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Growth rate and anticipated longevity of *Chrysopa phyllochroma* Wesmael (Neuroptera: Chrysopidae) larvae fed on *Aphis gossypii* Glover (Homoptera: Aphididae)

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Abstract

The growth rate and anticipated longevity of *Chrysopa phyllochroma* fed on *Aphis gossypii* were determined to test the two following hypotheses: a) When prey is quite sufficient, predators show the maximum growth rate; b) without prey provided, predators have a constant anticipated longevity. Considering assimilative efficiency (k), a new model was suggested: $G=G_0[1-e^{-k(I-C)}]$. Fitted to the new model, the maximum growth rate (G_0), respiration threshold (C) and assimilative efficiency of larvae (I) were 15.256, 0.529, and 17.624, respectively. There were significant linear correlations between the maximum growth rate and the development day-age of larvae (D), the respiration threshold and D, except between assimilative efficiency and D. Under the condition of no prey, stage mortality curves of larvae were fitted by Normal Distribution Curve. The anticipated longevity of larvae at 0.5, 1, 2, 3, 4, and 5 day-age was 29.56, 38.97, 46.79, 48.73, 53.15, and 59.77 h, respectively. There was a significant logarithmic correlation between the anticipated longevity of larvae and D. The accumulated weight loss of larvae increased as the survival time of larvae was prolonged, and there was a significant logarithmic correlation between the accumulated weight loss and survival time.

Key words: *Chrysopa phyllochroma*; *Aphis gossypii*; growth rate; feeding rate; anticipated longevity

INTRODUCTION

The green lacewing, *Chrysopa phyllochroma* Wesmael (Neuroptera: Chrysopidae), is a promising biological control agent in cotton fields in China (Mu et al., 1980). The larvae of *C. phyllochroma* fed on cotton aphids, *Aphis gossypii* Glover (Homoptera: Aphididae), were able to complete their life cycle. Besides aphids, this lacewing can eat mites and a wide variety of soft-bodied insects, including insect eggs, thrips, mealybugs, immature whiteflies, and small caterpillars (Zelený, 1965, 1969; Mu et al., 1980; Tulisalo, 1984; Peric and Dimic, 1997; Su and Sheng, 1999b). The measurements of fundamental life-cycle components are essential to develop a full understanding of the population dynamics of Chrysopids (Albuquerque et al., 1997; Tauber et al., 2000). The effective accumulated temperature and development rate of *C. phyllochroma* were determined in the laboratory (Su and Sheng, 1999a), but the growth rate (G) and stage mortality (M) were not determined; however, because the ways in which metabolism vary with different feeding rates in true predators, the relationship between the feeding rate and the growth rate appear to be complex, and the limited available evidence has been poorly documented (Beddington, 1976). Generally, the growth rate of a predator will depend on three main components, including the feeding rate (I), assimilated efficiency (δ), and the respiration threshold (C), which depend on the maintenance energy requirements of the predator. For some true predators, it can be assumed that the energy allocated to growth is a linear function of food intake (Turnbull, 1962; Mukerji and LeRoux, 1969; Toth and Chew, 1972).

$$G=\delta(I-C) \qquad (1)$$

Slightly more complex, non-linear relationships between G and I have been observed in other

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predatory poikliotherms, particularly fish (Davis and Warren, 1968), and Copepoda (Shushkina and Klekowski, 1968). A curvilinear relationship between G and I is to be expected as follows,

$$G=\delta(\ln I-C) \qquad (2)$$

For the two equations, if $I\to\infty$, then $G\to\infty$. These equations are neither ideal nor suitable enough to simulate the relationship between G and I so a hypothesis was put forward that: 1) when prey exposed to a predator is quite sufficient, because of confining factors, such as limited feeding time, limited ability of the ingesting system, limited activity of digesting enzymes, and other environmental factors, the growth rate of the predator does not increase infinitely, but it will be close to constant; 2) when no prey is provided to predators, they will lose weight with a negative growth rate. The aims of this study were as follows: first, to determine the stage mortality and growth rate of *C. phyllochroma* larvae in the laboratory and, second, to construct new models of the growth rate and the mortality rate of a predator under controlled conditions.

