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Survey of the native insect natural enemies of *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) in China

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Abstract

The fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), is an invasive and important pest in China. Investigations on insect natural enemies have been conducted from 1996 to 1999 in five provinces and one municipality of China in order to select effective species for biological control. Two carabid predators (Coleoptera) and 25 parasitoid species were found, among which 23 were parasitic wasps (Hymenoptera), including five hyperparasitic species and two tachinid flies (Diptera). The two carabids preyed on young larvae inside webs, two braconid wasps parasitized larvae, and 18 parasitoid species attacked the fall webworm during the pupal and/or 'larval-pupal' stages. Among these parasitoids, there were one genus and nine species that are new to science and four species new to China, which were described and published by the senior author Yang. The average parasitism rates of fall webworm pupae were 25.8% and 16.1% in the overwintering generation and the first generation (summer generation), respectively. These findings reveal that these natural enemies play an important role in the natural control of the pest. *Chouioia cunea* Yang (Hymenoptera: Eulophidae), a gregarious pupal endo-parasitoid, was recommended as a promising biological control agent against the fall webworm in China.

Keywords: fall webworm, insect natural enemies, parasitoids, predators, *Chouioia cunea*, biocontrol

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Introduction

The fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), is a serious invasive defoliator pest in China. It was first found in China in 1979 at Dandong City bordering North Korea, Liaoning Province (Yan & Wang, 1984; Wang, 1995). Since its invasion, the pest attacked most cultivated plants in infested areas in China, particularly the ornamentals, man-made forests and fruit trees. Soon it spread into Liaoning, Hebei, Shandong and Shaanxi Provinces, and the Tianjin and Shanghai Municipalities. Frequent outbreaks occur in these areas and great economic losses have been caused subsequently (Qu *et al.*, 1987; Wang, 1995; Zhang & Yu, 1985). The pest became a big problem to the planting projects in northern China (figs 1 and 2). The fall webworm usually has two generations per year. The first generation is in summer and the second one overwinters in

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Fig. 1. Ornamental trees severely attacked by the fall webworm.

the pupal stage and emerges in late April to early May of the following year. As an important invasive pest – it usually lives and damages ornamental trees around residential areas, towns and cities, it is essential to avoid using insecticides for control.

The fall webworm was also accidentally introduced into Europe, having been first reported in Hungary in 1940, and soon dispersed to many other European countries. Insect natural enemies of the fall webworm were surveyed in North America by Tadic (1963) and in other areas of the world by Warren and Tadic (1967). In a biological control program for the fall webworm in former Yugoslavia, Czechoslovakia and USSR, ten insect parasitoids (eight species of parasitic wasps and two species of tachinid flies) were imported from the USA and Canada, where the pest is native, between 1952 and 1966. However, these parasitoids all failed to establish in the new environments and the program was ultimately not successful (Tadic, 1958; Clausen, 1978).

From 1996 to 1999, a series of investigations on native insect natural enemies of the fall webworm was carried out in Yantai of Shandong Province, Dalian of Liaoning Province, Qinhuangdao of Hebei Province, Guanzhong area of Shaanxi Province and in the Tianjin Municipality (Yang, 1989, 1990b; Yang *et al*., 2001, 2002, 2003a,b, 2005; Yang & Wei, 2003; Yang & Baur, 2004). A great deal of native natural enemies have been found in China, and then an augmentative biological control program was carried out against this invasive pest (Yang *et al*., 2005, 2006).

Materials and methods

In the fall webworm damaged areas, i.e. Yantai of Shandong Province, Dalian of Liaoning Province, Qinhuangdao of Hebei Province, Guanzhong area of Shaanxi Province and in the Tianjin Municipality, a forest stand (0.1 ha) was selected as the investigated site where the favourable host trees of the fall webworm were distributed and predominate, e.g. populars (*Populus* spp.), elms (*Ulmus pumila*) and ashes (*Fraxinus velutina*). Every 7–10 days 30 trees were selected randomly for sampling during the field survey. The eggs, larvae and pupae of the fall webworm were randomly collected in both the damaged forest and ornamental tree

Fig. 2. Greening trees defoliated by the fall webworm larvae.

stands in those areas. They were reared in the laboratory at a temperature of 20–26°C, and checked each day to collect emerged parasitoids. Later, the natural enemies reared from every stage of the fall webworm were identified and their numbers, parasitic rates and sex ratio were assessed. At the same time, direct observations and collection of predators of the fall webworm were made.

