* rearing are the high mortality among parasitized larvae and an unfavourable sex ratio (>4 males:females) in laboratory-reared parasitoids (Patel, 1975). Basarkar and Nikam (1982) also reported a male-biased sex ratio in laboratory cultures.

Krishnamoorthy and Mani (1989) recommended using 4-day-old *S. litura* larvae as an alternative host for rearing *E. argenteopilosus* (Cameron) because laboratory cultures are less susceptible to viral and bacterial diseases. *S. litura* is readily accepted by the parasitoid.

Rearing methods for three tachinid parasitoids, *G. halli*, *S. illota* and *Palexorista* (as *Drino*) *munda* (Wiedemann), have been reported. *G. halli* must be reared on *H. armigera* larvae. Attempts to rear this species on alternative lepidopteran hosts were not successful (Patel & Singh, 1972). At 27°C egg-to-adult development was completed in 23 days. Only one parasitoid emerged from each host, but as many as 87% of the laboratory-reared puparia produced adults (Patel & Singh, 1972). Patel *et al.* (1970) reared *S. illota* at 27°C; egg-to-adult development was completed in 25 days and females produced an average of 168 eggs. At 32°C development was faster (22 days), but the emerging adult flies were unable to expand their wings. Higher parasitism levels were recorded when host larvae were infested with two or three parasitoid eggs (60 or 64% respectively) instead of one (48%). However, the percentage of parasitoid puparia obtained was higher when only one egg was placed in each host larva (48, 35 and 30% for one, two and three eggs respectively), because generally only one parasitoid maggot emerged from each host (Patel *et al.*, 1970). Host larvae were anaesthetized to reduce host defensive behaviour. A rearing method for *P. munda* was developed in the US after importation from India. Chauthani and Hamm (1967) reared this parasitoid at 26–28°C and 70–90% relative humidity on both *H. virescens* and *S. frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). Several authors have observed that tachinid parasitoids must be exposed to sunlight to stimulate mating (Achan *et al.*, 1968; Patel *et al.*, 1970; Patel & Singh, 1972). In contrast, Chauthani and Hamm (1967) reported that *P. munda* mated successfully under laboratory conditions without such exposure. The potential for using larval parasitoids in augmentative releases has been evaluated in the US with promising results (King *et al.*, 1982; King & Coleman, 1989), but no such effort has been made in India.

Mass rearing larval parasitoids on *H. armigera* is laborious and inefficient since parasitized larvae must be reared in isolation to avoid cannibalism (Nagarkatti, 1982). An effective and economical mass-rearing method must be developed before larval parasitoids can be used in biological control. Possible solutions would be to use factitious hosts or an artificial diet; some successful examples of the latter are listed by Greany *et al.* (1984). The larvae of *H. peltigera* (Denis & Schiffermüller) (Lepidoptera: Noctuidae) could be used as an alternative host for some parasitoids (N. J. Armes, personal communication, 1995). Larvae of *H. peltigera* are not cannibalistic and are hosts of important parasitoids such as *C. chlorideae* (Manjunath *et al.*, 1976).

NATIVE PUPAL PARASITOIDS

In contrast to the large number of larval parasitoids, only five pupal parasitoids have been recorded from *H. armigera* in India: the chalcid *Brachymeria albicrus* (Klug) (as *B. responsator*

Walker), the eulophid *Tetrastichus howardi* (Olliff) (as *T. ayyari* Rhower) and three ichneumonids (Table 1). Only negligible parasitism levels are reported for these pupal parasitoids (Cherian & Subramaniam, 1940; Achan *et al.*, 1968; CIBC, 1974).

However, in life-table studies, pupal mortality is underestimated. As *H. armigera* pupates under the soil surface (Ghosh *et al.*, 1986), pupae are only rarely sampled. Therefore, the pupal mortality reported in *H. armigera* life tables (e.g. Bilapate *et al.*, 1979; Nanthagopal & Uthamasamy, 1989; Tripathi & Singh, 1991) is caused by larval–pupal parasitoids and does not include the impact of true pupal parasitoids. The effect of pupal parasitoids may be important and should not be underestimated. For example, in Australia, Murray (1991) found that 8.2% of the pupae ($n = 124$) collected in chickpea were parasitized by *Ichneumon promissorius* Erichson (Hymenoptera: Ichneumonidae).

