

# Starvation resistance of invasive lace bug *Corythucha ciliata* (Hemiptera: Tingidae) in China

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Food shortage is a prevalent threat to insect survival and successful reproduction in natural settings. An insect species invading new areas may have a high capacity to survive and adapt to starvation. To test these hypotheses, we assessed the survival time of *Corythucha ciliata* (Say), in a laboratory under two starvation conditions: complete starvation (no food supplied) and gradual starvation (food provided once and not replenished). Under complete starvation, survival of 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs tended to decline steadily, whereas under gradual starvation this process was delayed in the initial stage. The average survival times increased as the instar increased under both conditions (14.0 h, 15.9 h and 24.4 h under complete starvation conditions; 27.8 h, 29.6 h and 33.6 h under gradual starvation conditions). The longest lived individual nymph survived for 49 hours. The results may partially explain the rapid global expansion of *C. ciliata*.

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## 1. Introduction

Food shortages negatively impact insect growth rates (Berrigan & Charnov 1994, Bauerfeind *et al.* 2005), maximum body size (Blanckenhorn 1998; Boggs & Freeman 2005) and reproductive output (Jiang & Lin 1965, Lin *et al.* 2003, Karl *et al.* 2007, Kehl & Fischer 2012) as well as other life history traits (Boggs & Ross 1993, Braby & Jones 1995, Bauerfeind *et al.* 2005, Daghli 2006, Ju *et al.* 2008, Zheng *et al.* 2011). Insects can suffer food shortages due to changes in food quality or availability, changes in food preferences, and food depletion. Insects have evolved several mechanisms to respond to starvation stress. These include delaying development until

sufficient resources have been secured, undergoing accelerated metamorphosis, and eclosing as smaller adults when resources are scarce during the larval stage (Chen & Gu 2006). The ability to address this stress is called starvation resistance.

Starvation resistance is of great interest to insect ecologists because of its close correlation with fitness in natural populations of many organisms and because it often co-varies with longevity (Stockhoff 1991, Johnson *et al.* 2001, Chen & Gu 2006, Sheng *et al.* 2007, Pijpe *et al.* 2008, Zhang *et al.* 2012). Body size, body composition and metabolic rate strongly affect starvation resistance (Stockhoff 1991, Lavy *et al.* 1997, Robinson *et al.* 2000, Vermeulen *et al.* 2006).

The current study concerns starvation resis-

tance in the sycamore lace bug *Corythucha ciliata* (Say) (Hemiptera: Tingidae), a recently recognised invasive pest in China (Ju *et al.* 2009). *Corythucha ciliata* is a native North American insect occurring east of the Rocky Mountains (Froeschner 1988). In Europe, it was first discovered in 1964 in Padova, Italy, and subsequently spread throughout Europe over the course of 20 years (Rabitsch 2008). *Corythucha ciliata* has also been introduced to Chile (Prado 1990), Korea (Chung *et al.* 1996), Japan (Tokihiko *et al.* 2003), Australia (Dominiak *et al.* 2008) and China (Ju *et al.* 2009). In China, it has dispersed throughout eastern China, mid-China and south-western China since it was first observed in 2006 in Wuhan, Hubei province (Li *et al.* 2007, Xiao *et al.* 2010, Liu *et al.* 2012, Ji *et al.* 2013, Wu *et al.* 2013). *Corythucha ciliata* has caused great damage in 12 other provinces (Shanghai, Zhejiang, Anhui, Jiangsu, Guizhou, Sichuan, Chongqing, Hunan, Hubei, Henan, Shandong and Beijing) in less than a decade (Ju *et al.* 2009).

The diffusion speed of *C. ciliata* has been very fast (Kukedi 2000, Mazzon & Girolami 2000, Hoffmann 2003) due to both the phenology of the invasive pest itself and to environmental factors (Ju *et al.* 2009). *Corythucha ciliata* can survive, develop, and reproduce over a wide range of temperatures (Ju *et al.* 2011a). In addition, exposure to high temperatures ranging from 35 to 41 °C for 2 h does not reduce the survival, longevity, or fecundity of *C. ciliata* adults, indicating that this species has great thermal tolerance (Ju *et al.* 2011b, 2013). Moreover, *C. ciliata* is extremely cold tolerant and can withstand temperatures as low as -23 °C in nature (Halbert & Meeker 1998). This insect also has extremely high fecundity: a female can lay 350 eggs in the wild (d'Aguilar *et al.* 1977). Collectively, these bioecological characteristics of *C. ciliata* may partially explain why it has rapidly spread on *Platanus* trees throughout the world.

