Energy budgets of the Chinese green lacewing (Neuroptera: Chrysopidae) and its potential for biological control of the cotton aphid (Homoptera: Aphididae)

FENG GAO^{1,2}, XIANG-HUI LIU¹ and FENG GE¹

¹State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences and ²Graduate University of Chinese Academy of Sciences, Beijing, China

Abstract Energy budgets of larval stages of the Chinese green lacewing, *Chrysopa sinica* (Tjeder) (Neuroptera: Chrysopidae) were determined under laboratory conditions at photoperiod of 14:10 L:D, 27 ± 1 °C and $75\% \pm 2\%$ RH. The energy used as ingestion, assimilation, respiration, productivity and feces was constructed for each developmental stage. In addition, under these experimental conditions, the potential of *C. sinica* as a biological control agent was evaluated according to the ingestion by this predator and the energy content of cotton aphid, *Aphis gossypii* (Glover) (Homoptera: Aphididae). The larval stage of *C. sinica* was able to consume 1281.4 1-day-old aphids, 1018.7 2-day-old aphids, 626.9 3-day-old aphids, 393.5 4-day-old aphids, 312.1 5-day-old aphids or 203.5 9-day-old aphids, respectively. No significant difference was detected between the estimated number of aphids consumed by the lacewings using energetic methods and the actual number of aphids consumed by the lacewings in this experiment. Our results showed that *C. sinica* is an important natural enemy of natural enemies.

Key words *Aphis gossypii*, biological control, *Chrysopa sinica*, ecological efficiency, energy budget, predation DOI 10.1111/j.1744-7917.2007.00178.x

Introduction

Natural enemies play an important role in controlling insect pests in agroecosystems. Many studies have discussed how to estimate the predaceous ability of predators on prey (Itioka *et al.*, 1997; Greenstone & Morgan, 1989). Constructing a life table and estimating functional response parameters are the main methods for evaluating the effect of predators on insect pests in the laboratory. However, laboratory life tables were usually constructed under nonlimiting conditions which differ from those in

Correspondence: Feng Ge, State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, China. Tel: +86 10 64807123; fax: +86 10 64807099; email: gef@ioz.ac.cn the field (Perdikis & Lykouressis, 2002). Determination of the functional response can be influenced by many factors (Wu *et al.*, 2004), and, therefore, the key question herein is how we could realistically estimate the parameters in the equation (Menezes *et al.*, 2005; Badii *et al.*, 2004).

The ecological efficiency with which a population converts its food into productivity, which then becomes available to other trophic levels, is of prime importance when considering the energy flow between trophic levels (Wiegert, 1976). A predator acquires all the energy it needs to complete its life cycle through food acquired by predation. In energetics, the energy consumed as food by a predator should be equal to the energy of the consumed prey. Hence, estimating the energy dynamics of predator and prey has the potential not only to assess the efficiency of utilization of prey by predators but also to estimate the potential of a predator as biological control agent (Ge & Ding, 1990). However, from the viewpoint of ecological energetics, few studies have been reported (Sinha *et al.*, 1986).

Cotton is a very important crop in China. The predator *Chrysopa sinica* (Tjeder) (Neuroptera: Chrysopidae) is considered an important natural enemy in cotton ecosystems (Dong *et al.*, 2003). It prefers to prey on cotton aphid, *Aphis gossypii* (Glover) (Homoptera: Aphididae). Few reports have focused on the energetics of this predator, especially on individual and population energy budgets. The objectives of this study were to: (i) determine how this predator utilizes energy from *A. gossypii*; and (ii) use energetic methods to quantify potential biological control by *C. sinica* on *A. gossypii*.

Materials and methods

Plant and insect culture

Cotton Transgenic Bt cottons (cultivar 'GK-12') were grown in 10-cm diameter plastic pots in a growth chamber from May to September in 2005. The chamber was maintained at $27 \pm 1^{\circ}$ C, $75\% \pm 2\%$ RH and with a photoperiod of 14:10 h L:D. The cotton was planted every week to provide fresh cotton plants for rearing aphids. Experimental plants were grown individually in each pot and were watered every 3 days.