For egg parasitoids, the egg clusters of the fall webworm (each stand has about ten egg clusters, which were laid about five days previous) were randomly collected and kept in glass test tubes (150 mm length and 45 mm diameter) sealed with absorbent cotton for rearing in the laboratory. The fall webworm larvae have 6–7 instars; the 1st–4th instar larvae live in the web, while the later instars disperse for feeding. Larvae of each instar (each stand has about 100 larvae) were, therefore, randomly collected for rearing separately in cages ($300 \times 250 \times 250$ mm with glass on all sides except for a door with metal gauze) and fed every day with host tree leaves. Because the fall webworm pupae were concealed in the crevices of host tree barks, building walls, litters etc. with loose cocoons, they were searched out and collected randomly for the survey of pupal parasitoids. The number collected in each stand is shown in tables 1 and 2, respectively. The fall webworm pupae were conserved in vials (75 mm in length and 10–13 mm in diameter) individually

Table 1. Parasitism of each parasitoid on the overwintering the fall webworm pupae (1996–1999).

Investigation site		Collection date	No. of host pupae collected	Parasitism percentage of main parasitoids (%)									Total parasitism rates (%)
				C. cunea	*P. elasmi*	*P. disparis*	*P. aethiops*	Tachinid flies*	*T. septentrionalis*	*A. magniventer*	*B. lasus*	*C. cuneae*	
Shangdong province	Sanhuai Rd.	Dec, 1996	620	15.81	14.68	9.03	0	0.16	0	0	0	0	39.68 (±3.85)
	Xinhuali	Dec, 1996	231	13.42	13.85	9.52	0	0	0	0	0	0	36.79 (±1.62)
	Zhuanghe	Dec, 1996	1531	7.18	4.51	5.75	0	0.78	0	0	0	0	18.22 (±1.93)
	Taipinling	Dec, 1996	683	10.98	0.73	11.57	0	0.29	0	0	0	0	23.57 (±3.18)
	Shishan	Dec, 1997	205	23.90	7.80	10.73	0	0	0.98	0	0	0	43.41 (±6.79)
	Zhifu Dist.[1]	Feb, 1997	816	3.06	3.19	6.62	0	6.74	0.49	0	0	0	20.10 (±2.75)
	Mupin	Feb, 1997	2975	17.48	2.99	2.82	0.17	0.47	0.47	0.74	0	0	25.14 (±1.56)
	Fushan	Feb, 1997	573	3.84	2.44	0	0	0	0.52	0	0	0	6.80 (±2.06)
	Zhifu Dist.[2]	Feb, 1998	112	1.79	0	0.89	0	0	0	0	0	0	2.68 (±2.99)
	Mupin	Feb, 1998	123	27.64	0	1.63	0	6.50	0	0	0	0	35.77 (±8.47)
	Zhifu Dist.[3]	Feb, 1999	1028	14.00	1.07	10.70	0	3.60	0	0	0.49	0	29.86 (±2.80)
	Yantai Univ.	Feb, 1999	292	12.67	0	0.69	0	6.85	0.34	0	19.86	2.74	43.15 (±5.68)
Hebei province	Shanhaiguan	Dec, 1996	1020	11.37	5.39	3.43	0	0.59	0	0	0	0	20.78 (±2.49)
	Haigangqu	Dec, 1996	1714	15.64	11.09	6.42	0.29	0.18	0	0	0	0	33.62 (±2.24)
	Haibin For. Farm	Dec, 1996	262	1.91	0.76	3.44	0	0.38	2.67	0	0	0	9.16 (±3.49)
	Tuanlin For. Farm	Feb, 1997	98	2.04	0	2.04	0	0	2.04	0	0	0	6.12 (±4.79)
	Shanhaiguan	Feb, 1998	164	15.85	6.10	10.98	0	9.15	0	0	0	0	42.08 (±7.56)
	Haibin For. Farm	Feb, 1998	167	20.96	3.59	2.40	0	5.99	0.60	0	0	0	33.53 (±7.16)
	Tuanlin For. Farm	Feb, 1998	500	14.80	13.40	0.80	0	0.20	0.80	0	0	0	30.00 (±4.02)
Mean parasitism rate (%)				12.33 (±1.73) a	4.82 (±1.15) b	5.23 (±0.94) b	0.024 (±0.017) c	2.20 (±0.72) c	0.47 (±0.17) c	0.039 (±0.039) c	1.07 (±1.04) c	0.14 (±0.14) c	–

[1]The numbers in bracket are the confidence interval value of parasitism rates at 95% confidence limit of binomial distribution.
[2]The same letters after the mean parasitism rate values of each parasitoid in the last line in the table showed no significant differences between enemies based on TSRT ($F = 21.59$, $P < 0.0001$).
[3],*Tachinid flies: *Exorista japonica*, *Compsilura concinnata*.

Table 2. Parasitism of each parasitoid on the fall webworm pupae of the summer generation (1996–1999).

