

An energy budget approach for evaluating the biocontrol potential of cotton aphid (*Aphis gossypii*) by the ladybeetle *Propylaea japonica*

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Abstract

Biological control of economically important crop pests is an important component of integrated pest management (IPM) strategies. Predator–prey energy relationships are critical to the success of biocontrol strategies; however, these relationships are often ignored in many IPM programs. In this study, the biocontrol potential of cotton aphid, *Aphis gossypii* (Glover) (Hemiptera: Aphididae), by the ladybeetle *Propylaea japonica* (Thunberg) (Coleoptera: Coccinellidae) was estimated in terms of energy budgets calculated at 27 ± 1 °C. The energy equivalent of prey subjects (aphids) consumed was estimated from bomb calorimetry and partitioned into the energy associated with ingestion, assimilation, respiration, reproduction, and waste for each developmental stage of the lady beetle. The average assimilation efficiencies for larval and adult ladybeetles were 88.2 and 91.1%, respectively, whereas net ecological efficiencies were 17.6% for larvae and 2.6% for adults. Similarly, assimilation efficiencies of cotton aphids were 71.5 and 74.4% for nymphs and adults, respectively. Based on energy budget calculations, approximately 520, 3-day-old aphids and 5 356, 3-day-old aphids were estimated to be consumed by the ladybeetle larval stage and the female adult stage, respectively. These estimates were similar to the actual number of aphids consumed by the ladybeetles, based on actual counts. The current data demonstrate that *P. japonica* is an important natural enemy of the cotton aphid, and that predator–prey energy relationships can play a critical role in biocontrol strategies and IPM programs.

Introduction

Energy transformations are important in ecology because they allow us to predict the outcomes of interactions among individuals and/or populations, as well as their impact on communities, based on the laws of thermodynamics (Wiegert, 1968; Gallucci, 1973; Singhal et al., 1976; Barlow, 1979). Furthermore, knowledge of the energetics of an individual or a population permits development of theories concerning efficiencies, foraging strategies, and evolution (Wiegert & Petersen, 1983). Hence, estimating the energy budgets or dynamics of predator and prey has the potential not only to assess the utilization efficiency of

prey by predators but also to estimate the potential of a predator as a biological control agent (Du et al., 2003; Gao et al., 2007, 2008a). However, energy budgets, utilization efficiency, and biological control potentials have not yet been extensively studied, especially not in the context of ecological efficiency. Natural enemies are an important component of integrated pest management (IPM) programs in many agroecosystems, and predator–prey energy relationships constitute a useful approach to quantify the biological control efficacy of natural enemies.

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. The proportion of food consumed that is actually assimilated (assimilation efficiency, AE) and the proportion of assimilated energy that is incorporated into biomass and/or used for reproduction (net ecological efficiency, NEE) are key

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determinants of gross ecological efficiency (GEE or Lindeman's Efficiency, LE), the efficiency with which organisms exploit food resources and convert them into biomass. Average AE values for many predatory species have been found to range from 50 to 90% because of variation in the digestibility of their diet. For insectivores, the chitin and exoskeletons of insect prey tend to reduce the AE to approximately 75%, whereas the AE of carnivores is approximately 90% (White et al., 1992).

Although energy-utilization efficiencies of predators are commonly limited by available energy, predatory populations generally make good use of the small amount of energy available to them (Singhal, 1980). Also important in predator-prey energy relationships is the number of prey individuals that a predator can consume in order to satisfy its energy requirements (Humphreys, 1979). This, in turn, will depend on the productive capacity of the prey, as well as the nature of the equilibrium among the different life history stages of the prey (Wiegert & Petersen, 1983). The relationship between production and respiratory energy losses in insect populations associated with age structure and life history has attracted considerable interest recently (Gao et al., 2007, 2008a).

Cotton [*Gossypium hirsutum* L. (Malvaceae)] is an important economic crop worldwide and chemical measures used to control important cotton pests such as the cotton aphid [*Aphis gossypii* (Glover) (Hemiptera: Aphididae)] are very costly. Integrated pest management strategies using natural enemies, such as the ladybeetle *Propylaea japonica* (Thunberg) (Coleoptera: Coccinellidae), are promising (Ge & Ding, 1995); however, the level of success is often mixed. Although the biological interactions between *P. japonica* and *A. gossypii* have been studied (Hagen & Bosch, 1968; Du et al., 2004; Zhu et al., 2006; Gao et al., 2008b), few investigations have considered the predator-prey energy relationships between these organisms as a measure of the biological control efficacy. The objectives of this study were therefore, to (1) quantify the energy utilization efficiency of *P. japonica* feeding on *A. gossypii*, and (2) evaluate potential biological control of *A. gossypii* by *P. japonica* using energy budget methods.