PREDATORS

In India more than 60 species of arthropods are recorded as predators of *H. armigera* (Table 7). However, this relationship has not been confirmed for about one-third of them under field conditions.

The biology of most of these predators is unknown, and their role in regulating *H. armigera* populations, individually or as a group, has not been quantified. Few studies have attempted to estimate the impact of potential predator species on *H. armigera* populations. In comparison, Van den Berg and Cock (1993a,b) have shown that in East Africa, predators, especially ants and anthocorids, are the most important group of natural enemies of *H. armigera* on maize, sorghum and sunflower.

Chrysopids have been the most extensively studied group of *H. armigera* predators. Singh *et al.* (1994b) studied the feeding potential of four native chrysopid predators in the laboratory. *Mallada boninensis* (Okamoto) was the most effective, and consumed up to 463 *H. armigera* eggs/first instar chrysopid larva, followed by *Apertochrysa* sp. (364 eggs/larva), *M. astur* (Banks) (244 eggs/larva) and *Chrysoperla carnea* Stephens (175 eggs/larva). During its larval development, a single larva of *Brinckochrysa* (as *Chrysopa*) *scelestes* (Banks) (Neuroptera: Chrysopidae) consumed 665 eggs or 410 young larvae. Its larval development was completed in 8.6 days when fed on eggs and 11.7 days when fed on larvae (Krishnamoorthy & Mani, 1982). However, the feeding potential of chrysopids has not been tested in the field.

Other predators such as the mud wasps, *Delta pyriforme* (Fabricius), *D. companiforme esuriens* Fabricius and *D. conoideus* (Gmelin) (Hymenoptera: Eumenidae), which prey on larvae of *H. armigera*, have only limited value in controlling the pest because of their long generation time. Their activity might be increased by providing sources of water and nesting sites protected from ants (Pawar & Jadhav, 1983). This type of habitat manipulation to augment natural enemies has not been investigated.

The feeding potential of the ant species recorded as predators on *H. armigera* is still unknown. Observations by King (1986) at ICRISAT indicated a high larval mortality by *Camponotus* sp. An ongoing study at ICRISAT indicates that ants may be important predators of *H. armigera* pupae (K. B. Tawar, personal communication, 1995). The host plant has an impact on the efficacy of ants and perhaps other predators. Romeis *et al.* (1996) observed *Paratrechina longicornis* (Latreille) removing *H. armigera* eggs from potted pigeonpea plants. Large numbers of eggs were removed from leaves, while eggs on flower-buds, flower-petals or pods suffered significantly less predation. The difference seems to be due to the type and distribution of trichomes on different pigeonpea plant structures.

Very few studies have investigated the abundance and within-plant distribution of different predators. Duffield (1993, 1995) studied predators in pigeonpea–sorghum fields and found the following predatory groups to be most abundant: neuropterans, mainly chrysopids; coccinellids, mainly *Chilomenes* (as *Menochilus*) *sexmaculatus* (Fabricius); anthocorids, mainly *Orius* spp. and spiders. Only the anthocorids showed a seasonal abundance and within-plant distribution pattern mirroring that of *H. armigera* eggs. Anthocorids may use *H. armigera* eggs as prey more