Investigation site	Collection date	No. of host pupae* collected	Parasitism percentage of main parasitoids (%)									Total parasitism rates (%)
			C. cunea	*P. elasmi*	*P. disparis*	*P. aethiops*	Tachinid flies*	*T. septentrionalis*	*A. magniventer*	*B. lasus*	*C. cuneae*	
Dock yard, Qinhuangdao	Jul, 1997	716	5.45	2.93	0.42	0	4.19	0	0	12.99	0	25.98 (±3.21)
Kunlongli	Jul, 1997	618	3.72	3.56	0.81	0	5.34	0	0	13.27	0	26.70 (±3.49)
Zhuanghe	Jul, 1998	222	15.31	1.35	0	0	15.77	0	0	0	0	32.43 (±6.16)
Xinfu 11th Mid. school	Jul, 1999	208	19.23	2.88	0.48	0	3.85	0	0	0	0	26.44 (±5.99)
Yantai Univ.	Jul, 1999	181	6.63	0	0	0	0.55	0	0	0	1.10	8.29 (±4.02)
Zhifu Dist.1	Jul, 1998	267	0.75	0	0.37	0	0.37	0	0	0	0	1.50 (±1.46)
Zhifu Dist.2	Jul, 1999	244	13.11	0	0.41	0	0.41	10.25	0	0	2.05	26.23 (±5.2)
Haibin For. Farm	Jul, 1998	1592	1.51	0	3.20	0	0.25	0.82	0	0	0	5.78 (±1.15)
Mean parasitism rate (%)	–	–	8.21 (±2.42) a	1.34 (±0.55) bc	0.71 (±0.37) bc	0 (±0) c	3.84 (±1.85) b	1.38 (±1.27) bc	0 (±0) c	3.28 (±2.15) bc	0.39 (±0.27) bc	–

The same letters after the mean parasitism rate values of each parasitoid in the last line in table showed no significant differences between enemies based on TSRT at 0.05 level ($F = 3.97$, $P = 0.0007$).
*Tachinid flies: *Exorista japonica and Compsilura concinnata*.

Table 3. Predator species of the fall webworm.

Species	Host stage of predation
1. *Parena laesipennis* Bates (Carabidae, Coleoptera)	1st–3rd instar larvae in web
2. *Parena latecincta* Bates (Carabidae, Coleoptera)	1st–3rd instar larvae in web

and plugged tightly with cotton in order to maintain moisture for rearing. The remains of the moth pupae, from which parasitoids had been reared, were later dissected carefully to examine whether or not they had contained primary or hyper parasitoids.

All experimental data were analyzed by means of the software Statistical Analysis System (SAS procedure, version 8.2) (Chen & Xu, 1997). Analyses of variance (GLM Procedure, SAS) followed by Tukey's Studentized Range Test (TSRT) were used to compare the differences in parasitism rates between natural enemies attacking the fall webworm. Regression analyses were used to determine the parasitism rates of all natural enemy species together, and the parasitism rates of every single parasitoid, whereby the goodness-of-fit of the equations were judged by the correlation coefficients and F-values at the $P = 0.05$ level of significance. Multiple comparisons were analyzed by using the T-method (Sokal & Rohlf, 1981).

The contribution of each species (variable x_i – with x_1 being *Chouioia cunea*, x_2 being *Pediobius elasmi*, x_3 being *Pimpla disparis*, x_5 being Tachinid flies, x_6 being *Tetrastichus septentrionalis*, x_8 being *Brachymeria lasus* and x_9 being *Conomorium cuneae*) to the total parasitism (variable y) was evaluated in a multiple regression analysis. According to the percent parasitism of each enemy and total parasitism percentage of all parasitoid species in the investigation plot, the correlation between them was analyzed using the method of multiple regression analysis, whereby parasitism rates were standardized by the formula $x_{ij}^2 = \arcsin\sqrt{x_{ij}}$. A linear regression model was obtained through a stepwise procedure of SAS Software (Proc Reg).

Results and discussion

Species of insect natural enemies

The species of predators and parasitoids of the fall webworm are given in tables 3 and 4, respectively. Although a scelionid species (Hymenoptera: Scelionidae) was observed in the field, of the inspect the eggs of the fall webworm, no egg parasitoid was reared out of a total 165 egg clusters containing about 132,000 eggs collected from many host tree stands. The probable reason was that the scale-like hairs secreted by the oviposition female covered the eggs and protected them from being parasitized. Two species of carabid predators (Coleoptera: Carabidae) and two braconid parasitoids (Hymenoptera: Braconidae) were discovered in the webworm larva stage. More natural enemies were still found in the pupal stage. Eighteen species of primary parasitoids (including two species of larval-pupal parasitoids) as well as five species of hyper-parasitoids were reared from pupae. A total of 23 species of parasitic wasps (Hymenoptera) and two species of tachinid flies (Diptera) were recovered. Among them, one genus and nine species are new to science, and four species were new to China

Table 4. Parasitoid species of the fall webworm.