Materials and methods

Plant and insect culture

Plant material. Cotton (*G. hirsutum* cv. 'GK-12') seeds were sown in well-drained plastic pots (16 cm diameter × 18 cm deep) filled with 8:3:1 loam:cowdung:earthworm frass (vol:vol:vol). Following germination, seedlings were thinned to one per pot and randomly placed in a reach-in growth chamber, which was maintained at 27 ± 1 °C, 75 ± 2% r.h., and a photoperiod of L14:D10.

Plants were watered at least once per day and fertilized with 40 ml of a complete water-soluble fertilizer (10N:1.4P:4.3K) every 2 days. All plants were used for experimental purposes when they reached ≥60 cm in height (the six- to eight-leaf stage). New seeds were sown every week in order to provide fresh cotton plants for rearing aphids.

Aphids. Cotton aphids (*A. gossypii*) were collected from infested cotton fields in Sanhe County, Hebei Province, China (35°57'N, 116°47'E), and maintained in colonies in a growth chamber set at 27 ± 1 °C, 75 ± 2% r.h., and L14:D10 on cotton plants for several generations. Aphids were transferred to cotton plants whenever the plants reached the six- to eight-leaf stage.

Ladybeetle. Ladybeetles (*P. japonica*) were obtained 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. Eggs produced by these first generation adults were maintained in a growth chamber at 27 ± 1 °C, 75 ± 2% r.h., and L14:D10 and were used for experiments after hatching.

Development of *Propylaea japonica* and *Aphis gossypii*

Four-hour-old aphid nymphs were individually transferred onto freshly picked cotton leaves in Petri dishes. Hoagland-Snyder solution was added to the dishes to keep the cotton leaves moist. The cotton leaves and Hoagland-Snyder solution were replaced twice weekly. A total of 100 replications (dishes) for aphids, divided into five blocks of replicates (20 dishes each), were used in this experiment. Similarly, newly hatched first instars of ladybeetles (*P. japonica*) were individually transferred into Petri dishes and fed with 3-day-old aphids daily in each dish. A total of 100 replications (dishes) for ladybeetles, divided into five groups (20 dishes each), were used in this experiment.

All dishes with aphids and ladybeetles were placed in the chamber under a photoperiod of L14:D10 at 27 ± 1 °C. The ladybeetles and aphids were examined twice daily, at 08:00 and 20:00 hours. Development time and mortality for each instar of the ladybeetle and the aphid were recorded. After eclosion, one male and one female ladybeetle were placed together in a glass arena (10 cm in diameter × 20 cm depth) to mate. The number of eggs produced by each pair of ladybeetles was recorded daily until the female died. Similarly, the number of nymphs produced by adult aphids in each arena was recorded until the adult aphid died. Life parameters of *P. japonica* and *A. gossypii* are listed in Table 1.

Table 1 Mean (\pm SE) development time (days) for each life stage and fecundity of the ladybeetle *Propylaea japonica* and cotton aphid, *Aphis gossypii*

Stage	Ladybeetle	Cotton aphid
First instar	1.26 \pm 0.07	1.18 \pm 0.04
Second instar	1.26 \pm 0.06	1.1 \pm 0.03
Third instar	1.09 \pm 0.05	1.28 \pm 0.03
Fourth instar	3.01 \pm 0.04	1.30 \pm 0.03
Pupa	2.50 \pm 0.04	—
Adult	37.9 \pm 4.41	16.3 \pm 0.79
Eggs/female	176 \pm 18.5	—
Nymphs/female	—	3.49 \pm 0.16

Individual energetic parameters

Biomass and caloric values. Ladybeetles and cotton aphids were reared as described above. Biomass of the ladybeetles and cotton aphids (i.e., insect body, exuviate, and feces) for each stage were collected from all experimental arenas. Live individuals were killed in a freezer (-20 °C), and then dried at 60 °C to a constant dry weight for 48 h. Fresh and dry weights (mg) of each sample were obtained using a Cahn 20 automatic electric balance (Cahn, St. Louis, MO, USA) to calculate biomass (mg per individual). The caloric value ($J\ mg^{-1}$) of each sample collection was determined with a bomb calorimeter (PARR 1281; Parr Instrument Company, Moline, IL, USA) following combustion of each sample. Energy contents (J per individual) of samples within each growth stage were recorded separately for each of the three replications. Biomass and caloric values of *P. japonica* and *A. gossypii* are listed in Tables 2 and 3, respectively.

