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Comparative study of temperature-dependent life histories of three economically important *Adelphocoris* spp.

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Abstract. Subsequent to the widespread adoption of Bt transgenic cotton in China and an associated reduction in pesticide use, *Adelphocoris* spp. (Hemiptera: Miridae) are the key pests of this crop. Three species (*Adelphocoris suturalis*, *Adelphocoris fasciaticollis* and *Adelphocoris lineolatus*) are found in Chinese Bt cotton fields, each with a distinct geographic distribution and phenology. In the present study, the development and fecundity of the three species are compared in the laboratory at various temperatures in the range 10–35 °C. Although nymphal development and adult moulting occurs under all temperature regimes, egg eclosion is not observed at 10 °C. In general, egg and nymphal development periods decrease with increasing temperature up to 30 °C. The lower and upper development thresholds are, respectively, 5.6 and 40.1 °C for *A. suturalis* eggs; 5.0 and 38.4 °C for nymphs; 6.3 and 39.0 °C for *A. fasciaticollis* eggs, 3.0 and 41.9 °C for nymphs; 5.6 and 41.3 °C for *A. lineolatus* eggs; and 6.2 and 38.8 °C for nymphs. Thermal constants are 189.9 degree days (DD) (egg) and 308.8 DD (nymph) for *A. suturalis*, 188.8 DD (egg) and 366.7 DD (nymph) for *A. fasciaticollis*, and 231.7 DD (egg) and 291.6 DD (nymph) for *A. lineolatus*. Temperatures above 30 °C affect egg development of *A. fasciaticollis* and *A. lineolatus* adversely, but not that of *A. suturalis*. At the same time, nymphal survival of *A. suturalis* is reduced at 10 °C. Longevity of all species declines with increasing temperature, whereas extremes of temperature (i.e. 10 and 35 °C) interfere with oviposition. The estimated optimum range for oviposition is 23–25 °C, irrespective of species. In general, development and fecundity of the three *Adelphocoris* spp. is consistent with their respective distribution and seasonal dynamics. The present study provides insight into the distribution and phenology of *Adelphocoris* spp., and contributes to the modelling of their population dynamics.

Key words. *Adelphocoris fasciaticollis*, *Adelphocoris lineolatus*, *Adelphocoris suturalis*, development, fecundity, longevity, life history, temperature.

Introduction

Three species of the genus *Adelphocoris* (Heteroptera: Miridae) are important herbivores of cotton in China: *Adelphocoris suturalis* (Jakovlev), *Adelphocoris fasciaticollis* (Reuter) and *Adelphocoris lineolatus* (Goeze) (Cao & Wan, 1983; Lu & Wu, 2008; Lu *et al.*, 2008a). Until recently *Adelphocoris* spp. were secondary pests in cotton fields, occurring at relatively low population levels and usually being controlled by insecticide sprays targeted against the cotton bollworm, *Helicoverpa armigera* (Wu & Guo, 2005). The development and subsequent widespread adoption of Bt cotton in the late 1990s, targeting *H. armigera* and pink bollworm, *Pectinophora gossypiella*, has led to a substantial reduction of the use of broad-spectrum insecticides in this crop (Huang *et al.*, 2002; Wu *et al.*, 2008).

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This reduction in insecticide usage means that *Adelphocoris* spp. population levels now surpass the economic threshold in various cotton-growing regions of China (Wu *et al.*, 2002; Lu *et al.*, 2007).

All three *Adelphocoris* species are distributed widely, and occur together commonly in cotton fields. However, *A. suturalis* is found principally in temperate regions, such as Changjiang River region and the southern part of Yellow River region, whereas *A. fasciaticollis* and *A. lineolatus* are confined to colder regions, such as the middle and northern parts of Yellow River region (Zhang & Zhao, 1996; Lu *et al.*, 2008a). *Adelphocoris suturalis* completes four to five generations annually in China, whereas both *A. fasciaticollis* and *A. lineolatus* have three to four generations (Lu & Wu, 2008). All there species overwinter as eggs, and egg hatching begins in early April for *A. suturalis* and in middle to late April for the other two species (Lu & Wu, 2008). These differences in geographical distribution and phenology are most likely related to species biology and ecology, adaptability to climatic conditions, and host-plant quality. Lu *et al.* (2009) reports that the flight capacity of *Adelphocoris* spp. correlates with each geographical distribution and occurrence.