Parasitoid species	Single or gregarious parasitism	Host stage parasitized	Parasitism rates (%)	Sex ratio (♀:♂)
1. Primary parasitoids				
Braconidae (Hymenoptera)				
1) *Dolichogenidea singularis* Yang et You*	Single	1st–3rd instar larvae in web	2.6	2:1
2) *Cotesia gregalis* Yang et Wei*	Gregarious	3rd–6th instar (mature) larvae	6.0–12.6	1.5:1
Pteromalidae (Hymenoptera)				
3) *Trichomalopsis genalis* Graham#	Gregarious	Larva-pupa	0.2	1.6:1
4) *Conomorium cuneae* Yang et Baur*	Gregarious	Pupa	1.2	7.5:1
5) *Pteromalus bifoveolatus* Foester	Gregarious	Pupa	0.2	5.5:1
Eulophidae (Hymenoptera)				
6) *Chouioia cunea* Yang$^{\Delta}$	Gregarious	Pupa	5.1–12.8	45–96:1
7) *Tetrastichus septentrionalis* Yang*	Gregarious	Pupa	3.2	10:1
8) *T. shandongensis* Yang*	Gregarious	Pupa	3.6	3.2:1
9) *T. nigricoxae* Yang*	Gregarious	Pupa	6.2	4.2:1
10) *T. litoreus* Yang*	Gregarious	Pupa	0.1	3.0:1
11) *Aprostocetus magniventer* Yang*	Gregarious	Pupa	3.5	2.6:1
12) *Pediobius elasmi* (Ashmead)#	Gregarious	Pupa	2.6	2.8–13.6:1
Eupelmidae (Hymenoptera)				
13) *Eupelmus fulvipes* Foester#	Gregarious	Pupa	0.1	Only ♀
Chalcididae (Hymenoptera)				
14) *Brachymeria lasus* (Walker)	Gregarious	Pupa (only in host summer generation)	6.6–16.7	6.4:1
Ichneumonidae (Hymenoptera)				
15) *Enicospilus lineolatus* (Roman)	Single	Larva-prepupa	1.5	1.8:1
16) *Coccygomimus disparis* (Viereck)	Single	Pupa	10.0	2.78:1
17) *C. parnarae* (Viereck)	Single	Pupa	0.34	2.0:1
18) *C. turionellae* L.	Single	Pupa	0.12	1.6:1
Tachinidae (Diptera)				
19) *Exorista japonica* (Townsend)	Single	Larva-pupa	4.0–15.7	1.5:1
20) *Compsilura concinnata* (Meigen)	Single or gregarious	Pupa	2.0	1.5:1
2. Hyper parasitoids				
Torymidae (Hymenoptera)				
21) *Monodontomerus minor* (Ratzeburg)	Gregarious	Larva-pupa of *Pimpla disparis, C. parnarae, C. turionellae*	0.15	1.4:1
Pteromalidae (Hymenoptera)				
22) *Dibrachys cavus* Walker	Gregarious	Larva-pupa of *Pimpla disparis, Enicospilus lineolatus, Exorista japonica*	0.15	8:1
23) *Trichomalopsis germanicus* Graham#	Gregarious	Pupa of *Cotesia gregalis*	15.0	2.0:1
Eurytomidae (Hymenoptera)				
24) *Eurytoma goidanichi* Boucek#	Gregarious	Pupa of *Cotesia gregalis*	22.0	2.2:1
Encyrtidae (Hymenoptera)				
25) *Exoristobia klinoclavata* Xu	Gregarious	Pupa of *Exorista japonica*	1.6	6.2:1

$^{\Delta}$New genus and species found in the present investigation; *new species found in the investigation; #new record for China.

(Yang, 1989; Yang *et al.*, 2001, 2002, 2003a,b; Yang & Wei, 2003; Yang & Baur, 2004).

Biology of insect natural enemies of the fall webworm

The two carabid species are predatory. All primary parasitoid species were endo-parasitic. However, two of the hyper-parasitoids were ecto-parasitic on the primary parasitic hosts inside fall webworm pupae.

Parena laesipennis *Bates (Carabidae)*

The carabid female adult lays eggs in webs of the fall webworm. These are ootheca-shaped, covered with a white foam material, with usually 3–5 eggs. Both larvae and adults prey on young larvae of the fall webworm and live inside the host web. Generally, two to three adult beetles live together in a web. Within the web there are usually 110–265 larvae, which are all consumed by the beetles. Subsequently, the beetles move to another web for feeding. They may consume

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host larvae from three to four webs, so many empty webs of the fall webworm were found on ornamental trees close to forest stand. The carabids destroy about 3.2% of the moth webs in the Dalian area, Liaoning Province.