Productivity

Growth productivity (P_g). The following formula (Wiegert, 1976; Gao et al., 2007) was used to calculate the growth productivity (P_g) of ladybeetles and aphids:

$$P_g = \Delta B + E, \quad (1)$$

where ΔB is the difference between initial and final biomass of each stage multiplied by the caloric value, and E is the biomass of exuviae multiplied by the caloric value for each stage.

Reproduction (Pr). The energy associated with adult reproduction (Pr) was measured by removing, counting, drying, and weighing all ladybeetle eggs and new-born aphid nymphs every 24 h. Methods used were the same as described above, under 'Development of *P. japonica* and *A. gossypii*'. Determination of caloric equivalents allowed the expression of these results as calories of young produced per 24 h per adult.

Productivity (P). The productivity of insects was calculated as the sum of P_g and Pr (Wiegert, 1976) using the formula:

$$P = P_g + Pr. \quad (2)$$

Respiration (R). Measurements of O_2 consumption rate were made in a Gilson single valve differential respirometer (IGRP-14; Gilson Medical Electronics, Paris, France) with a water bath controlled at 27 ± 0.2 °C as described by Gao et al. (2007). Ten percent KOH was used as a CO_2 absorbent in the center well of the flasks (Wu et al., 1990). Numbers of ladybeetles tested were 10, 8, 5, 3, 5, and 2 individuals for first, second, third, and fourth instars, pupae, and adults, respectively. Number of aphids tested were 150, 100, 80, 50, 30, and 20 individuals for 1-, 2-, 3-, 4-, 5-day-old nymphs, and 10-day-old adults, respectively. There were three replications for each treatment. Readings were taken every 5 min for 15 min for ladybeetles and for 30 min for aphids and the mean value was used in calculations. After the last reading, insects were removed from the

Table 2 Mean (\pm SE) caloric values ($J\ mg^{-1}$ dry weight) for the ladybeetle *Propylaea japonica* and cotton aphid, *Aphis gossypii*, of each developmental stage. 'Age' is time since hatching (days) of *A. gossypii*

Ladybeetle				Cotton aphid			
Stage	Body	Feces	Exuviae	Age	Body	Feces	Exuviae
Egg	21.7 \pm 1.49	—	—	—	—	—	—
First instar	30.4 \pm 2.11	20.2 \pm 1.29	28.3 \pm 1.48	1 day	20.6 \pm 1.14	22.9 \pm 0.49	—
Second instar	29.1 \pm 1.72	20.2 \pm 1.29	27.1 \pm 1.48	2 days	21.1 \pm 1.32	22.9 \pm 0.49	18.2 \pm 2.02
Third instar	28.1 \pm 0.48	20.4 \pm 0.75	27.0 \pm 1.48	3 days	21.4 \pm 1.38	20.2 \pm 1.85	18.2 \pm 2.02
Fourth instar	29.7 \pm 1.34	20.6 \pm 1.21	—	4 days	21.5 \pm 0.87	22.6 \pm 1.43	18.2 \pm 2.02
Pupa	28.0 \pm 1.67	—	31.9 \pm 1.48	5 days	21.5 \pm 0.87	20.0 \pm 1.46	—
Male	25.9 \pm 1.60	20.9 \pm 1.43	—	—	—	—	—
Female	26.8 \pm 1.05	20.9 \pm 1.43	—	10 days	21.5 \pm 1.16	20.7 \pm 1.28	—

Table 3 Mean (\pm SE) biomass (body, exuviae, and feces) (mg dry weight) of the ladybeetle *Propylaea japonica* and cotton aphid, *Aphis gossypii*, at different development stages. 'Age' is time since hatching (days) of *A. gossypii*