The long-distance diffusion of *C. ciliata* populations likely occurs primarily by artificial propagation via host plants, vehicles, or other biological and non-biological carriers (Halbert & Meeker 1998). During diffusion, the lace bug suffers food shortages or even the absence of food. We hypothesise that this species has a great capacity to adapt to starvation and that its starvation

resistance plays an important role in its invasive process.

There may be a very complex mechanism for the adults to cope with starvation. For example, overwintering adults of *C. ciliata* can survive more than 150 days in the absence of any food (Arzone 1975; Kim & Jeong 1999; Xiao *et al.* 2010). In the present study, we conducted laboratory analyses to assess the effects of starvation on newly emerged 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs of *C. ciliata*. We restricted our study to 3<sup>rd</sup> to 5<sup>th</sup> instars, because it was too hard to get newly emerged nymphs (<3 h old) of all the instars at the same time. Even if using just those three nymphal instars, the study most likely aids understanding some basic rules on starvation resistance for the sycamore lace bug, especially the longest surviving time of those nymphs. We will investigate the starvation resistance of adults at different generations in future studies.

We answered the following questions. (1) What are the survival patterns of *C. ciliata* nymphs under complete starvation conditions (no food supplied) and gradual starvation conditions (food provided once and not replenished)? (2) How long can they live under the two conditions?

## 2. Materials and methods

### 2.1. Insects

A laboratory colony of *C. ciliata* was established in May 2015 from nymphs collected from London plane trees (*Platanus acerifolia* (Ait.) Willd.) in Jinan, China (36.687 °N, 117.070 °E). The insects were reared on leaves of *P. acerifolia* in a mesh cage (100 × 60 × 60 cm). One branch with 5 – 6 leaves was placed in the cage with the cut end of the branch placed in a water-filled bottle. Fresh branches from London plane trees and the water in the bottle were changed as needed to ensure food availability and to prevent desiccation. Each cage held approximately 200 individuals. The stock culture was maintained in the laboratory at 26 ± 0.5 °C with a relative humidity of 70 ± 5% and a 14 h:10 h (L:D) photoperiod (see Ju *et al.* 2011c). Newly emerged 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs (<3 h old) of the F2 generation were used in the following experiments.

## 2.2. Measurement of starvation resistance

Newly emerged 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs (<3 h old) from stock cultures were transferred to empty plastic insect-rearing boxes (12 × 9 × 10 cm) using a small brush, which were then placed in an intelligent artificial climate chamber (Model: RXZ-280C, Ningbo Jiangnan Instrument Co., Ltd.) at 26 ± 0.5 °C with a relative humidity of 80 ± 5% and a 14:10 L:D photoperiod. In complete starvation treatment, no food was provided during the tests. In gradual starvation treatment, a fresh leaf was placed in the rearing box before newly emerged 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs were transferred to the box to supply food for nymphs in the initial stage of the experiment. The leaf was not replaced during the experiment, resulting in gradual starvation. *Corythucha ciliata* reared in the box containing a fresh leaf of *P. acerifolia* were used as a control; their leaf was changed as needed to ensure a steady food supply, and all other conditions were the same as above.

The numbers of dead nymphs and moulting nymphs were recorded every hour. A nymph was considered dead, if none of its appendages moved after all appendages were touched with a brush (Ju *et al.* 2013). Three replicates with at least 30 individuals of each instar per replicate were evaluated for each treatment. All rearings were performed simultaneously in the same single climate chamber with an interspersed spatial arrangement of the replicates of the different treatments (and control).

## 2.3. Statistical analyses

The survival patterns of the *C. ciliata* nymphs under complete starvation conditions and gradual starvation conditions were assessed by curves that described age-specific survivorship over hours. The results are presented as the mean values ± SE (n=3 replicates per treatment).

Differences in developmental time for control nymphs were tested by one-way analysis of variance (ANOVA). The mean survival time for the starved nymphs was analysed using two-way ANOVA with age and starvation condition as fixed factors. Statistical analyses were performed with SPSS 15.0 (SPSS, 2006). Prior to ANOVA,