Aphis gossypii Aphids were collected from cotton fields. The colony was maintained in a growth chamber at $27 \pm 1^{\circ}$ C, $75\% \pm 2\%$ RH and 14:10 h L:D on cotton plants. Aphids were placed on cotton plants at the 7-leaf stage.

Chrysopa sinica The lacewing adults were purchased from the Laboratory of Biological Control, Beijing Academy of Agricultural and Forest Sciences, Beijing, China. Newly hatched larvae of the first generation were placed in a cage in the growth chamber, and were fed with sufficient cotton aphids until they matured. The number of eggs produced by these first generation adults were maintained in a growth chamber at $27 \pm 1^{\circ}$ C, $75\% \pm 2\%$ RH and 14: 10 h (L:D) and were used for experiments.

Development of C. sinica

A total of 100 newly hatched 1st instar larvae were transferred individually into Petri dishes. Sufficient 3-dayold aphids were supplied daily for lacewing larvae (1–8 days old) in each dish. A total of 100 replications (dishes), divided into five groups (20 dishes each), were used in this experiment. All dishes with aphids and lacewings were placed in the chamber under a photoperiod of 14:10 h L:D at $27 \pm 1^{\circ}$ C. The lacewing larvae were examined twice daily at 8:00 am and 8:00 pm. Hoagland-Snyder solution was added to the dishes to keep the cotton leaves fresh. The cotton leaves and Hoagland-Snyder solution were replaced twice weekly. Development time and mortality for each instar of the lacewing larvae were recorded. After eclosion, one male and one female lacewing were placed together in a glass arena (10 cm diameter by 20 cm depth) to allow them to mate for 7 days. Then the number of eggs produced by the pair of lacewings in each arena was recorded daily until the female died.

Individual energetic parameters

Biomass and caloric values The lacewings and cotton aphids were reared as described previously. Biomass of the lacewings and cotton aphids (i.e., insect body, exuviae, and feces) for each stage were collected from all experimental arenas. The live individuals were killed in a refrigerator (-20°C) , and they were then dried at 60°C for 48 h to obtain a constant dry weight. Fresh weight (mg) and dry weight (mg) for each sample were obtained using a Cahn 20 automatic electribalance (Cahn, St. Louis, MO, US) to calculate biomass (mg/individual). The caloric value (J/mg) of each sample collection was determined with a bomb calorimeter (PARR 1281, Parr Instrument Company, Moline, IL, USA) from combustion of the sample. Energy content (J/individual) of all samples of each stage was recorded separately for each of the three replications. Energy content of aphid bodies is listed in Appendix 1.

Growth productivity (P) We used the following formula to calculate growth productivity (P) of lacewings (Wiegert, 1976):

$$P = \Delta B + E,$$

where ΔB = the difference between initial and final biomass of each stage × the caloric value, and *E* = biomass of exuviae × caloric value for each stage.

Respiration (*R*) Measurements of O₂ consumption rate were made in a Gilson single valve differential respirometer (IGRP-14, Gilson Medical Electronics, Inc., Paris, France) with a water bath controlled at 27 \pm 0.2°C. Ten percent KOH was used as a CO₂ absorbent in the center well of the flasks (Wu et al., 1990). Numbers of lacewing larvae tested were 5, 5, 4, 4, 3, 2, 2, and 1 individuals for 1-, 2-, 3-, 4-, 5-, 6-, 7-, and 8-day-old larvae, respectively; and the number of pupae and adults tested were 5 and 1, respectively. Readings were taken every 5 min for 15 min for lacewings, and the mean value was used in calculations. After the last reading, insects were removed from the flasks, weighed, dried and reweighed. These samples were then used for the caloric content calculation to determine productivity. We converted oxygen consumption measurements to calories by an oxycaloric coefficient of 20.36 J/mL (Brody, 1945).