MATERIALS AND METHODS

Cotton, cotton aphids and green lacewing. Six wood-framed cages (100 cm×100 cm×100 cm) covered by fly-proof nylon gauze were constructed. In each cage, four plastic pots (40 cm high and 20 cm ID) with soil were used to grow cotton plants (variety: Simian 3). When the plants were ca. 40 cm high, adult aphids obtained from a laboratory colony were introduced onto plants after removing other herbivorous pests and natural enemies. The aphids used as prey in the experiments were 3–4-day-old nymphs infesting plants and laid by adult cotton aphids.

Adult green lacewings were collected from an apple orchard (N37°10′, E118°7′, Boxing County, Shandong Province, China) and were fed with honey solution (5% v/v) in the laboratory. The oviposition unit for adult lacewings was a cylindrical glass tube (12 cm high and 15 cm ID). At the ends of each tube, a piece of black cloth and a piece of nylon gauze were held by rubber bands. Five pairs of adult lacewing were introduced into each unit with honey solution. The eggs were collected daily and then transferred into Petri dishes where they were allowed to hatch. The newly-hatched and other different day-age lacewing larvae were used in the experiments.

Stage mortality and accumulated weight loss. This experiment (Exp1) was conducted in a climatic chamber (LRH-250-GS, Donglian Co., Harbin, China) with 28±0.2°C, 13L : 11D and 70±5% RH). There were six different day-age treatment groups (0.5-, 1-, 2-, 3-, 4-, and 5-day-old groups, respectively) with 20 larvae in each group. The initial weight of each larva (WT_0) was record and then the larvae were isolated in glass tubes (7 cm high and 2 cm ID) individually without any prey. The number of dead larvae (those which did not move when touched lightly with a brush pen or respond behaviorally when their mouthparts were touched with agar dipped in the body fluid of cotton aphids) in the ith group (NT_i) was recorded at a time interval of 6 h. Surviving larvae in the ith group (WT_i) were weighed using an electric balance (FA2104N, Shanghai Balance Instruments Co. Ltd., Shanghai, China) at 12 h time intervals until all larvae died or pupated. Meanwhile, another 120 larvae at six different developed day-ages (mentioned above) were used as a control. These control larvae were reared individually in glass tubes with abundant prey. The number of dead larvae in the ith group (NC_i) was recorded at 6 h time intervals until all surviving larvae pupated. Exp1 was replicated three times.

Growth rate. This experiment (Exp2) was carried out in another climatic chamber (with similar conditions to Exp1). One hundred and twenty newly-hatched larvae were separated into six groups. These larvae were reared individually in glass tubes with cotton aphids of a designated number (Table 1). Newly-hatched larvae (WL_1) and aphids (WA_1) were weighed on the first day. From the second to the eighth day, the weight of the larva (WL_i) and the remaining aphids (WR_i) in each tube were recorded and then, the larva was placed into a clean tube and reared with fresh aphids of different weight (WA_i) daily. Exp2 was replicated three times.

Statistical analysis. In the ith group of Exp1, the stage mortality of lacewing larvae (M_i) was calculated by $M_i=(NT_i-NC_i)/N\times100\%$ (N=initial number of larvae), and the accumulated weight loss of larvae (W_i) was calculated by $W_i=WT_i-WT_0$; average M_i and W_i of three replications was recorded followed by standard diversity (SD), and

Table 1. Number of cotton aphids for *Chrysopa phyllochroma* larvae of different day-ages

Day-age of *C. phyllochroma* larvae	Number of cotton aphids					
	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
1	5	10	15	20	25	30
2	5	10	15	20	25	30
3	10	20	30	40	50	60
4	10	20	30	40	50	60
5	15	30	45	60	75	90
6	15	30	45	60	75	90
7	20	40	60	80	100	120
8	20	40	60	80	100	120