Ladybeetle				Cotton aphid			
Stage	Body	Exuviae	Feces	Age	Body	Exuviae	Feces
First instar	0.09 \pm 0.006	0.007 \pm 0.001	0.075 \pm 0.006	1 day	0.012 \pm 0.001	0.005 \pm 0.000	0.008 \pm 0.001
Second instar	0.3 \pm 0.011	0.018 \pm 0.001	0.150 \pm 0.000	2 days	0.015 \pm 0.001	0.006 \pm 0.000	0.015 \pm 0.001
Third instar	0.569 \pm 0.043	0.022 \pm 0.001	0.225 \pm 0.036	3 days	0.024 \pm 0.000	0.01 \pm 0.004	0.031 \pm 0.011
Fourth instar	0.899 \pm 0.034	—	0.301 \pm 0.074	4 days	0.038 \pm 0.000	0.02 \pm 0.001	0.04 \pm 0.019
Pupa	1.46 \pm 0.013	0.156 \pm 0.021	—	5 days	0.048 \pm 0.000	—	0.049 \pm 0.015
Male	2.585 \pm 0.184	—	0.222 \pm 0.031	—	—	—	—
Female	3.568 \pm 0.15	—	0.222 \pm 0.031	10 days	0.074 \pm 0.001	—	0.067 \pm 0.009

flasks, weighed, dried, and reweighed. These samples were then used for the caloric content calculations to determine productivity. We converted oxygen consumption measurements to calories by an oxycaloric coefficient of 20.36 J ml⁻¹ (Brody, 1945).

The main energy budget components of aphids and ladybeetles were ingestion (I), assimilation (A), feces (FU), productivity (P), and respiration (R). Energy budgets for each insect were estimated using the following equation (Wiegert & Petersen, 1983):

$$I = A + FU = R + P + FU = R + Pg + Pr + FU, \quad (3)$$

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

Ecological efficiencies. Energy budget results were evaluated from the following ecological efficiency formulae:

$$\text{assimilation efficiency, } AE = A/I,$$

$$\text{gross ecological efficiency, } GEE = P/I, \text{ and}$$

$$\text{net ecological efficiency, } NEE = P/A,$$

where A, I, and P are as defined above [see description in Gao et al. (2007)].

Predation of Propylaea japonica on Aphis gossypii. Under the rearing conditions described above, 30 newly hatched first instars of ladybeetles were transferred individually to Petri dishes and fed on 3-day-old aphids, using about 20, 50, 80, 150, and 200 aphids for first, second, third, and fourth instars, and adult ladybeetles every day, respectively. There were three blocks (groups) of 10 dishes each. The numbers of aphid consumed by the ladybeetles were

recorded by counting surviving and dead aphids daily, and new 3-day-old aphids were introduced into the dishes every 24 h. Using energy budget methods, based on the energy content of aphids and ingestion by the ladybeetle, the number of aphids consumed by a ladybeetle at each stage was evaluated by dividing the ingestion value (I) at each stage by the energy content of cotton aphids when compared with the number as actually observed.

Statistical analysis

All data were analyzed using general linear model (GLM) procedures (SAS Institute, Cary, NC, USA). The prey numbers actually consumed by ladybeetles and estimated number of aphids consumed based on caloric calculations were compared using analysis of covariance (ANCOVA) at $P = 0.05$ level.

Results

Energy budgets of Propylaea japonica and Aphis gossypii

For the aphids, growth productivity (Pg), the energy for honeydew (FU), and respiration (R) increased with age (Figure 1). Respiratory consumption of energy was a dominant proportion of the aphid energy budget.

For the ladybeetle, the energy budget components were generally very high due to the lengthy developmental period of adults (approximately 38 days; Table 1). Therefore, only 24-h energy budgets are presented for the adult ladybeetle. The total amount of energy used for respiration (R) increased exponentially during the larval stage. The respiration and productivity of female adults (123.1 J) was much higher than that of male adults (64.6 J; Figure 2). Ingestion (I) followed the same pattern as assimilation, which increased with age in the immature stages and varied in the adult stage with higher energy content in the female than in the male.

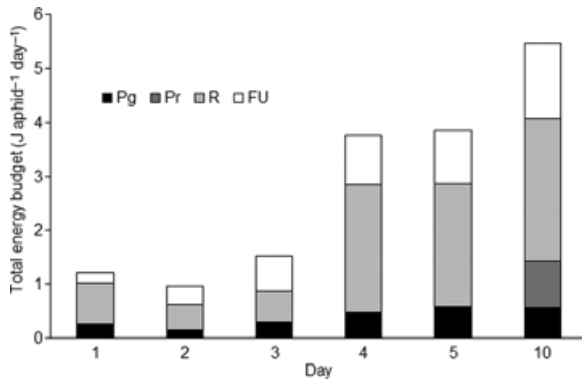


Figure 1 Energy budgets for the cotton aphid, *Aphis gossypii*, at different developmental stages (Pg, growth productivity; Pr, reproductivity; R, respiration; FU, feces and urine).