Energy budgets for lacewings were estimated using the following equation (Wiegert & Petersen, 1983):

$$\mathbf{I} = \mathbf{A} + \mathbf{FU} = \mathbf{R} + \mathbf{P} + \mathbf{FU},$$

where A, the amount of energy assimilated, was taken to be equivalent to the sum of productivity (P) and the energy loss through respiration (R); I = energy of food ingested, R = energy loss through respiration; P = energy stored as secondary productivity; and FU = energy egested as feces.

Ecological efficiencies Energy budget results were evaluated from the following ecological efficiency formulas: assimilation efficiency (AE) =A/I, gross ecological efficiency (GEE) =P/I, net ecological efficiency (NEE) =P/A (A, I, and P as defined above).

Predation of C. sinica on A. gossypii

Under the rearing conditions mentioned previously, 30 newly hatched 1st instar larvae of *C. sinica* were transferred individually to Petri dishes and fed on 3-day-old aphids, using about 10, 30, 50, 80, 100, 150, 200, and 250 aphids for 1-8-day-old larvae every day, respectively. These Petri dishes were separated into three groups (replicates), 10 dishes each. Numbers of aphids consumed by the lacewings were recorded daily, and new 3-day-old aphids were introduced into the dishes every 24 h.

The number of aphids consumed by a lacewing larva at each stage is the quotient of dividing ingestion of lacewing larvae at each stage by the energy content of cotton aphids (Appendix 1).

Data analysis

All data collected in this study were analyzed using SPSS for Windows, Version 12.0 (SPSS, Chicago, IL, USA) statistical software. The prey numbers actually consumed by *C. sinica* and estimated number of aphids consumed based on caloric calculations were compared using Chi-square test at P = 0.05 level. Values were log transformed for analyses to stabilize variance. Regression analyses were performed to examine the correlation of respiration rate and energy ingestion with age of *C. sinica*.

Results

Development of C. sinica

Individual lacewings molted twice during larval development. The average development time of a lacewing was 201.1 ± 28.1 , 247.9 ± 38.8 , and 925.6 ± 209.6 h in the larval, pupal, and adult stage, respectively (Table 1).

Energetic parameters of C. sinica

In general, the caloric values of lacewing body and exuviae were higher than those of the feces (Table 2). The biomass of lacewing body, exuviae and feces increased with the increase of age (Table 3).

Respiration rate decreased log-arithmetically (y, log μ L O₂/dry mg/h) with increasing age (x, days) from 1 to 8 days (y = -0.2279x + 2.9619, $r^2 = 0.825$, F = 28.354, df =1,6, and P = 0.002, Fig. 1).

Energy budgets and ecological efficiencies

The basic components of lacewing energy budgets

Table 1 Development time (h) and fecundity (mean \pm SE) of *C*. *sinica* at 27°C.

Stage	$Mean \pm SE$	Stage	$Mean \pm SE$
1st instar	51.3 ± 12.6	Pupa	247.9 ± 38.8
2nd instar	54.8 ± 16.6	Adult	925.6 ± 209.6
3rd instar	95.0 ± 22.1	Eggs/female	$647.0~\pm~~16.1$
Larval stage	201.1 ± 28.1		

Table 2 Caloric values (J/mg) (mean \pm SE) for *C. sinica* at different developmental stages.

Stage	Body	Feces	Exuviae
Egg	24.5 ± 1.73	_	_
1st instar	29.6 ± 1.25	17.6 ± 0.64	27.1 ± 0.94
2nd instar	25.8 ± 0.91	17.6 ± 0.64	26.9 ± 1.22
3rd instar	26.0 ± 1.14	20.9 ± 1.26	_
Pupa	22.4 ± 1.12	_	29.2 ± 1.37
Male	21.5 ± 0.77	20.9 ± 1.26	_
Female	22.3 ± 0.65	20.9 ± 1.26	_

Table 3 Biomass (dry weight mg) (Mean \pm SE) of *C. sinica* at different development stages.