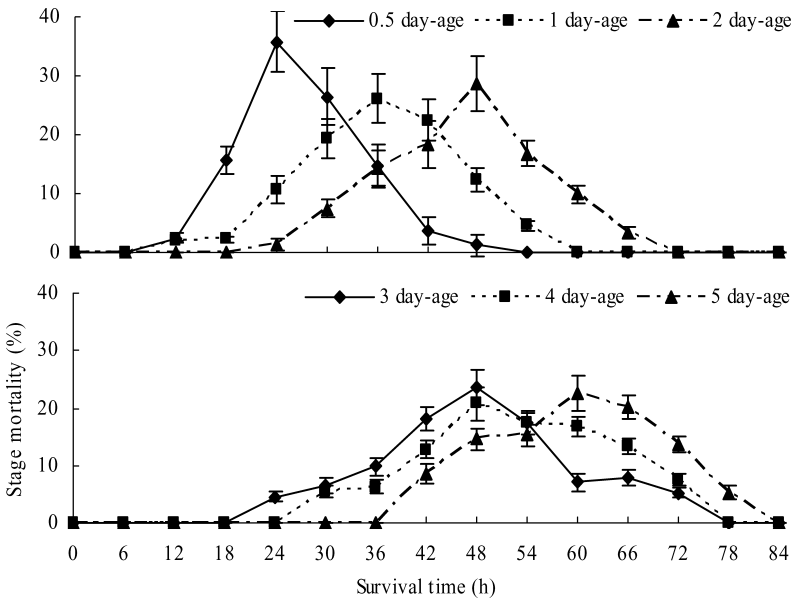

Fig. 1. The correlation between average stage mortality of three replicates (mean±SD) and the survival time of *Chrysopa phyllochroma* larvae in six treatment groups (different development day-ages).

then Eqs. (3) and (4) (mentioned later) were fitted. In the *i*th group of Exp2, the weight of prey ingested by lacewing larvae (I_i) was calculated by $I_i=WA_i-WR_{i+1}$, the growth weight of larvae (G_i) was calculated by $G_i=WL_{i+1}-WL_i$, average I_i and G_i of three replications were recorded, and then the growth rate models (1) and (2) and new model (5) (suggested later) were performed (SPSS Ver. 10, SPSS Inc., Chicago, Illinois).

RESULTS

Stage mortality and anticipated longevity

When the feeding rate (I)=0 or I was less than the respiration threshold (C), the larvae lost body weight continuously and finally died. The stage mortality of lacewing larvae in different development day-age groups was different (Fig. 1).

Correlation between the survival time (T_i) and stage mortality (M_i) was fitted by the Normal Distribution Curve as follows,

$$M_i = \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(T_i-\mu)^2}{2\sigma^2}} \qquad (3)$$

where both μ and σ are constants.

There was a significant logarithmic correlation between M_i and T_i (Table 2). The parameter (μ) of the Normal Distribution Curve was regarded as the anticipated longevity of lacewing larvae; mean-

Table 2. Average survival time, anticipated longevity (μ) and standard deviation (σ) of *Chrysopa phyllochroma* larvae fitted by Normal Distribution Curve (no prey)

Development time of larvae (day-age)	Average survival time (h)	Anticipated longevity (μ) (h)	Standard deviation (σ)	Correlation coefficient (R^2)
0.5	27.08	29.56	6.10	0.8534**
1	36.31	38.97	9.51	0.9031***
2	46.33	46.79	14.33	0.8465**
3	48.09	48.73	13.65	0.8628**
4	52.77	53.15	14.96	0.8901***
5	59.59	59.77	15.37	0.8543**

df=8, $\alpha_{0.05}$=0.6319; $\alpha_{0.01}$=0.7646; $\alpha_{0.001}$=0.8721; R^2 is the correlation coefficient (**: p=0.01; ***: p=0.001).