Temperature is one of the main factors determining the biology and physiology of arthropods and, accordingly, is one of the most important variables regulating their life history, as well as their geographical distribution and phenology (Messenger, 1959; Howe, 1967). Although several references are available on the development of *Adelphocoris* species (Ting, 1963; Li *et al.*, 1994a, b; Fu *et al.*, 2008; Guo *et al.*, 2008), there are no comparative studies concerning the temperature-dependent life history of *Adelphocoris* spp. In the present study, egg and nymphal development, survival, adult fecundity and longevity are compared in the three *Adelphocoris* spp., at six temperature regimes. It is suggested that the results obtained can be used to understand the distribution and phenology of *Adelphocoris* spp., as well as to predict population dynamics, establish forecasting protocols and optimize laboratory rearing.

Materials and methods

Insects and temperatures

Laboratory colonies of the three *Adelphocoris* species were established with field-collected individuals. Nymphs and adults of *A. suturalis* were collected from cotton fields in Xinxiang (Henan Province) (35°32′N, 113°85′E), in July 2006, whereas nymphs and adults of *A. fasciaticollis* and *A. lineolatus* were collected from alfalfa fields in Chanzhou (38°33′N, 116°83′E) and Langfang (39°53′N, 116°70′E) (Hebei Province), respectively, during July–August 2006. Each laboratory colony was initiated using 500–800 field-collected individuals. Insects were reared on green beans (*Phaseolus vulgaris*) and a 10% sucrose solution (Lu *et al.*, 2008b). Each rearing container ($20 \times 10 \times 6$ cm) housed 60–80 adults. Green beans also served as the oviposition substrate and were changed every other day. Beans with eggs attached were placed subsequently in rearing containers lined with filter paper and kept in the incubator until first-instar nymphs emerged. Nymphs were placed in similar containers, covered with nylon mesh to allow air circulation, and provided with fresh food every 2 days until adult emergence. Each rearing container housed 100 nymphs. Laboratory colonies were maintained under an LD 14 : 10 h photoperiod and 60 ± 5% relative humidity (RH) at 29 ± 1 °C.

The study was conducted at six constant temperatures (10, 15, 20, 25, 30 and 35 °C) in environmental growth chambers (Ningbo Jiangnan Instrument Factory, China) under an LD 14 : 10 h period and 60% RH. Temperatures were maintained at ±0.5 °C around the set point, whereas RH fluctuated in the range 55–65%. For each chamber, humidity was maintained using a single humidifier (Beijing Yadu Science & Technology Co., China) and each temperature regime was considered as a separate treatment.

Immature development and survival

The methodology used was similar to that employed in the study of *Lygus elisus* by Bommireddy *et al.* (2004). Prior to the experiment, several 4-cm long green bean sections were placed in adult rearing containers for 24 h. Upon removal of bean sections, the number of eggs was counted under the microscope, and bean sections with a known number of eggs were placed in a rearing container at a given temperature. Egg hatching was recorded daily for 25 days and newly-emerged nymphs were removed from containers. A single batch of eggs (i.e. 30–80 eggs) was considered as a replicate, and a total of three replicates were included per temperature regime. Successive replicates were established at weekly intervals.

Upon emergence (egg hatching), nymphs were placed singly into (height 5 cm, diameter 1.5 cm) glass vials covered with a nylon screen. Each vial contained a small section of bean and a long paper strip (1.5×5 cm). Nymphal development and survival were recorded daily until adult moulting or death, for the various temperature treatments and species. Each replicate for nymphal development comprised a total of 20–30 individuals, and each temperature treatment consisted of three replicates.