TABLE 7. Arthropod predators of *H. armigera* reported from India

Order, family and species	Reported stage attacked[a]	Reference
COLEOPTERA		
Anthicidae		
Formicomus sp.	E	Sigsgaard, 1996
Carabidae		
Calosoma indicum Hope[b]	?	Singh *et al.*, 1990
Coccinellidae		
Chilomenes (as *Menochilus*) *sexmaculatus* Fabricius	E, L	Bhatnagar *et al.*, 1983
Coccinella septempunctata (Linnaeus)	E, L	Mehto *et al.*, 1986
Staphilinidae		
Unidentified species	L	Singh, 1994
DERMAPTERA		
Carcinophoridae		
Euborellia annulata (Fabricius) (as *E. stalli* (Dohrn))	L	Bhatnagar *et al.*, 1983
Euborellia annulipes (Lucas)	L	Bhatnagar *et al.*, 1983
Labiduridae		
Nala lividipes (Dufour)	L	Bhatnagar *et al.*, 1983
ORTHOPTERA		
Mantidae		
Humbertiella sp.	L	Bhatnagar *et al.*, 1983
HEMIPTERA		
Anthocoridae		
Orius albidipennis (Reuter)[b]	E, L	Salim *et al.*, 1987
Orius maxidentex (Ghauri)	E, L	Bhatnagar *et al.*, 1983
Orius tantillus (Motschulsky)	E, L	Sigsgaard & Esbjerg, 1994
Lygaeidae		
Paromius gracilis (Rambur)	L	Bhatnagar *et al.*, 1983
Miridae		
Cyrtopeltis (as *Nesidiocoris*) *tenuis* (Reuter)[b]	?	Chari *et al.*, 1992
Nabidae		
Nabis spp.	L	Yadav, 1990
Nabis (as *Tropiconabis*) *capsiformis* Germar	L	Bhatnagar *et al.*, 1983
Pentatomidae		
Andrallus spinidens (Fabricius)[b]	L	Rajendra & Patel, 1971
Cantheconidea (*Eocanthecona*) (as *Canthecona*) sp.	L	Bhatnagar & Davies, 1978
Cantheconidea (*Eocanthecona*) *furcellata* (Wolff)	L	Bhatnagar *et al.*, 1983
Reduviidae		
Acanthaspis pedestris Stål[b]	L	Sahayaraj & Ambrose, 1994
Acanthaspis quinquespinosa (Fabricius)[b]	L	Sahayaraj, 1991 (in Ambrose, 1995)
Catamiarus brevipennis (Serville)	L	Bhatnagar *et al.*, 1983
Coranus sp.	L	Yadav, 1980
Coranus spiniscutis Reuter	L	CIBC, 1974
Ectomocoris tibialis Distant[b]	L	Ambrose, 1985 (in Ambrose, 1995)
Ectomocoris xavierei Vennison & Ambrose[b,c]	L	Vennison, 1988 (in Ambrose, 1995)
Ectrychotes dispar Reuter	L	Bhatnagar *et al.*, 1983
Edocla slateri Distant[b]	L	Ambrose, 1985 (in Ambrose, 1995)
Endochus inornatus Stål[b]	L	Lakkundi, 1989 (in Ambrose, 1995)