Ecological efficiencies of *Propylaea japonica* and *Aphis gossypii*

The AE reflects the ability of an insect to use consumed energy for maintenance of life and growth. The assimilation efficiencies (A/I) of immature ladybeetles were very similar to those of the mature stages (Table 4). Second instars of ladybeetles had higher gross ecological efficiencies (P/I), averaging approximately 22.1%, while the other larval stages had efficiencies ranging from 5.73 to 18.7%. However, male and female adults had relatively low efficiencies, averaging 1.88 and 2.42%, respectively. The net ecological efficiency (P/A) of the ladybeetle was 17.6% for larvae and 2.36% for the adult stages.

The assimilation efficiencies (A/I) of aphids were relatively low, with average values of approximately 72% for the larval stages and 75% for the adult stages. Gross ecological efficiency (P/I) and net ecological efficiency (P/A) of

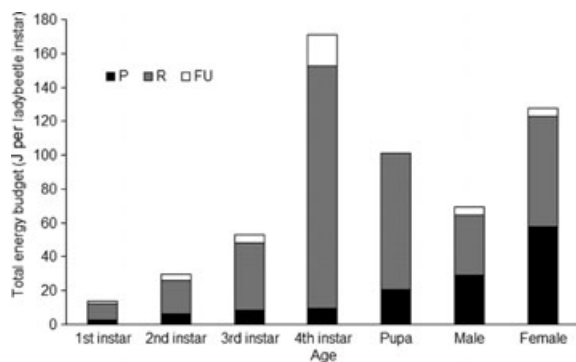


Figure 2 Energy budgets for the ladybeetle *Propylaea japonica* at different developmental stages (total energy for larvae and pupae; 24-h value for adults because the energy budget components were very high as a result of the lengthy developmental period of adults (see Results); P, productivity; R, respiration; FU, feces and urine).

10-day-old aphids (26.2 and 35.2%, respectively) were higher than those of the larval stages (16.9 and 24.1%, respectively).

Potential predaceous ability of *Propylaea japonica* on *Aphis gossypii*

The measured energy contents (body biomass multiplied by caloric value) of aphids were 0.25, 0.32, 0.51, 0.82, 1.03, and 1.58 J for 1-, 2-, 3-, 4-, 5-, and 10-day-old aphids, respectively. Based on the energy content of aphids and ingestion by the ladybeetle, the number of aphids consumed by a ladybeetle at each stage was evaluated (Table 5). Based on the energy budget calculations, female adult ladybeetles consumed nearly twice as many prey subjects as male adults. No significant difference was found between the estimated 3-day-old aphid numbers ingested by ladybeetles using energy budget methods and the actual number of aphids consumed (actual experimental observation: $F_{21} = 0.18$, $P = 0.812$).

Discussion

The current data clearly demonstrated that the amount of energy of food ingested by *P. japonica* is high, which means that *P. japonica*, as a biocontrol agent, consumed many cotton aphids. Approximately 1 607, 3-day-old aphids and 5 767, 3-day-old aphids were consumed on average by the ladybeetle larval stage and the adult stage, respectively. Energy budget methods provided further evidence that the estimated number of aphids was statistically similar to the actual number of aphids consumed by the ladybeetles. A previous study reported that *Chrysopa sinica* Tjeder was an important natural enemy of the cotton aphid and consumed about 627 cotton aphids, calculated using energetic methods (Gao et al., 2007). *Propylaea japonica* has stronger predaceous capability on cotton aphids than *C. sinica* because only *C. sinica* larvae prey on cotton aphids.

The current data also demonstrated that, in this biological control agent, different stages varied in their predation on cotton aphids from the viewpoint of energy budgets. The number of aphids consumed by ladybeetles increased with the development of the larval stages, ingestion being over 10 times higher during the fourth instar than the first instar. Adult *P. japonica* were even better than larvae as control agents, especially the females, which were able to consume 5 356 cotton aphids; this was the highest ingestion among all growth stages. Obviously, a ladybeetle adult needs more prey to convert energy for its searching, mating, oviposition, and other activities during its long life (Wiegert & Petersen, 1983).