Adult longevity and reproduction

Adults were reared from nymphs under each of the different temperature regimes, using the above methodology. Newly-emerged adults were paired and placed into (height 3 cm, diameter 3 cm) glass vials with a nylon screen. Within each vial, a 4-cm long section of green bean and a 10% sucrose solution was provided as food. Green bean sections also acted as an oviposition substrate, and were changed and inspected for the eggs daily. Adult mortality was recorded daily, and adult longevity was determined. Dead individuals were removed from the vials and not replaced. For each temperature regime and species, adult longevity and fecundity was determined. Each replicate included a total of 20–40 mating pairs, and each treatment consisted of three replicates.

Statistical analysis and model development

To determine the effect of temperature on immature development, adult fecundity and longevity, a Kruskal–Wallis test was used because the data did not meet assumptions of normality or homogeneity of variances (Zar, 1999; Sokal & Rohlf, 2001). Percentage data (i.e. nymphal survival, egg hatching rate) were arcsine transformed. Next, nymphal survival and egg hatching rate were compared between the different treatments using a one-way analysis of variance followed by a Tukey's honestly significant difference test ($P < 0.05$). To determine the effect of temperature on nymphal development and adult fecundity, nymphs that died prior to adult moulting and adults that produced no eggs were excluded from the analysis, respectively. All statistical analyses were conducted using SAS software (SAS Institute, 2005).

The effect of temperature on the developmental rate of various stages of a given species was characterized by linear regressions using the model $y = bx + a$, where y is development rate (1/development time), x is temperature, and a and b are parameters obtained from the regression. Lower development thresholds (T_o) and thermal constant requirements, degree days (DD), were estimated using the parameters: $T_o = -a/b$ and $DD = 1/b$ (Campbell *et al.*, 1974). Estimations of the constants T_o and DD were based on data obtained from the range 10–30 °C. Because of known inherent deficiencies in the linear model (Kontodimas *et al.*, 2004), the nonlinear Logan model 6 was used to describe the relationship between temperature (10–35 °C) and rate of development (Logan *et al.*, 1976). According to this model, Y or $1/D = P_1 \times \{\exp [P_2 \times (X - T_0)] - \exp [P_2 \times (T_{\max} - T_0) - P_3 \times (T_{\max} - X)]\}$, where X is temperature, T_0 is the lower temperature developmental threshold, $T_{\max}$ is the upper (lethal) temperature, and P_1, P_2 and P_3 are coefficients. The optimum temperature for development was calculated by setting the first derivative of the Logan equation to zero. Curve fitting in nonlinear regression was performed using JMP IN software (SAS Institute, 2005).

Results

Immature development and survival

Nymphs of all three *Adelphocoris* spp. developed successfully into adults in the temperature range 10–35 °C. However, egg hatching did not occur at 10 °C (Table 1). The developmental time of each stage differed significantly between the various temperature regimes (Kruskal–Wallis test; $P < 0.001$ for each) (Table 1) and decreased gradually with increasing temperature in the range 10–30 °C.

The relationship between development rates of egg and nymphal stages and temperature (15–30 °C for egg, 10–30 °C for nymph) was linear for each of the *Adelphocoris* spp. (Fig. 1). The minimum (lower) development thresholds and DD accumulations were determined for egg and nymphal

Table 1. Developmental time (days) of immature stages of *Adelphocoris suturalis*, *Adelphocoris fasciaticollis* and *Adelphocoris lineolatus* at different constant temperatures (60 ± 5% relative humidity and an LD 14 : 10 h photoperiod).