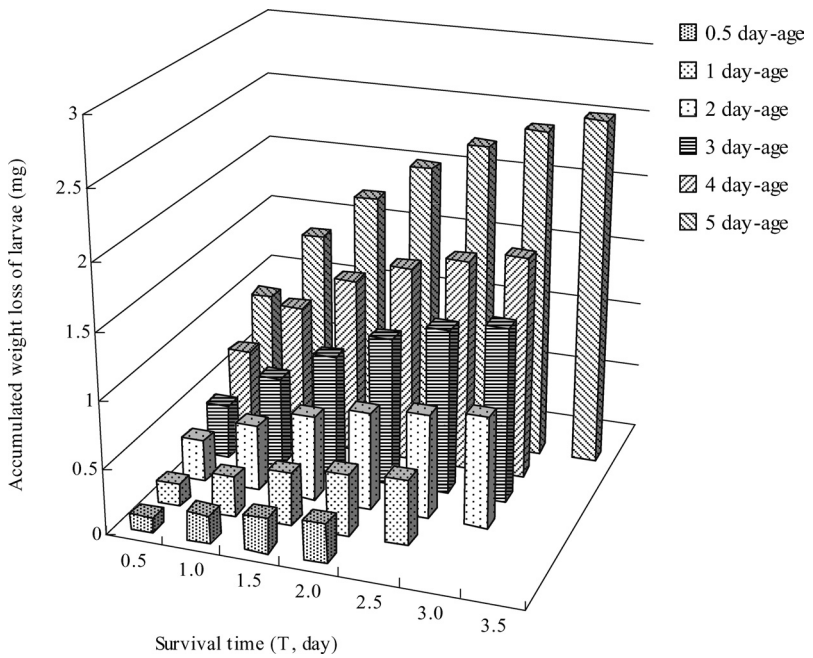

Fig. 2. Average accumulated weight loss of *Chrysopa phyllochroma* larvae (three replicates) in six treatment development day-age groups (0.5, 1, 2, 3, 4 and 5 days old, respectively) increased with the survival time under the condition of no prey (cotton aphid) provided.

while, the older the day-age (D) lacewing larvae, the longer the anticipated longevity. There was a significant logarithmic correlation between anticipated longevity and D of lacewing larvae (df=4, anticipated longevity=$11.928\ln D+38.022$, the correlation coefficient $R^2=0.973>R^2_{0.01}=0.917$).

Accumulated weight loss

The accumulated lost weight of lacewing larvae of 6 treatment groups is shown in Fig. 2. For larvae of the ith group, when the survival time (T_i) of larvae was prolonged, the accumulated weight loss (W_i) increased gradually. The relationship was simulated by a logarithmic equation as follows,

$$W_i=K\ln(T_i)+W_0 \quad (4)$$

where K and W_0 were constants, then

Larvae of 0.5D, $W_{0.5}=0.132\ln(T)+0.120$, $R^2=0.961$ (df=3, $R^2_{0.01}=0.959$)

Larvae of 1D, $W_1=0.205\ln(T)+0.168$, $R^2=0.952$ (df=4, $R^2_{0.01}=0.917$)

Larvae of 2D, $W_2=0.296\ln(T)+0.312$, $R^2=0.978$ (df=5, $R^2_{0.001}=0.951$)

Larvae of 3D, $W_3=0.530\ln(T)+0.372$, $R^2=0.966$ (df=5)

Larvae of 4D, $W_4=0.577\ln(T)+0.684$, $R^2=0.981$ (df=5)

Larvae of 5D, $W_5=0.863\ln(T)+0.926$, $R^2=$

Table 3. Simulation of the growth rates of *Chrysopa phyllochroma* larvae by three models