Parena latecincta *Bates (Carabidae)*

The biology of this species is similar to the above species, *P. laesipennis*, and the two predators are found together in the same web.

Dolichogenidea singularis *Yang & You (Braconidae)*

This braconid is a solitary endoparasitoid of 1st–3rd instar larvae of the fall webworm; the mature larva of the wasp kills its host larva, makes its way out of host body, spins a cocoon and pupates inside the host. The white cocoon frequently is attached to the web far away from the remains of its host (Yang *et al*., 2002).

Cotesia gregalis *Yang & Wei (Braconidae)*

This braconid is a gregarious endoparasitoid of the mid-instar to mature larvae of the fall webworm (Yang *et al*., 2002). When its larvae finish development in the late larval stage of their host, they kill the host, emerge and spin white cocoons that surround their host mummy. As many as 18–38 adult wasps emerge from one host mature larva.

Trichomalopsis genalis *Graham (Pteromalidae)*

This species overwinters as a full-grown larva in host pupa. The female wasp lays her eggs into the 4th instar host larvae and the offspring complete their development in the host pupa. Adults emerge from the host pupae the following spring. From one pupa, 15 wasps were reared. This species is also a parasitoid of gypsy moth larvae in China. However, when Graham (1969) described the species, he mentioned that it was reared from *Masicera senilis* (Meigen) (Diptera: Tachinidae) on *Pyrausta nubilalis* Hübner (Lepidoptera: Pyralidae), which would suggest a hyperparasitic lifestyle not in accordance with our observations.

Conomorium cuneae *Yang & Baur (Pteromalidae)*

This gregarious species overwinters as mature larvae in the host pupa and emerges in May of following year. From one host, 14–30 wasps, with an average of 17, were reared. Parasitism rate is low (usually 1.2%) in the overwintering host pupae, but reaches 12% in some local areas, e.g. Yantai, Shandong Province (Yang & Baur, 2004).

Pteromalus bifoveolatus *Foester (Pteromalidae)*

This species gregariously parasitizes pupae of the fall webworm, and 11–22 individuals of the wasp may be reared from one host pupa. It overwinteres as a mature larva in the pupal stage of the fall webworm and emerges in the next spring.

Chouioia cuneae *Yang (Eulophidae)*

This gregarious pupal parasitoid of the fall webworm (Yang, 1989, 1990b) develops from the egg to the pre-oviposition adult stage inside its host pupa (figs 3 and 4). It is only 1.1–1.5 mm in length. From a single host pupa, an average of 124 adult wasps, with a maximum of 365, was reared (Yang, 1990a). For oviposition, the female wasp attaches itself to the body of the mature fall webworm larva by hidding in the thick hair of the host larvae. This causes its host to pupate about one week earlier than normal. When the host spins its cocoon, the female wasp(s) is enclosed inside it. The parasitoid inserts her eggs into the pupa only after the host pupates. Alternatively, the female wasp can also access the host pupa for oviposition by biting a hole in the host cocoon. The wasp overwinters as a mature larva in the host pupa. The larva pupates the next spring, usually in early May. The adult wasps first mate inside their host pupa, and then bite a hole in the host pupal shell. The other wasps find their way out by using this same hole. Thus, the adult females can parasitize new hosts soon after their 'emergence' (Yang & Xie, 1998). The species is predominant in all areas of the fall webworm. Its parasitism rates in overwintering pupae and in those of the summer generation of the fall webworms are 12.76% and 5.09%, respectively. Besides the fall webworm, this species also parasitizes other lepidopterous forest defoliators, e.g. *Clostera anachoreta* (Fabricius), *Micromilalopha troglodyta* (Graeser) (Notodontidae), *Stilpnotia salicis* (L.), *S. candida* Staudinger, *Ivela*

Fig. 3. Female wasp of *Chouioia cunea* Yang is laying eggs into a pupa of the fall webworm.

Fig. 4. Larvae of *Chouioia cunea* Yang consumed up all contents of the fall webworm pupa.

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ochropoda (Fabricius) (Lymantriidae), *Clania variegeta* Snelleny (Psychidae) (Yang, 1989). Since its description, the wasp also has been founded to parasitize fall webworm in Japan (Kamijo, 1991) and Europe (Boriani, 1991).