TABLE 7. *Continued*

Order, family and species	Reported stage attacked[a]	Reference
Endochus parvispinus Distant[b]	L	Lakkundi, 1989 (in Ambrose, 1995)
Endochus umbrinus Distant[b]	L	Sahayaraj, 1991 (in Ambrose, 1995)
Euagoras plagiatus (Burmeister)[b]	L	Vennison, 1988 (in Ambrose, 1995)
Isyndus heros Fabricius[b]	L	Lakkundi, 1989 (in Ambrose, 1995)
Lestomerus (as *Pirates*) *affinis* (Serville)[b]	L	Ambrose, 1985 (in Ambrose, 1995)
Oncocephalus annulipes Stål	L	CIBC, 1974
Rhynocoris (as *Harpactor*) *costalis* (Stål)[b]	L	Krishnananda & Satyanarayana, 1984 (in Chari *et al.*, 1992)
Rhynocoris fuscipes (Fabricius)	L	CIBC, 1974
Rhynocoris kumarii Ambrose & Livingstone[b,c]	L	Ambrose, 1985 (in Ambrose, 1995)
Rhynocoris lapidicola Samuel & Joseph[b]	L	Joseph, 1959
Rhynocoris marginatus (Fabricius)	L	Bhatnagar *et al.*, 1983
Rhynocoris scualis[b,c]	L	Krishnananda & Satyanarayana, 1984 (in Chari *et al.*, 1992)
Sycanus indagator Stål	L	CIBC, 1974
Sycanus reclinatus Dohrn[b]	L	Vennison & Ambrose, 1992 (in Ambrose, 1995)
Sycanus versicolor Dohrn[b]	L	Kumaraswami & Ambrose, 1992
HYMENOPTERA		
Eumenidae		
Delta companiforme esuriens Fabricius	L	Pawar & Jadhav, 1983
Delta conoideus (Gmelin)	L	Pawar & Jadhav, 1983
Delta pyriformis (Fabricius)	L	Pawar & Jadhav, 1983
Formicidae		
Camponotus sp.	L	King, 1986
Camponotus sericeus (Fabricius)[d]	L	Manjunath *et al.*, 1976
Cataglyphis bicolor (Fabricius)	L	Khan & Sharma, 1972
Dorylus labiatus Shuckard	L	Mehto *et al.*, 1986
Paratrechina longicornis (Latreille)	E	Romeis *et al.*, 1995
Pheidole sp.	E	Romeis *et al.*, 1995
Solenopsis geminata (Fabricius)	L	Dhandapani *et al.*, 1994
Tapinoma melanocephalum (Fabricius)	E, L	Musthak Ali, personal communication, 1995
Sphecidae		
Sphex argentatus Fabricius	L	Bhatnagar *et al.*, 1983
Vespidae		
Polistes olivaceus (DeGeer)	L	Bhatnagar *et al.*, 1983
Polistes olivaceus (DeGeer)[b] (as *P. hebraeus* Fabricius)	L	Singh *et al.*, 1990
Ropalidia marginata (Lepeletier)	L	Bhatnagar *et al.*, 1983
Vespa orientalis (Linnaeus)	L	Bhatnagar *et al.*, 1983
Vespa sincta[b,c]	L	Bhat & Virupakshappa, 1992
Vespa tropica haemotodes Bequaert	L	Bhatnagar *et al.*, 1983
NEUROPTERA		
Chrysopidae		
Apertochrysa sp.[b]	E	Singh *et al.*, 1994b
Brinckochrysa (as *Chrysopa*) *scelestes* (Banks)	E, L	Krishnamoorthy & Mani, 1982
Chrysopa sp.	E, L	Bhatnagar *et al.*, 1983
Chrysoperla sp.	E, L	Srinivas & Jayraj, 1989
Chrysoperla carnea (Stephens)[d]	E, L	Manjunath *et al.*, 1976
Mallada astur (Banks)[b]	E	Singh *et al.*, 1994b
Mallada boninensis (Okamoto)[b]	E	Singh *et al.*, 1994b

TABLE 7. *Continued*

Order, family and species	Reported stage attacked[a]	Reference
ARACHNIDA: ARANEAE		
Araneidae		
Leucauge tessellata (Thorell)	L	Bhatnagar *et al.*, 1983
Neoscona theisi (Walckenaer)	L	Bhatnagar *et al.*, 1983
Clubionidae		
Cheiracanthium inornatum O. P. Cambridge	E, L	Sigsgaard, 1996
Clubiona sp.	L	Bhatnagar *et al.*, 1983
Oxyopidae		
Oxyopes sp.	L	Singh, 1994
Oxyopes ratnae Tikader	L	Dhulia & Yadav, 1991
Thomisidae		
Ozyptila reenae Basu	L	Bhatnagar *et al.*, 1983
Thomisus sp.	L	Bhatnagar *et al.*, 1983

[a]E = egg; L = larvae; ? = unknown.
[b]These species were either observed preying on *H. armigera* in the laboratory or the location of the observation (field or laboratory) is unknown.
[c]These species names are probably not valid (G. R. Stonedahl and A. Polaszek, personal communication, 1996).
[d]First reported to attack *H. peltigera* but now recognized as also attacking *H. armigera*.

readily than other generalist predators. The abundance of all predators was much lower on pigeonpea than on sorghum, although pigeonpea supported higher densities of *H. armigera*. For example, anthocorids were found at a peak 'per plant' density of 3.6 on sorghum and only 0.5 on pigeonpea. Similar crop-specific differences were reported for adult coccinellids (1.6 versus 0.6), neuropteran eggs (3.0 versus 0.2) and spiders (1.2 versus 0.7) (Duffield, 1995). Sigsgaard and Esbjerg (1994) also found *O. tantillus* (Motschulsky) to be a more effective predator on sorghum than on pigeonpea. The predator was more active on reproductive than vegetative structures of both plants, and fed on eggs and first instar larvae of *H. armigera*.