Development time of larvae (day-age)	Model (1) $G=\delta(I-C)$			Model (2) $G=\delta(\ln I-C)$			New model $G=G_0[1-e^{-k(I-C)}]$			
	δ	C	R^2	δ	C	R^2	G_0	k	C	R^2
1	0.028	−5.834	0.7593*	0.126	−0.851	0.7998**	0.365	0.449	0.386	0.7807*
2	0.035	−7.002	0.6798*	0.121	−1.877	0.6057	0.498	0.559	0.728	0.7694*
3	0.099	−2.048	0.7915**	0.311	−0.541	0.7545*	0.713	0.573	0.808	0.8657**
4	0.041	−14.642	0.6181	0.217	−2.213	0.5925	1.106	0.441	1.285	0.6838*
5	0.079	−8.227	0.7263*	0.412	−0.957	0.7582*	1.225	0.536	1.084	0.7737*
6	0.278	−1.903	0.7676**	1.766	−0.503	0.7290*	3.554	0.467	3.406	0.8024**
7	0.222	−8.130	0.6770*	1.848	0.098	0.6253	4.907	0.572	5.419	0.7547*
8	0.196	−9.278	0.8413**	1.470	0.274	0.7972**	4.285	0.537	4.067	0.7998**
Total period	0.103	−77.650	0.8759**	4.331	0.861	0.8600**	15.256	0.529	17.624	0.7686*

For model (1) and model (2), df=8, $\alpha_{0.05}=0.632$, $\alpha_{0.01}=0.765$; for new model, df = 7, $\alpha_{0.05}=0.666$, $\alpha_{0.01}=0.798$; R^2 is the correlation coefficient (*: $p=0.05$; **: $p=0.01$).

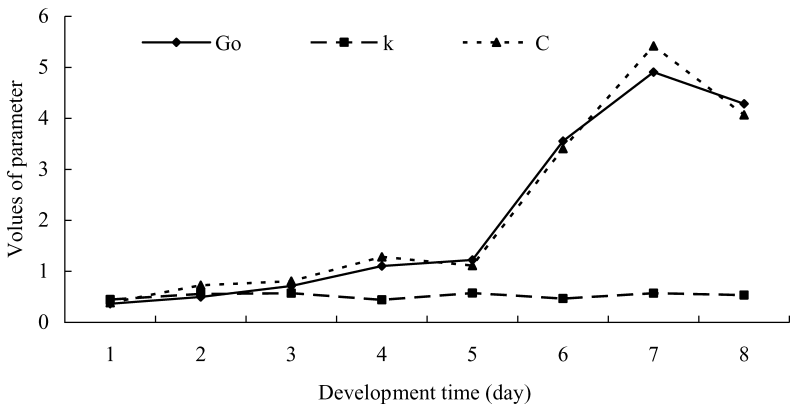

Fig. 3. Correlations between the maximum growth rate (G_0), assimilative efficiency (k), respiration threshold (C), and development day-age (D) of *Chrysopa phyllochroma* larvae (df=6, $\alpha_{0.05}=0.7067$, $\alpha_{0.01}=0.8343$, and R^2 is the correlation coefficient; $G_0=0.692D-1.032$, $R^2=0.8393$; $k=0.006D+0.495$, $R^2=0.0602$; $C=0.667D-0.894$, $R^2=0.7789$).

0.972 (df=6, $R^2_{0.001}=0.925$)

Growth rate of lacewing larvae simulated by Eqs. (1) and (2)

Simulations of growth rate models (1) and (2) for lacewing larvae are shown in Table 3. For model (1), if $C<0$, the linear regression lines crossed the y-axis with a positive value (larvae could grow in the absence of prey), and so the model was neither ideal nor suitable. The actual data (Fig. 1) suggest that the growth of larvae decreased gradually to death, and the larvae could not complete their life history under such a condition. For model (2), $C<0$ on six of eight test days, and correlation coefficients were not significant on three test days, so the model was also not ideal to simulate the growth process of lacewing larvae.