Assimilation reflects the proportion of ingested food by a biological control agent that is in fact absorbed and used

Table 4 Percent ecological efficiencies (mean \pm SE) of the ladybeetle *Propylaea japonica* and cotton aphid, *Aphis gossypii*, at different stages based on individual energy budgets (A/I, assimilation efficiency; P/I, gross ecological efficiency; P/A, net ecological efficiency). 'Age' is time since hatching (days) of *A. gossypii*

Ladybeetle				Cotton aphid			
Stage	A/I	P/I	P/A	Age	A/I	P/I	P/A
First instar	86.2 \pm 9.4	18.7 \pm 6.0	21.7 \pm 7.5	1 day	84.5 \pm 7.8	20.9 \pm 5.3	24.7 \pm 4.7
Second instar	87.1 \pm 4.2	22.1 \pm 5.4	25.3 \pm 5.6	2 days	64.3 \pm 11.3	15.6 \pm 4.5	24.2 \pm 10.0
Third instar	90.6 \pm 4.1	15.5 \pm 3.5	17.1 \pm 6.4	3 days	58.2 \pm 9.6	19.9 \pm 7.4	34.2 \pm 8.5
Fourth instar	89.1 \pm 3.4	5.73 \pm 3.0	6.43 \pm 2.8	4 days	75.6 \pm 7.4	13.0 \pm 5.7	17.2 \pm 3.3
Laval mean	88.3 \pm 5.3	15.5 \pm 2.4	17.6 \pm 6.4	5 days	74.7 \pm 12.7	15.0 \pm 7.2	20.1 \pm 6.1
Male	88.6 \pm 2.8	1.88 \pm 0.3	2.12 \pm 0.7	Larval mean	71.5 \pm 6.4	16.9 \pm 5.9	24.1 \pm 5.5
Female	93.5 \pm 3.1	2.42 \pm 0.7	2.59 \pm 0.6	10 days	74.4 \pm 9.9	26.2 \pm 8.4	35.2 \pm 7.3
Adult mean	91.1 \pm 3.0	2.15 \pm 0.6	2.36 \pm 0.6	—	—	—	—

for growth, repair and maintenance, and reproduction. Assimilation efficiencies vary widely depending upon ecosystem, trophic levels, and growth stages of the subjects under consideration (Wiegert & Petersen, 1983). Edgar (1971) reported that the AE of the wolf spider (*Pardosa* spec.) was 100%, but this did not include excretion as part of ingestion. Furthermore, for predators such as spiders, the ingested material comprises all the easily digested liquid content of the prey, and the major non-assimilable material is simply not eaten. Thus, by comparison with more 'conventional' predators that chew and swallow the entire prey, or a greater proportion of it, spiders will exhibit higher assimilation efficiencies. In the current study, the mean assimilation efficiencies of larval ladybeetles were high (88.2–91.1%), in part because during feeding, the entire aphid is swallowed, and also because of the high sugar and amino acid contents of aphids.

The current data also demonstrated that net ecological efficiency (P/A) of *P. japonica* was only 17.6% in the larval stage, which fell within the value range of 13.8–66.3% for terrestrial predators reported by Wiegert & Petersen (1983). Interestingly, net ecological efficiency was only 2.36% in *P. japonica* adults. The relationship between productivity and respiratory energy losses in animal populations has been the subject of considerable interest (Golley & Gentry, 1964; Wiegert, 1964; Wiegert & Evans, 1967; Mackay, 1985). In this study, the net ecological efficiency decreased with increased body weight at the larval stage. To fulfill their productivity energy (P) needs, *P. japonica* needed to prey on more aphids. Female adult ladybeetles consume large numbers of aphids because they need more productivity energy (P) to maintain not only their development but fecundity as well. Our earlier study showed that the net ecological efficiency (P/A) of *C. sinica* was 28.2% (Gao et al., 2007), which was higher than *P. japonica*.

As a biocontrol agent, *P. japonica* is thus better than *C. sinica*.