On black gram (*Vigna mungo* (Linnaeus) Hepper), Dhuri *et al.* (1986) found a significantly higher density of the coccinellid *C. septempunctata* (Linnaeus) when it was inter-cropped with sorghum and a larger number of the predatory wasp *Polistes olivaceus* (DeGeer) (as *P. hebraeus* Fabricius) (Hymenoptera: Vespidae) on plants inter-cropped with green gram (*V. radiata* Linnaeus) in comparison with sole crops.

Mehto *et al.* (1986) recorded a maximum of 0.3 spiders and 0.7 *C. septempunctata* per chickpea plant. Other studies have noted the abundance of predatory spiders, but without recording their efficacy (Singh & Singh, 1977; Dhulia & Yadav, 1991). Laboratory studies of the feeding potential of *Clubiona* sp. (Acarina: Clubionidae) showed that these spiders can consume a large number of *H. armigera* eggs (59/day) and young larvae (three/day) (ICRISAT, 1982).

The usefulness of ants, anthocorids and chrysopids as egg predators must be weighted against the possible disadvantage of them feeding on parasitized eggs. Egg predation may be an important mortality factor for egg parasitoids because parasitized eggs remain in the field up to three times longer than unparasitized eggs, and are therefore exposed to predators for a longer period. Krishnamoorthy and Mani (1985) observed the feeding behaviour of larvae of *B. scelestes* on *H. armigera* eggs parasitized by *T. chilonis*. There was no difference in consumption between fresh unparasitized eggs and 1-day-old parasitized eggs, but the predator consumed significantly more parasitized eggs when the eggs were greater than 3 days old. However, it is unclear if this has an impact on the combined use of these natural enemies in the field.

There are other examples of mutual interference among *H. armigera* natural enemies. Ants have been reported to remove chrysopid larvae from the plants (Singh *et al.*, 1994b) and chrysopid eggs are parasitized by *Trichogramma* sp. (Pawar *et al.*, 1985b; Kapadia & Puri, 1991).

Chrysopids are the only *H. armigera* predators to be mass produced in India. Life tables have been constructed under laboratory conditions for *C. carnea, M. boninensis, M. astur* and *Apertochrysa* sp. (Bakthavatsalam *et al.*, 1994). The highest net reproductive rate was for *C. carnea* ($R_0 = 559$). Chrysopid larvae are easy to rear on *C. cephalonica* eggs, but they are cannibalistic and must be separated (Krishnamoorthy & Nagarkatti, 1981; Patel *et al.*, 1988b; Singh *et al.*, 1994c). Adults are maintained on an artificial diet. For *C. carnea,* Singh *et al.* (1994b) reported the highest fecundity (about 900 eggs/female) with a diet containing black gram flour, honey, yeast and sugar in equal proportions by volume. According to Singh *et al.* (1994b), eggs of *C. carnea* can be stored at 10°C for 15 days without a reduction in the proportion hatching; storage beyond 30 days significantly reduced hatching. The age of the eggs (up to 60 h) at the time of storage had no impact on their ability to hatch.

Singh *et al.* (1994c) recommended releasing *C. carnea* or *M. boninensis* at 50 000 ha^{-1} in cotton, twice during a season, at an interval of 15 days. No data on the success of such field releases in cotton have been reported. In a 2-year study, Venkatesan *et al.* (1994) made three releases of first instar larvae of *B. scelestes* (one $head^{-1}$) on sunflower at 10-day intervals. They reported complete suppression of the *H. armigera* larval population in both years. However, the study was carried out using small plots and the results should be confirmed in larger field studies. Dhandapani *et al.* (1992) released *B. scelestes* (50 000 ha^{-1}) together with *T. chilonis* (100 000 ha^{-1}) in cotton and reported a 40% reduction in *H. armigera* larvae (Table 4). Unfortunately, the impact of the two biocontrol agents was not separated.