		Temperature (°C)						
Species	Stage	10	15	20	25	30	35	Kruskal–Wallis test statistic
Adelphocoris suturalis	Egg	–†	20.0 ± 0.3^{a}	13.8 ± 0.1^{b}	9.8 ± 0.1^{c}	7.9 ± 0.1^{d}	8.4 ± 0.3^{cd}	KW = 195.3, d.f. = 4,212, $P < 0.001$
	First instar	10.1 ± 0.3^{a}	8.8 ± 0.4^{a}	5.3 ± 0.1^{b}	4.0 ± 0.1^{c}	3.1 ± 0.1^{c}	4.0 ± 0.4^{bc}	KW = 244.3, d.f. = 5,294, $P < 0.001$
	Second instar	8.1 ± 0.5^{a}	6.8 ± 0.2^{a}	3.1 ± 0.1^{b}	2.1 ± 0.1^{c}	2.0 ± 0.2^{c}	3.3 ± 0.2^{ab}	KW = 242.8, d.f. = 5,294, $P < 0.001$
	Third instar	9.2 ± 0.4^{a}	5.3 ± 0.2^{b}	3.0 ± 0.1^{c}	2.5 ± 0.1^{d}	1.8 ± 0.1^{d}	1.7 ± 0.2^{d}	KW = 238.6, d.f. = 5,294, $P < 0.001$
	Fourth instar	8.5 ± 0.5^{a}	7.7 ± 0.2^{a}	3.2 ± 0.1^{b}	2.6 ± 0.1^{c}	2.3 ± 0.1^{c}	1.7 ± 0.2^{c}	KW = 222.5, d.f. = 5,294, $P < 0.001$
	Fifth instar	13.4 ± 0.4^{a}	12.3 ± 0.2^{a}	4.3 ± 0.1^{b}	3.8 ± 0.1^{bc}	3.1 ± 0.1^{c}	3.3 ± 0.2^{bc}	KW = 239.2, d.f. = 5,294, $P < 0.001$
	Total nymph	49.4 ± 0.6^{a}	41.0 ± 0.4^{a}	19.0 ± 0.2^{b}	14.9 ± 0.1^{c}	12.3 ± 0.2^{d}	14.0 ± 0.6^{cd}	KW = 279.7, d.f. = 5,294, $P < 0.001$
Adelphocoris fasciaticollis	Egg	–	20.1 ± 0.4^{a}	14.5 ± 0.1^{a}	9.8 ± 0.1^{b}	7.8 ± 0.1^{c}	8.5 ± 0.1^{c}	KW = 178.4, d.f. = 4,206, $P < 0.001$
	First instar	9.9 ± 0.2^{a}	6.4 ± 0.2^{a}	4.3 ± 0.2^{b}	3.9 ± 0.3^{bc}	3.0 ± 0.2^{c}	2.5 ± 0.2^{c}	KW = 128.1, d.f. = 5,156, $P < 0.001$
	Second instar	6.9 ± 0.2^{a}	4.9 ± 0.2^{ab}	3.8 ± 0.1^{bc}	2.4 ± 0.1^{c}	2.2 ± 0.2^{c}	2.6 ± 0.2^{c}	KW = 129.7, d.f. = 5,156, $P < 0.001$
	Third instar	8.5 ± 0.5^{a}	4.7 ± 0.2^{b}	4.1 ± 0.1^{b}	2.8 ± 0.1^{c}	2.2 ± 0.2^{c}	1.7 ± 0.1^{c}	KW = 132.6, d.f. = 5,156, $P < 0.001$
	Fourth instar	11.1 ± 0.5^{a}	8.5 ± 0.3^{ab}	4.5 ± 0.1^{b}	2.9 ± 0.1^{c}	2.5 ± 0.2^{c}	2.7 ± 0.1^{c}	KW = 129.5, d.f. = 5,156, $P < 0.001$
	Fifth instar	11.6 ± 0.2^{a}	7.7 ± 0.2^{ab}	6.2 ± 0.1^{b}	4.5 ± 0.1^{c}	3.7 ± 0.1^{c}	3.6 ± 0.2^{c}	KW = 146.3, d.f. = 5,156, $P < 0.001$
	Total nymph	47.9 ± 0.4^{a}	32.2 ± 0.3^{ab}	22.9 ± 0.2^{bc}	16.5 ± 0.4^{c}	13.6 ± 0.4^{c}	13.0 ± 0.1^{c}	KW = 152.1, d.f. = 5,156, $P < 0.001$
Adelphocoris lineolatus	Egg	–	24.5 ± 0.3^{a}	15.8 ± 0.1^{a}	12.3 ± 0.1^{b}	9.4 ± 0.1^{c}	9.1 ± 0.1^{c}	KW = 195.8, d.f. = 4,210, $P < 0.001$
	First instar	15.1 ± 0.3^{a}	10.3 ± 0.3^{a}	4.3 ± 0.1^{b}	3.0 ± 0.1^{c}	2.4 ± 0.1^{c}	2.2 ± 0.1^{c}	KW = 228.8, d.f. = 5,248, $P < 0.001$
	Second instar	9.6 ± 0.4^{a}	8.6 ± 0.3^{a}	3.1 ± 0.1^{b}	2.3 ± 0.1^{c}	1.7 ± 0.1^{c}	2.1 ± 0.1^{c}	KW = 199.3, d.f. = 5,248, $P < 0.001$
	Third instar	7.9 ± 0.3^{a}	7.2 ± 0.3^{a}	3.3 ± 0.1^{b}	2.5 ± 0.1^{c}	2.0 ± 0.1^{c}	2.0 ± 0.2^{c}	KW = 200.9, d.f. = 5,248, $P < 0.001$
	Fourth instar	10.4 ± 0.5^{a}	9.4 ± 0.3^{a}	4.0 ± 0.1^{b}	3.1 ± 0.1^{c}	2.3 ± 0.1^{c}	2.6 ± 0.2^{c}	KW = 204.8, d.f. = 5,248, $P < 0.001$
	Fifth instar	11.3 ± 0.4^{a}	10.3 ± 0.3^{a}	5.6 ± 0.2^{b}	4.4 ± 0.1^{c}	3.5 ± 0.1^{c}	3.9 ± 0.3^{c}	KW = 203.5, d.f. = 5,248, $P < 0.001$
	Total nymph	54.3 ± 0.7^{a}	45.8 ± 0.4^{a}	20.3 ± 0.2^{b}	15.3 ± 0.1^{c}	12.0 ± 0.2^{d}	12.8 ± 0.4^{cd}	KW = 240.2, d.f. = 5,248, $P < 0.001$