Stage	Body	Exuviae	Feces
Egg	0.02 ± 0.001	_	_
1st instar	0.04 ± 0.010	_	0.10 ± 0.001
1st instar	0.07 ± 0.010	0.01 ± 0.001	0.10 ± 0.001
2nd instar	0.24 ± 0.080	_	0.19 ± 0.003
2nd instar	0.61 ± 0.080	_	0.19 ± 0.003
2nd instar	1.10 ± 0.730	_	0.19 ± 0.003
3rd instar	1.34 ± 0.210	0.02 ± 0.001	0.32 ± 0.007
3rd instar	2.46 ± 0.490	_	0.32 ± 0.007
3rd instar	4.15 ± 0.910	_	0.32 ± 0.007
Pupa	3.07 ± 0.090	0.80 ± 0.11	_
Adult	6.44 ± 0.800	_	0.27 ± 0.008
Adult	3.76 ± 0.460	_	0.27 ± 0.008
	Stage Egg 1st instar 1st instar 2nd instar 2nd instar 2nd instar 3rd instar 3rd instar 9rd instar Pupa Adult Adult	Stage Body Egg 0.02 ± 0.001 1st instar 0.04 ± 0.010 1st instar 0.07 ± 0.010 2nd instar 0.24 ± 0.080 2nd instar 0.61 ± 0.080 2nd instar 1.10 ± 0.730 3rd instar 1.34 ± 0.210 3rd instar 2.46 ± 0.490 3rd instar 4.15 ± 0.910 Pupa 3.07 ± 0.090 Adult 5.44 ± 0.460	StageBodyExuviaeEgg 0.02 ± 0.001 -1st instar 0.04 ± 0.010 -1st instar 0.07 ± 0.010 0.01 ± 0.001 2nd instar 0.24 ± 0.080 -2nd instar 0.61 ± 0.080 -2nd instar 1.10 ± 0.730 -3rd instar 1.34 ± 0.210 0.02 ± 0.001 3rd instar 2.46 ± 0.490 -3rd instar 4.15 ± 0.910 -Pupa 3.07 ± 0.090 0.80 ± 0.11 Adult 6.44 ± 0.800 -



Fig. 1 Log respiration rate for C. sinica at different larval ages.

including ingestion (I), assimilation (A), feces (F), productivity (P), and respiration (R) were constructed (Figs. 2,3). Ingestion (y, log J) increased log-arithmetically with age (x, days) from 1 to 8 days (Fig. 3, y = 0.1066x + 1.0719; $r^2 = 0.777$; F = 20.884, df = 1,6; and P < 0.05). Total energy used for respiration (Fig. 3) increased exponentially in 3-, 6-, and 8-day-old larvae, respectively. Productivity of an individual lacewing larva increased with age, and much higher productivity was found in 3rd instars (6-, 7- and 8day-old larvae).

The assimilation efficiencies (A/I) were similar among the lacewing larvae of different ages, with a mean value of $89.2\% \pm 6.25\%$ (Table 4). The mean gross ecological



Fig. 2 Log ingestion for *C. sinica* at different larval ages.



Fig. 3 Energy budgets for *C. sinica* at different larval ages. R is loss energy for respiration; FU is loss energy for feces and urine; and P is prodctivity.

efficiency (P/I) and net ecological efficiency (P/A) for the whole larval stage were $25.3\% \pm 3.78\%$ and $28.2\% \pm 4.23\%$, respectively.

Evaluation of potential predaceous ability by C. sinica on A. gossypii

Table 4 Ecological efficiencies (mean \pm SE) of *C. sinica* at different larval ages.

Age	A/I	P/I	P/A
1 day	88.7 ± 6.03	3.03 ± 0.63	3.42 ± 0.73
2 days	86.6 ± 5.72	8.26 ± 1.77	9.54 ± 1.34
3 days	93.0 ± 6.43	9.19 ± 1.64	9.89 ± 1.78
4 days	88.8 ± 3.73	31.9 ± 4.38	35.9 ± 5.76
5 days	88.7 ± 7.05	45.0 ± 4.93	50.8 ± 6.73
6 days	85.8 ± 8.36	13.0 ± 1.67	15.1 ± 3.06
7 days	88.7 ± 7.51	48.7 ± 6.15	54.9 ± 7.55
8 days	93.4 ± 9.58	43.0 ± 4.22	46.1 ± 4.16
Larvae mean	89.2 ± 6.25	25.3 ± 3.78	28.2 ± 4.23

A, the amount of energy assimilated; P, energy stored as secondary productivity; I, energy of food ingested; A/I is assimilation efficiency; P/I is gross ecological efficiency; and P/A is net ecological efficiency.