EXOTIC PARASITOIDS

The first introduction to India of an exotic natural enemy to control *H. armigera* was the egg parasitoid *T. pretiosum* Riley (Hymenoptera: Trichogrammatidae) in 1964 (Sankaran, 1974). A total of 16 hymenopteran and two dipteran parasitoids of *H. armigera* has been introduced from the Americas, Africa and Europe (Table 8). From the limited records available, it appears that only one larval parasitoid, the tachinid *Eucelatoria bryani* Sabrosky (introduced as *Eucelatoria* sp. near *armigera* (Coquillett)), is established on *H. armigera.*

The effectiveness of exotic *Trichogramma* spp. is still in doubt. Among the species introduced into India, *T. brasiliense* is the most frequently released. This species has been successfully used in an inundative release programme on tomato (Singh *et al.*, 1994b; Table 4). Singh *et al.* (1994a) recommended weekly releases of *T. brasiliense* at 50 000 females ha^{-1} in this crop. *T. brasiliense* was not effective in cotton. Between 1974 and 1976, Raodeo *et al.* (1978) made weekly releases at a rate of 50 000 parasitoids ha^{-1} in cotton fields at different locations in Maharashtra. Almost six million parasitoids were released in total. *T. brasiliense* was recovered on *C. cephalonica* egg cards during the cotton growing season, but no recovery was made in subsequent years. Singh and Jalali (1992) released *T. brasiliense* on potted cotton plants artificially infested with *H. armigera* eggs. The experiment was conducted outdoors but it is not clear if it was in a cotton field. Even at the highest release rate of 250 000 parasitoids ha^{-1}, fewer than 8% of the eggs were parasitized by *T. brasiliense*, compared with at least 70% parasitism caused by the indigenous *T. chilonis* and *T. achaeae.* Divakar and Pawar (1987) were not able to recover *T. brasiliense* after inundative releases of between 300 000 and 6 million parasitoids/year between 1977 and 1983 around Bangalore (Karnataka) in different crops. Unfortunately, the authors only gave the total area covered by the release but did not report the actual number of parasitoids released/unit area. Kaker *et al.* (1990) reported that no adult parasitoids emerged from *H. armigera* eggs parasitized in the laboratory by *T. brasiliense*, *T. perkinsi* Girault and *T. minutum* Riley. No parasitoids emerged from parasitized eggs (black egg stage) collected in tomato fields after releasing the three species.

Balasubramanian *et al.* (1989) recorded up to 62% parasitism by *T. pretiosum* in chickpea after mass releases. This is the only record of high levels of parasitized *H. armigera* eggs collected parasitoids have either not been maintained in culture after their initial introduction or have not been released.

CONCLUSIONS

H. armigera is a devastating pest on several crops in India, despite the sometimes high levels of parasitism reported for some parasitoids. Though the parasitoid and predator lists given in this paper appear to be extensive, new species continue to be discovered. The taxonomic status of many species must be clarified as there have been many misidentifications, as demonstrated for the most important larval parasitoid, *C. chlorideae*. Records of species belonging to the Sarcophagidae as parasitoids of *H. armigera* may not be correct. This group deposit larvae in wounds, damaged tissues, and dead animals and plants (see Van den Berg *et al.*, 1988). Nonetheless, species of Sarcophagidae are listed as parasitoids of *Heliothis* spp. from the Americas (Kogan *et al.*, 1989) and *H. armigera* from Africa (Van den Berg *et al.*, 1988).