Tetrastichus septentrionalis *Yang (Eulophidae)*

This gregarious species overwinters as mature larvae in the host pupa and pupates in late April of the following year. Usually the adult wasps emerge in May. From one pupa of the fall webworm, 118–248 wasps have been reared, with an average of 149. The species also parasitizes pupae of *Clostera anachoreta* Fabricius (Lepidoptera: Notodontidae), *Stilpnotia candida* Staudinger and *S. salicis* (L.) (Lepidoptera: Lymantridae). It is also found in Korea as a parasitoid of the fall webworm (Yang *et al*., 2001).

Tetrastichus shandongensis *Yang (Eulophidae)*

This gregarious species overwinters as mature larvae in fall webworm pupa, and emerges in May of the next year. From one host pupa, 48–115, with an average of 77, wasps were reared. The female can survive for 12–15 days at 25°C (Yang & Wei, 2003).

Tetrastichus nigricoxae *Yang (Eulophidae)*

This gregarious species overwinters as mature larvae in fall webworm pupa (Yang & Wei, 2003). From one host pupa, 86–168 wasps have been reared, with an average of 124. In addition, within the distribution of the fall webworm, the species also parasitizes the pupae of *Micromelalopha troglodyta* Graeser (Lepidoptera: Notodontidae) and *Stilpnotia candida* Staudinger (Lepidoptera: Lymantridae).

Tetrastichus litoreus *Yang (Eulophidae)*

This species has been found only in Qinhuangdao, Hebei Province. Six wasps were reared from one fall webworm pupa (Yang *et al*., 2003a).

Aprostocetus magniventer *Yang (Eulophidae)*

This gregarious species overwinters in pupae of the fall webworm as mature larvae and emerges from its host in May. From one host pupa, 45–105 wasps were reared, with an average of 64. The species has only been found in Yantai, Shandong Province (Yang *et al*., 2003b).

Pediobius elasmi *(Ashmead) (Eulophidae)*

This species overwinters in the pupa of the fall webworm as mature larvae and pupates in late April. Usually the adult wasp emerges in May. One host pupa produces an average of 62 wasps with a maximum of 154. The species is common in areas where the fall webworm occurs.

Eupelmus fulvipes *Foester (Eupelmidae)*

Only three female wasps of this species were reared from a single fall webworm pupa overwintering in Qinhuangdao, Hebei Province. The species occurs in western Europe, where it parasitizes the gall midge *Perrisia bupleuri* Wachtl (Diptera: Cecidomyiidae) (Nikolskaya, 1952).

Brachymeria lasus *(Walker) (Chalcididae)*

This species parasitizes the pupae of the summer generation of the fall webworm. In most cases, only one adult wasp emerges per host pupa, rarely two. Its parasitism rate avereged 6.56%, but in Hangu District, Tianjin Municipality, it reached 16.7%.

Enicospilus lineolatus *(Roman) (Ichneumonidae)*

This species is a solitary endo-parasitoid in the larval to pre-pupal stages of the fall webworm. It does not kill its host in the larval stage until the host cocoons, then emerges from the host pre-pupa and spins a cocoon inside the host to overwinter as a pupa. Thus, a thick, dark brown cocoon of the parasitoid is found on the mummy of host pre-pupa inside the cocoon of the fall webworm. The species also parasitizes many other lepidopterous defoliators, including *Dendrolimus punctatus* Walker (Lepidoptera: Lasiocampidae) and *Spilarctia subcarnea* Walker (Lepidoptera: Arctiidae) (Tang, 1990).

Pimpla disparis *(Viereck) (Ichneumonidae)*

The species overwinters as a mature larva inside the host pupa. The exoskeleton of the parasitized host pupa, thereby, becomes thin and stretched between the segments, which make it easy to distinguish between healthy and paraisitized host pupae. After emergence in May of the next year, the emerging adult wasp completely consumes the host pupal integument. In China, the species is found to parasitize 36 other lepidopterous defoliators, e.g. *Malocosoma neustria* (L.), *Dendrolimus punctatus* Walker, *D. tabulaeformis* Tsai et Liu, *D. spectabilis* Butler (Lasiocampidae), *Lymantria dispar* (L.) (Lymantridae) (He *et al*., 1996).

P. aethiops *Curtis (Ichneumonidae)*

The biology of this species is similar to that of *P. disparis*, but its parasitism percentage is only 0.34% in the overwintering pupa of the pest. Besides the fall webworm, it has a broad host range, with 17 species of lepidopterous defoliators, e.g. *Canephora asiatica* Staudinger (Psychidae), *Malocosoma Neustria* (L.) (Lasiocampidae) etc. (He *et al*., 1996).

P. turionellae *L. (Ichneumonidae)*

The biology of the species is similar to that of *P. disparis*. It rarely occurred in the investigation areas and only 12 specimens were collected in the course of the entire study.