Based on the energy content of cotton aphids (Appendix 1) and ingestion by lacewing larvae, the number of aphids consumed by a lacewing larva at each stage was evaluated (Table 5). A larva could consume 1281.4 1-day-old, 1018.7 2-day-old, 626.9 3-day-old, 393.5 4-day-old, 312.1 5-day-old or 203.5 9-day-old aphids during its lifespan. No significant difference was found between the number of 3-day-old aphids ingested by lacewings estimated using energetic methods and the actual number of 3-day-old aphids consumed in the experiment ($\chi^2 = 20.597$, df =15, P = 0.195).

Discussion

Compared and estimated energy utilization and ecological efficiency

The efficiency with which a population converts its food into productivity, which then becomes available to higher trophic levels, is of prime importance when considering the energy flow between trophic levels. Assimilation reflects the percent of ingested food that is absorbed as nourishment. Assimilation efficiency exhibits a wide range (Wiegert & Petersen, 1983). Some of this variability is caused by difficulty in defining ingestion. Edgar (1971) reported that

Age of I C. sinica		Estimated consumption of aphids in different age groups					Actual aphid consumption	
		1 day	2 days	3 days	4 days	5 days	9 days	3 days
1 day	11.8 ± 4.39	47.2 ± 16.3	36.9 ± 9.19	$23.1\pm4.22^{\rm a}$	14.3 ± 5.44	11.5 ± 5.31	7.5 ± 6.02	$11.6\pm2.35^{\rm a}$
2 days	13.3 ± 3.22	52.8 ± 11.7	42.1 ± 5.28	$25.8\pm2.35^{\scriptscriptstyle a}$	16.2 ± 4.24	12.9 ± 5.22	8.4 ± 3.34	$16.7\pm6.39^{\rm a}$
3 days	27.6 ± 5.37	110.4 ± 31.4	86.3 ± 27.4	$54.1\pm15.3^{\rm a}$	33.7 ± 7.56	26.8 ± 6.35	17.5 ± 4.89	$39.7\pm12.8^{\rm a}$
4 days	29.9 ± 6.19	118.8 ± 26.1	94.7 ± 36.2	$58.1\pm11.6^{\rm a}$	36.5 ± 11.2	28.9 ± 4.66	18.9 ± 6.11	$53.6\pm12.1^{\rm a}$
5 days	29.5 ± 6.64	117.4 ± 33.8	93.5 ± 278	$57.4\pm9.39^{\rm a}$	36.1 ± 9.87	28.6 ± 6.65	18.6 ± 5.68	$56.0\pm24.1^{\rm a}$
6 days	47.9 ± 7.33	190.2 ± 45.9	151.6 ± 32.3	$93.1\pm16.6^{\rm a}$	58.5 ± 16.4	46.3 ± 11.0	30.2 ± 9.89	$90.9\pm19.5^{\rm a}$
7 days	59.9 ± 8.38	238.0 ± 39.2	189.6 ± 47.1	$116.4\pm33.3^{\text{a}}$	73.2 ± 21.6	58.0 ± 9.89	37.8 ± 10.3	$138.7\pm32.3^{\rm a}$
8 days	102.3 ± 26.3	406.6 ± 103.7	324.0 ± 69.4	$198.9\pm42.5^{\scriptscriptstyle a}$	125.0 ± 36.1	99.0 ± 26.6	64.6 ± 25.9	171.1 ± 24.7^{a}
Total	322.2 ± 76.7	1281.4 ± 212.4	1018.7 ± 198.3	$626.9\pm126.2^{\rm a}$	393.5 ± 106.3	312.1 ± 77.9	$203.5~\pm~72.8$	$578.3\pm134.3^{\text{a}}$

Table 5 Numbers of aphid consumed by *C. sinica* based on energetic values.