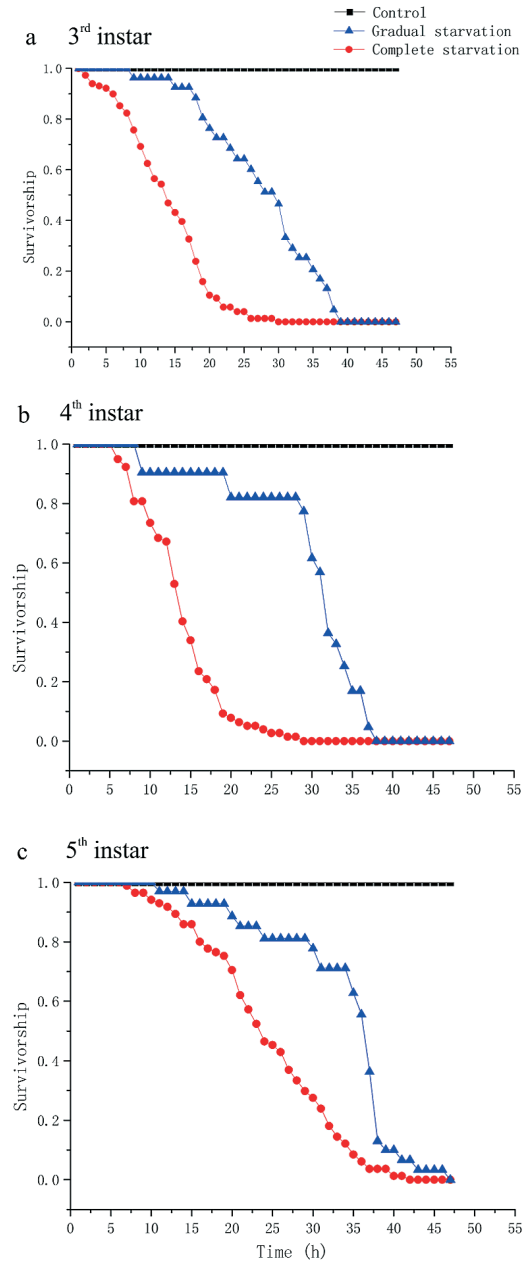


Fig. 1. Age-specific survivorship curves for three instars of *Corythucha ciliata* nymphs under complete, gradual or no starvation conditions. – a. 3<sup>rd</sup> instar. – b. 4<sup>th</sup> instar. – c. 5<sup>th</sup> instar.

all data were checked for normality and equal variance. When treatment effects were significant ( $P < 0.05$ ), the means were compared using Tukey's test. All survival percentages were arcsine-transformed prior to statistical analysis (Ju *et al.* 2011c, 2014).

Table 1. Means  $\pm$  SE for survival time of the starved nymphs and developmental time of control nymphs (all survived in control) for *Corythucha ciliata*.

	Survival time (h)		Developmental time (h)
	Complete starvation*	Gradual starvation*	Control*
3 <sup>rd</sup> instar	13.0 $\pm$ 1.34 b	27.8 $\pm$ 2.74 a	52.0 $\pm$ 5.32 b
4 <sup>th</sup> instar	15.9 $\pm$ 0.68 b	29.6 $\pm$ 1.97 a	61.5 $\pm$ 6.47 b
5 <sup>th</sup> instar	24.4 $\pm$ 1.74 a	33.6 $\pm$ 1.81 a	100.5 $\pm$ 3.91 a
F	17.5	1.8	23.1
P	0.003	0.24	0.002

\* Means within the same column followed by a different letter are significantly different (Tukey's test:  $P < 0.05$ ).

### 3. Results

#### 3.1. Survival patterns under complete and gradual starvation conditions

The shapes of the age-specific survivorship curves for the instars differed considerably under complete starvation and gradual starvation conditions (Fig. 1). Each instar exposed to complete starvation exhibited a type II age-specific survivorship curve (steady mortality throughout life). The nymphs exposed to gradual starvation initially exhibited type I curves (good initial survival but high death rates at later stages) but progressively exhibited type II curves. In the control, all nymphs of all three instars survived and developed to the next stage during the experiment.

#### 3.2. Survival time under complete and gradual starvation conditions

No control nymphs died and their mean developmental time increased with the increase of age (3<sup>rd</sup> instar: 52.0 h; 4<sup>th</sup> instar: 61.5 h; 5<sup>th</sup> instar: 100.5 h). The mean developmental time of 5<sup>th</sup> instar nymphs was significantly longer than that of 3<sup>rd</sup> and 4<sup>th</sup> instar nymphs, but there were no significant differences between 3<sup>rd</sup> and 4<sup>th</sup> instar nymphs (Table 1). As expected, both the starvation condition and the age of the nymphs had a significant effect on the mean survival time, but their interactions was not significant (Starvation condition:  $F_{1,18} = 67.3$ ,  $P < 0.001$ ; Age:  $F_{2,18} = 10.9$ ,  $P < 0.001$ ; Starvation condition\*Age:  $F_{2,18} = 1.1$ ,  $P = 0.38$ ) (Table 1).