Exorista japonica *(Townsend) (Tachinidae)*

This species parasitizes larvae of the fall webworm but does not kill the host larvae until they pupate. The parasitoid overwinters inside the host pupa as a full-grown larva, and emerges to pupate beside its host pupa the following spring. Generally, only one parasitoid develops from a host pupa. Its parasitism rate in the fall webworm is usually 4.0% but reaches 15.7% in some survey areas of Yantai City, Shandong Province. The species has a wide host range and has been recorded from more than 20 species of lepidopterous defoliators (Fan, 1992; Zhao & Liang, 1984).

Compsilura concinnata *(Meigen) (Tachinidae)*

This species overwinters inside fall webworm pupae as mature larvae or pupae. The next spring, the adult fly emerges from the host pupa, with one to three individuals per host, depending on the host size. This species is recorded from 104 lepidopterous host species (Zhao & Liang, 1984).

Monodontomerus minor *(Ratzeburg) (Torymidae)*

This hyper-parasitic species is an ecto-parasitioid of several ichneumonid species, such as *Pimpla disparis*, *P. aethiops* and *P. turionellae*, which are primary solitary parasitoids of the fall webworm. *M. minor* overwinters as a mature larva beside its killed host larva or pupa, inside the pupa of the fall webworm. In the next spring, usually in early May, the larvae pupate. The emergence holes made by the adult wasps on the pupal shell of the fall webworm led to the wrong conclusion that it is a primary parasitoid (Tadic, 1963; Warren & Tadic, 1967). From one pupa of the fall webworm, on average 12 wasps, ranging from 9 to 14, emerge.

Dibrachys cavus *Walker (Pteromalidae)*

This hyper-parasitic species ecto-parasitizes larvae and/or pupae of the primary parasitoids *Pimpla disparis*, *Enicospilus lineolatus* and *Exorista japonica* inside pupae of the fall webworm. From one pupa of the fall webworm that is parasitized by *P. disparis*, 18–26 wasps, with an average of 20, were reared. The female to male adult sex ratio was 8 : 1 with a parasitism rate of 0.5% on the host species. From one cocoon of *E. lineolatus*, an average of 34 wasps of the species was reared. The sex ratio of female to male adults was 7 : 1; its parasitism rate was 3.2% on the ichneumonid host. After emergence, the adult wasps make their way out from the brown thick cocoon of the ichneumonid by biting a hole. From one puparium of *E. japonica*, an average of 35 wasps of the species emerges. The female to male adult sex ratio is 2.5 : 1 and the parasitism rate is 4.2% on the tachinid host.

Trichomalopsis germanicus *Graham (Pteromalidae)*

This hyper-parasitic species parasitizes the pupa of *Cotesia gregalis* inside the cocoon. Its biology is similar to that of *Eurytoma goidanichi* Boucek below. Its parasitism rate for all cocoons of a web was 0.3%. The species was originally described by Graham (1969) as parasitizing *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae) on *Pieris brassicae* (L.) (Lepidoptera: Pieridae) in Europe.

Eurytoma goidanichi *Boucek (Eurytomidae)*

This species hyperparasitizes pupae of *Cotesia gregalis*, which gregariously cocoon around the dead larva of the fall webworm. Its overall parasitism percentage is 0.6%; the parasitism rate among the cocoons of an infected web is 65%, with a maximum of 85%. Only one wasp develops from each host cocoon. The parasitized host cocoons change from white to brown and become harder. After emergence, the adult wasp bites an irregular exit hole, which differs from its host's emergence hole, which is round and always at the top of the cocoon. Thus, for survey purposes, it is easy to distinguish the two types of emergence holes. The species was originally described by Boucek (1970) from Italy, where it parasitized *Apanteles glomeratus* (L.) *Apanteles orobena* (Hymenoptera: Braconidae) on *Pieris brassicae* (L.) (Lepidoptera: Pieridae).

Exoristobia klinoclavata *Xu (Encyrtidae)*

This hyper-parasitic species gregariously parasitizes larvae or pupae of the tachinid fly, *Exorista japonica*. From one host puparium, an average of 47 wasps was reared. The species had originally been described by Xu and Lou (2000).

Parasitism and control effects of the parasitoids of the fall webworm pupae

Although the classical biological control was considered as the first choice in China to manage the invasive pest, it means that the natural enemies of the fall webworm should be introduced from its native countries (USA and Canada). However, as the lessons in former USSR etc. mentioned above, we focused on searching for native insect enemies of the fall webworm in different areas in China, trying to find effective species as potential biological control agents. From 1996 to 1999, 13,114 overwintering pupae, and from 1997 to 1999, 4,048 1st generation pupae of the fall webworm were collected and reared out in laboratory. As the natural enemies developed and emerged from the collections, the species were identified, and taxonomic studies on the parasitic wasps were undertaken. The numbers of each species, the female/male ratio of the adults, the parasitism percentages and other data were recorded from the rearing (tables 1 and 2).