I, energy of food ingested. Means within a row indicated by the same lowercase letters are not significantly different (Chi-square test: df = 15, P > 0.05).

the assimilation efficiency of the wolf spider Pardosa sp. was 100%, which did not include excretion as part of ingestion. For predators, such as spiders, the ingested material comprises all readily digestible liquid content of the prey, and non-assimilable material, such as exoskeleton, which is not being consumed. Thus, by comparison with more "conventional" kinds of predators that chew and swallow the entire prey, spiders will always have consistently higher assimilation efficiency. In our study, the mean assimilation efficiency of larval lacewings was 89.21%. This high efficiency may be the result of the lacewing larvae having digested the liquid content of the aphids which have large quantities of sugar and amino acids. In addition, lacewing larvae have a strong ability to assimilate this type of food and to convert the energy for maintenance, searching, developing and other behaviors.

The relationship between productivity and respiratory energy losses in animal populations has attracted considerable interest in the past. Humphreys (1979) found the P/A ratio in nonsocial insects was 41%, and the ratios varied from 39% for herbivores to 56% for carnivores. Wiegert and Petersen (1983) reported that the ratios for terrestrial predators were 13.8%-66.3% with a mean 38%, and the ratios for herbivores were 43.6%. Ge and Ding (1990) and Wu et al. (1986) believe that the same insect species has different ecological efficiencies in different life history stages, and in general, assimilation and gross ecological efficiency decreased with increased body weight. The value for lacewing larvae (28.19%) fell within the range of 13.8%-66.3% reported by Wiegert and Petersen (1983). Gross ecological efficiencies (25.25%) of lacewing larvae coincided with the values of several terrestrial predator insects (ranging from 24.7% to 45.6%) as reported by Wiegert and Petersen (1983).

Estimating predation effect and biological control potential of C. sinica

Since a predator acquires all the energy it needs to complete its life cycle through food ingested, the energy consumed as food by a predator should be equal to the energy of the consumed prey. Thus, using ingestion energy of a predator to evaluate its value for biological control of pests is a very useful method. Benestad (1970) reported that Syrphus corollae larvae consumed 307-385 Myzus persicae (Sulzer), but he did not state the method of presentation of aphids or their size. In this study, the estimated number and size of aphids consumed by the lacewing larvae are reported in detail by energetics. We compared the numbers of 3-day-old aphids consumed by estimation and the actual numbers ingested by lacewings, and found that these numbers did not differ significantly. These results represent a much greater potential consumption of aphid biomass than that observed in the previous case, and suggest that this ecological energetic method was very useful for evaluating the potential biological control ability of lacewings feeding on aphids.

This study is a valuable advance in understanding of energy dynamics of *C. sinica*. Energy dynamics is a synthetic reflection of population density, mortality and caloric values. If the energy budgets of pests and natural enemies are constructed, then we may estimate the damage ability by herbivores and control potential of natural enemies more accurately. So, one of the key further study areas should focus on understanding energy allocation and conversion of various insect pests as prey for a predator as a potential biological control agent. To our knowledge, this is the first effort to quantify *C. sinica* as a potential biological control agent for *A. gossypii*. We believe that this methodology is very useful for quantifying the potential of natural enemies as biological control agents of crop pests, and this method will provide valuable basic information to facilitate the formulation of future integrated pest control strategies.

Acknowledgments

We are grateful to Dr. J. E. Slosser (Texas Agricultural Experiment Station, Agricultural Research and Extension Center at Chillicothe-Vernon) and Dr. T. -X. Liu (Texas A & M University) for their constructive comments on earlier versions of the manuscript. This project was supported by "National Basic Research Program of China" (973 Program) (No.2006CB102006), National Key Technology R&D Program (2006BAD08A07-3-2).