Because a predator acquires all the energy it needs to complete its life cycle through food obtained from prey individuals, the energy consumed as food by a predator should theoretically be very close to the energy equivalent of the prey consumed, assuming a high conversion efficiency. However, and consistent with the law of thermodynamics, some energy is always lost during this transformation. Consequently, predators must consume a large number of prey in order to satisfy their energy requirements. Through calculations based on energy equivalents of prey subjects, several researchers have attempted to predict the number of prey subjects that a predator would have to consume to fulfill its energy needs (e.g., Benestad, 1970; Gao et al., 2007). For instance, Benestad (1970) predicted that *S. corollae* larvae would consume a mean of 307–385 *Myzus persicae* (Sulzer); however, the method used to make the prediction was not presented. In the current study, calculations based on energy equivalents of prey subjects allowed us to estimate that approximately 520, 3-day-old aphids and 5 356, 3-day-old aphids were consumed by the ladybeetle larval stage and the female adult stage, respectively. The estimated aphid numbers consumed by the ladybeetles were similar to the actual aphid numbers ingested by ladybeetles. The results herein represent a much greater and more accurate potential consumption of aphid biomass than has been reported in previous studies (Benestad, 1970) and thus demonstrates that energy budget methods can be useful in evaluating the potential biological control ability of ladybeetles on cotton aphids. Our results are also consistent with the previous conclusion reported by Gao et al. (2007), who used the energetic methods to quantify biological control efficacy of *C. sinica*.

In summary, the net ecological and assimilation efficiencies of the ladybeetle *P. japonica* and its main prey, the

Table 5 Mean (\pm SE) estimated potential predaceous ability of *Propylaea japonica* on *Aphis gossypii* based on energetic values and observed numbers of *A. gossypii* consumed by *P. japonica*

Stage	Ingestion	Estimated number							Observed number	
		1-day-old aphid	2-day-old aphid	3-day-old aphid	4-day-old aphid	5-day-old aphid	10-day-old aphid	3-day-old aphid	3-day-old aphid	
First instar	13.9 \pm 2.19	55.3 \pm 12.4	44.1 \pm 10.7	27.1 \pm 2.89	17.0 \pm 4.91	13.5 \pm 2.03	8.79 \pm 1.86	7.02 \pm 2.36		
Second instar	29.7 \pm 8.33	118 \pm 25.2	93.9 \pm 28.3	57.7 \pm 20.0	36.3 \pm 10.2	28.7 \pm 6.31	18.7 \pm 3.41	41.2 \pm 7.35		
Third instar	53.0 \pm 12.6	211 \pm 53.3	168 \pm 32.4	103 \pm 23.4	64.8 \pm 11.3	51.3 \pm 13.1	33.5 \pm 9.01	54.0 \pm 13.9		
Fourth instar	171 \pm 27.3	679 \pm 106	541 \pm 99.3	332 \pm 88.5	209 \pm 86.3	165 \pm 53.6	108 \pm 33.8	276 \pm 26.8		
Larval	268 \pm 42.7	1 063 \pm 227	847 \pm 241	520 \pm 105	327 \pm 102	259 \pm 76.4	169 \pm 54.7	1 607 \pm 358		
Male	1 548 \pm 247	6 154 \pm 2 036	4 903 \pm 1 206	3 010 \pm 1 263	1 892 \pm 337	1 499 \pm 311	977 \pm 139	5 322 \pm 1 082		
Female	2 755 \pm 1 125	10 950 \pm 2 672	8 724 \pm 2 117	5 356 \pm 1 422	3 367 \pm 1 323	2 667 \pm 1 215	1 739 \pm 840	6 212 \pm 997		
Adult	2 137 \pm 561	8 552 \pm 2 304	6 813 \pm 1 656	4 183 \pm 1 364	2 630 \pm 835	2 083 \pm 763	1 358 \pm 488	5 767 \pm 1 040		

cotton aphid *A. gossypii*, calculated using energy budget methods, were found to vary depending on gender and developmental stage. *Propylaea japonica* is an important natural enemy of the cotton aphid, and energetic methods are very useful to quantify biological control efficacy of natural enemies.

Future studies will concentrate on developing simulation models using these data. Currently, we are working on other natural enemies as biological control agents. A better understanding of energy allocation and conversion of various insect pests as prey for predators as potential biological control agents should improve the usefulness of this methodology for quantifying the potential of natural enemies as biological control agents of crop pests.