†No eggs incubated at 10 °C. Means ± SEM followed by different superscript letters within a row are significantly different [Kruskal–Wallis (KW) test, $P < 0.05$].

stages of the three *Adelphocoris* spp. (Fig. 1). The nonlinear Logan model 6 gave a good fit to the data for development rates of egg and nymphal stages (Table 2). The optimum temperature for development and the upper limit temperature differed between developmental stages and species (Table 2).

The percentage of egg hatch and nymphal survival rates varied significantly with temperature (Tukey's honestly significant difference; $P < 0.05$) (Fig. 2). For *A. suturalis*, the lowest egg incubation rate was recorded at 15 °C, whereas nymphal survival rate was greatest at 15 °C. For *A. fasciaticollis*, both low and high temperatures adversely affected egg hatch, and high temperatures also influenced nymphal survival. Similar findings were obtained for *A. lineolatus* (Fig. 2).

Adult longevity and fecundity

For the *Adelphocoris* species studied, female and male adult longevity declined with increasing temperatures (Kruskal–Wallis test; $P < 0.001$ for each) (Table 3). For *A. suturalis*, the female and male longevity fitted the linear equations $y = -2.02x + 80.78$ and $y = -1.61x + 68.74$, respectively (where y is longevity and x is temperature). For *A. fasciaticollis*, female and male adult longevity fitted the linear equations: $y = -0.93x + 53.67$ and $y = -0.83x + 48.82$, respectively. For *A. lineolatus*, the relationships between female and male longevity and temperature were described by $y = -1.69x + 70.29$ and $y = -1.19x + 55.07$, respectively (Table 3). However, no differences were noted in longevity between gender for a given species at each temperature (Kruskal–Wallis test; $P > 0.05$ for each), except for *A. lineolatus* at 15 °C (Kruskal–Wallis test; KW=8.71, d.f. = 1, 118, $P < 0.003$) (Table 3).