References

- Badii, M.H., Hernández-Ortiz, E., Flores, A.E. and Landeros, J. (2004) Prey stage preference and functional response of *Euseius hibisci* to *Tetranychus urticae* (Acari: Phytoseiidae, Tetranychidae). *Experimental and Applied Acarology*, 34, 263–273.
- Benestad, E. (1970) Food consumption at various temperature conditions in larvae of S. corollae. Norsk Geologisk Tidsskrift, 17, 87–91.
- Brody, S. (1945) *Bioenergetics and Growth*. Reinhold, New York, 33.
- Dong, L., Wan, F.H. and Zhang, G.F. (2003) Impacts of transgenic Bt cotton on the development and fecundity of *Chrysopa sinica* Tjeder. *Chinese Journal of Eco-Agriculture*, 11, 16–18.
- Edgar, W.D. (1971) Aspects of the ecological energetics of the wolf spider *Pardosa* (*Lycosa*) lugubris (*Walckenaer*). *Oecologia*, 7, 136–154.
- Ge, F. and Ding, Y.Q. (1990) The energy flow through rich brown planthopper-*Theridion octomaculatum* ecosystem. *Acta Entomologica Sinica*, 10, 167–172. (in Chinese)
- Greenstone, M.H. and Morgan, C.E. (1989) Predation on *Heliothis* zea (Lepidopera: Noctuidae): intraspecific ELISA assay for stomach analysis. Annals of the Entomological Society of America, 82, 45–49.

Humphreys, W.F. (1979) Production and respiration in animal

populations. Journal of Animal Ecology, 48, 427-453.

- Itioka, T., Inoue, T., Matsumoto, T. and Ishida, N. (1997) Biological control by two exotic parasitoids: eight-year population dynamics and life tables of the arrowhead scale. *Entomologia Experimentalis et Applicata*, 85, 65–74.
- Menezes, Luciana C.C.R., Rossi, M.N. and Reigada, C. (2005) Consequences of refuge for the functional response of *Dermestes ater* (Coleoptera: Dermestidae) to *Musca domestica* (Diptera: Muscidae). *Population Ecology*, 47, 213–219.
- Perdikis, D.C. and Lykouressis, D.P. (2002) Life table and biological characteristics of *Macrolophus pygmaeus* when feeding on *Myzus persicae* and *Trialeurodes vaporariorum*. *Entomologia Experimentalis et Applicata*, 102, 261–272.
- Sinha, R.N., Madrid, F.J. and White, N.D.G. (1986) Bioenergetics of *Ephestia cautella* (Walker) (Lepidoptera: Phycitidae) feeding on stored wheat. *Annals of the Entomological Society* of America, 79, 622–628.
- Wiegert, R.G. and Petersen, C.E. (1983) Energy transfer in insects. *Annual Review of Entomology*, 28, 455–486.
- Wiegert, R.G. (1976) *Ecological Energetics*. Pennsylvania, Halsted Press, 290–301.
- Wu, K.J., Gong, P.Y. and Li, X.Z. (1986) The energy budget of *Heliothis armigera*. Acta Entomologica Sinica, 29, 149–157. (in Chinese)
- Wu, K.J., Gong, P.Y. and Li, X.Z. (1990) Energy utilization and transfer in the cutworm, *Agrots segetum* Schiff. *Acta Entomologica Sinica*, 33, 416–423. (in Chinese)
- Wu, K.J., Sheng, C.F. and Gong, P.Y. (2004) Equation of predator functional response and estimation of the parameters in it. *Entomological Knowledge*, 41, 267–269. (in Chinese)

Accepted September 19, 2007

Appendix 1 Energy content (mean \pm SE) of *A. gossypii* bodies at different ages.

Day	Biomass (mg)	Caloric value (J/mg)	Energy content (J)
1	$0.012\ \pm\ 0.001$	20.59 ± 0.64	0.25 ± 0.01
2	0.015 ± 0.001	21.05 ± 1.06	0.32 ± 0.04
3	0.024 ± 0.002	21.43 ± 0.87	0.51 ± 0.07
4	0.038 ± 0.006	21.48 ± 1.02	0.82 ± 0.15
5	0.048 ± 0.008	21.52 ± 1.25	1.03 ± 0.28
10	0.074 ± 0.011	21.53 ± 1.47	1.58 ± 0.31