Table 1 shows that the parasitism percentages of the natural enemies in the overwintering pupae of the fall webworm at the 19 study sites varied, and ranged from 2.68% to 43.41%, with a mean of 25.80%. For parasitism rates of the natural enemies of the 1st generation pupae of the fall webworm (i.e. 1st generation pupa) at various sites, see table 2. They ranged from 1.50% to 32.43% and averaged 16.13% and were generally lower than those on overwintering host pupae.

The percent parasitism of most parasitoids in the overwintering host pupae was generally higher than the one of the summer generation, and percentages for *Chоioia cunea* were significantly higher than those of the other species in both host pupae of the overwintering generation and the 1st generation, with 12.76% and 5.09%, respectively. The parasitism rate of *Pimpla disparis* in the overwintering host pupae was also relatively high, reaching 6.38%.

The parasitism by *Brachymeria lasus* and the tachinid flies were higher in the 1st generation host pupae than in the overwintering host pupae. Where tree and bush diversity was rich, the total parasitism rate among all natural enemies was particularly high and reached 40% in some plots. However, rates were lower (below 10%) in plots with monocultures of trees or poor biodiversity.

Regression analysis of parasitism rates of the main parasitoid species

First, the parasitism rate (table 1) of the main parasitoid species in each study plot was calculated from data in tables 3 and 4 collected from 1996 to 1999. Then, according to the percent parasitism of each enemy and total parasitism percentage of all parasitoid species in the investigation plot,

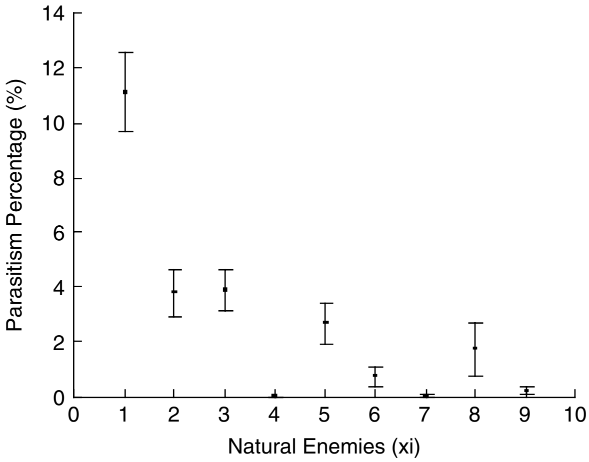

Fig. 5. Comparison of the mean parasitism rates for the nine parasitoids. Xi, parasitoids; 1, *Chouioia cunea*; 2, *Pediobius elasmi*; 3, *Pimpla disparis*; 4, *Pimpla parnasae*; 5, Tachinid flies; 6, *Tetrastichus septentrionalis*; 7, *Aprostocetus magniventer*; 8, *Brachymeria lasus*; 9, *Conomorium cuneae*.

the correlation between them was analyzed using the method of multiple regression analysis. A linear regression model was obtained as follows:

$$\hat{y} = 0.0171 + 0.7953x_1 + 0.4538x_2 + 0.3978x_3 + 0.4030x_5 + 0.2986x_6 + 0.3905x_8 + 0.4578x_9$$

$$(R^2 = 0.9837,\ F = 163.7,\ \text{df} = 7{,}19,\ P < 0.0001)$$

From the results above, it is clear that the regression model established the parasitism rates of each parasitoid species to the total parasitism rate ($\hat{y}$) on the fall webworm were highly significant. The coefficient of *Chouioia cunea* was the highest (0.7953), indicating that the parasitism rate of *C. cunea* was the largest contribution to the total parasitism rate.

Multiple comparison analysis of the parasitism of parasitoid species on the fall webworm

Based on the standardized original data in table 1 with the parasitoid species as x-values and different sites as repetitions, the mean parasitism rates of every parasitoid were compared. Results showed that the rate of parasitism for *Chouioia cunea* was significantly different with those for every other parasitoid species (df = 8, 234, $F = 21.808$, $P < 0.0001$). Comparison of the mean parasitism rates for the nine parasitoid species (the mean values of two generations of the fall webworm pupae in all survey sites), showed that percent parasitism of *Chouioia cunea* was much higher than that of all other parasitoids (fig. 5). This parasitoid has been successfully used in the subsequent biological control program in China as an augmentative strategy (Fuester, 2004; Yang *et al.*, 2005, 2006; Murphy, 2006).

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