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References

- Barlow CA (1979) Energy utilization by larvae of flower fly, *Syrphus corollae* (Diptera: Syrphidae). Canadian Entomologist 111: 897–904.
- Benestad E (1970) Food consumption at various temperature conditions in larvae of *S. corollae*. Norsk Entomologisk Tidsskrift 17: 87–91.
- Brody S (1945) Bioenergetics and Growth. Reinhold, New York, NY, USA.
- Du L, Ge F, Ding YQ & Wu KJ (2003) Using population energetics to evaluate potential damage to cotton by cotton bollworm *Helicoverpa armigera* (Lepidoptera: Noctuidae) in North China. Applied Entomology and Zoology 38: 57–64.
- Du L, Ge F, Zhu SR & Parajulee MN (2004) Effect of cotton cultivar on development and reproduction of *Aphis gossypii* (Homoptera: Aphididae) and its predator *Propylaea japonica* (Coleoptera: Coccinellidae). Journal of Economic Entomology 97: 1278–1283.
- Edgar WD (1971) Aspects of the ecological energetics of the wolf spider *Pardosa (Lycosa) lugubris* (Walckenaer). Oecologia 7: 136–154.

- Gallucci VF (1973) On the principles of thermodynamics and ecology. *Annual Review of Ecology and Systematics* 4: 439–457.
- Gao F, Liu XH & Ge F (2007) Energy budgets of the Chinese green lacewing (Neuroptera: Chrysopidae) and its potential for biological control of the cotton aphid (Homoptera: Aphididae). *Insect Science* 14: 497–502.
- Gao F, Ge F, Liu XH & Song Y (2008a) Impact of insecticides on the structure and productivity of insect pest and natural enemy communities associated with intercropping in cotton agroecosystems. *International Journal of Pest Management* 54: 103–114.
- Gao F, Zhu SR, Du L, Parajulee MN, Kang L & Ge F (2008b) Interactive effect of elevated CO₂ and cotton cultivar on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Propylaea japonica*. *Environmental Entomology* 37: 29–37.
- Ge F & Ding YQ (1995) The foraging behavior of lady beetle *Propylaea japonica* towards cotton aphids *Aphis gossypii*. *Acta Entomologica Sinica* 38: 436–441. (in Chinese).
- Golley RB & Gentry JB (1964) Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. *Ecology* 45: 217–225.
- Hagen KS & van den Bosch R (1968) Impact of pathogens, parasites and predators on aphids. *Annual Review of Entomology* 13: 325–384.
- Humphreys WF (1979) Production and respiration in animal populations. *Journal of Animal Ecology* 48: 427–453.
- Mackay WP (1985) A comparison of the energy budgets of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Oecologia* 66: 484–494.
- Singhal RN (1980) Relationship between ecological efficiencies of a herbivore and a carnivore insect. *Indian Journal of Ecology* 7: 71–76.
- Singhal RZ, Vats LK & Singh JS (1976) Food consumption energy budget for the Ak grasshopper, *Poeciloceris pictus*. Fabr. (Acrididae: Orthoptera). *Indian Journal of Ecology* 3: 119–124.
- White ID, Harrison SJ & Mottershead DN (1992) *Environmental Systems*, 2nd edn. Chapman & Hall, New York, NY, USA.
- Wiegert RG (1964) Population energetics of meadow spittlebugs (*Philaenus spumarius* L.) as affected by migration and habitat. *Ecological Monographs* 34: 217–241.
- Wiegert RG (1968) Thermodynamic considerations in animal nutrition. *American Zoologist* 8: 71–81.
- Wiegert RG (1976) *Ecological Energetics*. Pennsylvania, Halsted Press, 290–301.
- Wiegert RG & Evans FC (1967) Investigations of secondary productivity in grasslands. *Secondary Productivity of Terrestrial Ecosystems* (ed. by K Petruszewics), pp. 449–518. Panstwowe Wydawnictwo Naukowe, Warszawa, Poland.
- Wiegert RG & Petersen CE (1983) Energy transfer in insects. *Annual Review of Entomology* 28: 455–486.
- Wu RG, Gong PY & Li XZ (1990) Energy utilization and transfer in the cutworm, *Agrotis segetum* Schiff. *Acta Entomologica Sinica* 33: 416–423. (in Chinese).
- Zhu SR, Su JW, Liu XH, Du L, Yardim EN & Ge F (2006) Development and reproduction of *Propylaea japonica* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) on transgenic cotton. *Zoological Studies* 45: 98–103.