New growth rate model

Because of the limitations of models (1) and (2), the growth rate of lacewing larvae was redefined as,

$$G=G_0[1-e^{-k(I-C)}] \quad (5)$$

where G_0=the maximum growth rate, k=the assimilation efficiency, both G_0 and k are constants.

This is a new model of growth rate, and the relation between the growth rate and the feeding rate is not linear, but a curvilinear asymptote curve. Simulation of the growth rates of larvae with the new model is shown in Table 3.

Correlations between G_0, k, C, and D

The value of G_0 increased with the value of D of larvae. In addition, the value of C should always be a positive value and increase gradually with the de-

velopment of larvae (Fig. 3). In contrast, assimilation efficiency (k) was stable. There were significant linear relations between G_0 and D, C and D, respectively.

DISCUSSION

The anticipated longevity of lacewing larvae means that half of all larvae died; the higher the value of the anticipated longevity, the stronger the survival ability of larvae to endure the absence of prey. Sundby (1966) reported the survival ability of newly-hatched larvae of three species (*Coccinella septempunctata* L., *Chrysoperla carnea* Step., and *Syrphus ribesii* L.) in which, under the condition of no prey but with water provided, the anticipated longevity of *C. carnea* was 3.8 d (range: 2–9 d). In our study, the anticipated longevity of newly-hatched *C. phyllochroma* was 29.56 h≈1.25 d (range: 0.5–2.3 d). The difference of the anticipated longevity between the two species of lacewing larvae was due to Chrysopidae species characteristics and also the test conditions, such as test temperature and activity space, but no water supply. Meanwhile, Su and Sheng (1999b) suggested that the attack rate of lacewing larvae decreased after a long non-feeding period; in contrast, the handling time (T_h) of larvae was prolonged. It is known that the anticipated longevity of predators is affected by the use of insecticides. Although the resistance of *Chrysopa* spp. to insecticides is stronger than that of spider, ladybug, syrphid, and assassin bug; insecticides with lower toxicity should be an alternative to control insect pests in cotton fields (Lingren and Ridgway, 1967; Pree and Hagley, 1985). In addition, the spraying time and period of validity of insecticides should miss the growth period of *C. phylochroma* larvae to protect larvae from injury from insecticides (Su et al., 2003).

Equations (4) and (5) are new models suggested in this study. If $I=0$, then $G=G_0[1-e^{-k(I-C)}]=G_0[1-e^{-kC}]<0$. The growth rate model and weight loss equation can be used simultaneously to explain the same phenomena in which green lacewing larvae lose weight when larvae are exposed to conditions of no prey. For example, when a lacewing larva was 5 days old, the next day, the growth rate was $G=1.225[1-e^{0.539\times1.084}]=-0.965$ (data from Tables 2 and 3) after one day. According to the accumulated weight loss equation for a larva of 5 days old, $W_5=0.863\ln T+0.926=0.926$ (where $T=1$), and the lost weight was 0.926. Although $G+W_5=-0.039$, it does no harm to conclude that green lacewing larvae of 5 days old will lose weight of approximately 1 mg the next day. If the larvae lose weight on consecutive days, half will die after 2.5 days (Table 2).

Chrysopids are a group of important natural predators in cotton fields (Debach, 1974; Canard et al., 1984; Hagley and Miles, 1987; Boo et al., 1998). In North China, *C. phyllochroma* is an efficient natural enemy to control cotton aphids in cotton fields (Wuhan Teachers College, 1976; Mu et al., 1980; Zhao, 1987; Yang, 1988; Su et al., 2003). Further investigation and tests should be undertaken to explore the relationship between the growth rate and feeding rate as physiological and ecological studies. Modified parameters such as k and C in a growth rate model (5), and K and W_0 in lost weight Eq. (4) produced a more perfect regression model that fit more predators, suggesting that this could be a valuable model for predicting the population dynamics of predaceous natural enemies, if confirmed.

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