Under complete starvation, 3<sup>rd</sup> instar nymphs of *C. ciliata* had a mean survival time of 14.0 h, whereas 4<sup>th</sup> and 5<sup>th</sup> instar nymphs of *C. ciliata* survived an average of 15.9 h and 24.4 h, respectively. The average survival times of 3<sup>rd</sup> and 4<sup>th</sup> instar nymphs under complete starvation did not differ significantly but were both significantly shorter than that of 5<sup>th</sup> instar nymphs. Under gradual starvation conditions, the average survival times of 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs were 27.8 h, 29.6 h and 33.6 h, and there were no significant differences between instars (Table 1). The longest-lived individual was a 5<sup>th</sup> instar nymph subjected to gradual starvation, which died when it was 49 hours old.

### 4. Discussion

Many studies have reported that older instars survive longer under starvation conditions and are therefore more resistant to starvation stress than younger instars (Huang *et al.* 1985, Cao *et al.* 2010). For example, older instars of *Epiblema strenuana* (Walker) nymphs survive longer under starvation (Ma *et al.* 2002). Newly hatched larvae of *Actinote antea*s (Doubleday) and *Actinote thaliapyrrha* (Fabricius) survive under starvation for an average of 3 d, whereas 2<sup>nd</sup> and 4<sup>th</sup> instar larvae survive for an average of 6 d and longer than 8 d, respectively (Li *et al.* 2005). Similarly, in this study, 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> instar nymphs survived under complete starvation for an average of 14.0 h, 15.9 h and 24.4 h, respectively. Similar survival was observed under gradual starvation, with average survival times of 27.8 h, 29.6 h and 33.6 h,

respectively (Table 1). These results thus further support the longer survival of older instars under starvation.

The age-specific survivorship curves generated under gradual starvation conditions considerably differed from those generated under complete starvation conditions for each instar stage. As there was no mortality in control, these two logically differed crucially also from the control. Under complete starvation conditions (no food supplied), the survival of 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs tended to decline steadily (i.e., a type II survivorship curve). Under gradual starvation conditions (food provided once and not replenished), this process was delayed, and all nymphs exhibited type I curves (good initial survival but high death rates at later stages) in the initial stage (Fig. 1). This may be due to the similar conditions as the control at the initial stage (both were provided by food). These differences demonstrate that a certain amount of feeding may allow them to store more energy, thus enhancing their starvation resistance (Rion & Kawichi 2007).

*Corythucha ciliata* can spread very quickly. For example, in Italy, the distribution of the sycamore lace bug was confined to areas surrounding the Venice port in 1960. By 1974, they had spread to the northern and central regions of Italy (Venturi 1974). By 2000, they were distributed throughout the whole country, including two islands, Sardinia and Sicily (Mazzon *et al.* 2000). Similarly, *C. ciliata* spread over 80,000 km<sup>2</sup> in 10 years in Hungary, and 25 cities were populated by the insect by 2000 (Kozar & Nagyne 1985, Kukedi 2000). *Corythucha ciliata* may have spread from North America to Italy via transport on oceanic vessels (Özsi *et al.* 2005). In addition, other vehicles (trucks, buses) may also carry *C. ciliata* adults or nymphs to other trees when they come into contact with infested branches and leaves, causing the spread of the bug (Arzone 1975). Human transportation of plants and logs with bark attached were ultimately identified as the main cause of long-distance spread (Ju *et al.* 2009).

The ability of an exotic insect species to overcome stressful starvation conditions during transport is a prerequisite for successful colonisation. In this study, we demonstrated that 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs of *C. ciliata* can survive without food for

at least 13 h at an average temperature of 26 °C and a relative humidity of 80%. If the nymphs were transported with their host tree (even one leaf), they would survive for longer periods, at least 27 h. The survival time of this species is likely to be longer at lower temperatures (Ji *et al.* 2010). Assuming that the average speed of a vehicle is only 60 km/h, 3<sup>rd</sup> to 5<sup>th</sup> instar nymphs of *C. ciliata* may arrive at a new location 780 km away. This survival capacity explains why *C. ciliata* has undergone such rapid global spread.

Phytosanitary measures are very common for preventing the diffusion of alien species to pest-free areas (Hallman 2007). The longest-lived individual nymph in the test groups in this study did not die until 49 hours after exposure to starvation at a constant temperature of 26 °C (a developmental reference temperature, see Ju *et al.* 2011b, c, 2013). Although the starvation-resistant capacity of this species under different temperature conditions requires further study, quarantine regulations should be strengthened to prevent *C. ciliata* diffusion into pest-free areas.

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