Of greater importance is the paucity of information concerning the impact of known natural enemies of *H. armigera* populations in the field. The identification of key natural enemies and knowledge of their effectiveness is essential for the development and implementation of management strategies (Bellows *et al.*, 1992; Room *et al.*, 1990). Life-table studies of *H. armigera* conducted by Bilapate and others (Bilapate *et al.*, 1979, 1988; Bilapate, 1981a,c) report generation survival rates of 37–94%. The mortality of the different life stages is highly underestimated because of the design of these studies (see Fitt, 1989 for discussion). In comparison, life-table studies of *H. armigera* conducted in East Africa revealed generation survival rates of only 7–18% (Van den Berg & Cock, 1993a). Two *H. armigera* life-table studies from India report generation survival rates similar to Van den Berg and Cock (1993a). Tripathi and Singh (1991) recorded generation survival between 13 and 28% in larvae exposed to field conditions. Only parasitism was recorded in this study; no impact of predators (or unknown causes) was given. Nanthagopal and Uthamasamy (1989) reported generation survival of 2–5% for *H. armigera* on cotton. The impact of parasitoids was generally low and mortality from "migration and unknown" causes was high. This may be indirect evidence for the existence of chewing predators. Indirect evidence suggests that natural enemies and/or abiotic factors have the greatest impact on *H. armigera* populations on sorghum; reported egg densities are high, but larval populations are often low (Pawar *et al.*, 1989a). The population-regulating mechanisms that keep *H. armigera* at sub-economic levels in sorghum are unknown. Understanding these mechanisms in sorghum could provide an insight into the reasons why they fail to regulate *H. armigera* populations in other crops.

To understand *H. armigera* population dynamics, accurate and complete life-table studies are needed. This would include experiments to evaluate the impact of natural enemies using exclusion techniques, observations of egg and larval cohorts and feeding trace methods (Kiritani & Dempster, 1973; Luck *et al.*, 1988; Bellows *et al.*, 1992). Currently, in the absence of these studies, the full impact of natural enemies on *H. armigera* population dynamics in India is unknown.

Attempts to suppress *Heliothis* spp. populations by augmenting natural enemy populations have been inconsistent, and economic feasibility has rarely been demonstrated (King *et al.*, 1982; King & Coleman, 1989). A highly fecund, polyphagous and mobile insect such as *H. armigera* can increase in number rapidly and disperse to new host plants. Large quantities of natural enemies are needed at field release sites soon after eggs or early instar larvae are observed. For these reasons, *Trichogramma* spp. and, to some extent, chrysopids have been the preferred candidates for augmentative-release programmes. In India, the only successful examples of the practical use of natural enemies to control *H. armigera* have utilized *Trichogramma* spp. In the most well-documented example, inundative releases of *T. chilonis* on cotton, combined with the release of the predator *B. scelestes*, were as successful in suppressing *H. armigera* as insecticides, and had a similar cost–benefit ratio (Dhandapani *et al.*, 1992). Though successful, widespread adoption of these strategies has not occurred. Until an analysis of the reasons for lack of adoption is made, the constraints to using this pest control strategy will remain unknown.

The introduction of exotic natural enemies into India may still be useful, especially the strategy of finding new host–parasite associations (Pimentel, 1963). It is difficult to recommend a specific parasitoid guild, as suggested by Greathead and Girling (1982), as a candidate species for an *H. armigera* biological control programme in India, for two reasons. Firstly, as previously discussed, the impact of indigenous parasitoids is unknown, so it is not clear which guild is ineffective. Secondly, the parasitoid fauna for *H. armigera* differs between crops and therefore 'gaps' in the parasitoid guild may be crop-specific. One possibility could be the introduction of *Telenomus* egg parasitoids from Africa or Australia. In Africa the widespread, host-specific *T. ullyetti* Nixon is abundant, with a second species, *T. laeviceps* (Förster), occurring in North Africa and Europe. In Australia, an additional (undescribed) species of *Telenomus* is common on *H. armigera* (A. Polaszek, personal communication, 1996). Future classical biological control programmes must be carried out carefully and reported in far greater detail than has previously been the case, including an analysis of reasons in the case of failure (Stiling, 1993). This is essential if these programmes are to advance beyond the 'try-it-and-see' stage (Cock, 1986).

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