Female fecundity differed significantly between the different temperature regimes (Kruskal–Wallis test; $P < 0.001$) (Fig. 3). The nonlinear models describing mean fecundity (y) as a function of temperature (x) were: $y = -0.27x^2 + 12.41x - 75.32$ for *A. suturalis*, $y = -0.25x^2 + 11.57x - 76.98$ for *A. fasciaticollis*, and $y = -0.40x^2 + 19.57x - 137.26$ for *A. lineolatus*. The optimum temperatures for oviposition were estimated as 23.2 °C for *A. suturalis*, 23.4 °C for *A. fasciaticollis* and 24.2 °C for *A. lineolatus*, respectively (Fig. 3).

Discussion

The period of immature development for mirid species is generally inversely proportional to temperature, with developmental rates outside low and high temperature extremes being linear in relation to temperature (Wheeler, 2001; Bommireddy *et al.*, 2004). Temperature also greatly affects survival, fecundity and longevity of mirids (Wheeler, 2001; Bommireddy *et al.*, 2004). The present study describes the relationship between temperature and survival, development and fecundity for three *Adelphocoris* spp.

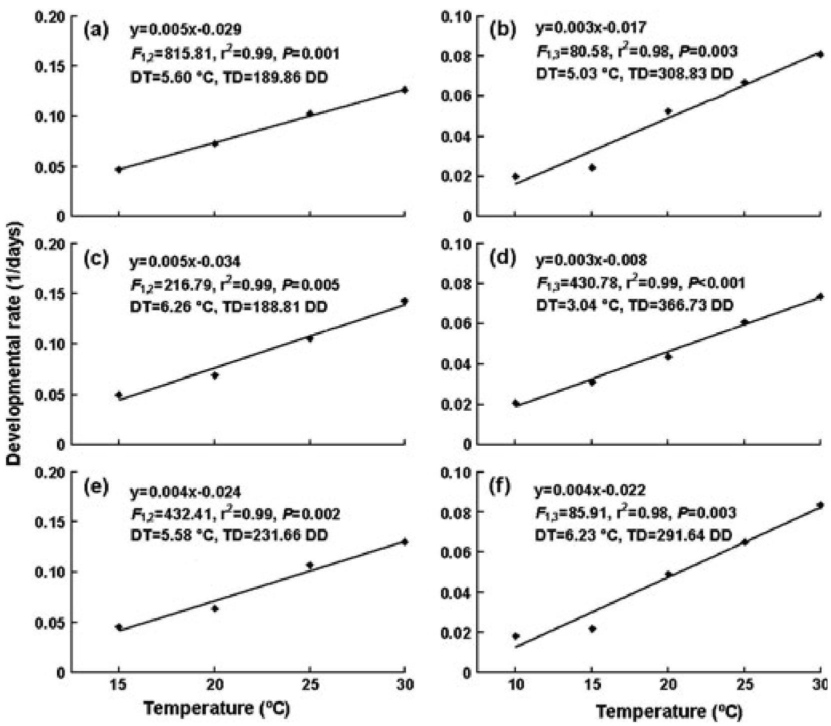

Fig. 1. Relationship between development rate and temperature for immature stages of three different *Adelphocoris* spp. For each species and the developmental stage, the development threshold and thermal duration are calculated. The lower development threshold (DT) is calculated as the x-intercept of regression model. Thermal constant (TD) is calculated as 1/slope of regression model. (a) *Adelphocoris suturalis* eggs; (b) *A. suturalis* nymphs; (c) *Adelphocoris fasciaticollis* eggs; (d) *A. fasciaticollis* nymphs; (e) *Adelphocoris lineolatus* eggs; (f) *A. lineolatus* nymphs.

Table 2. Parameters of the Logan VI equation, upper temperature thresholds and optimum developmental temperatures for the immature stages of three different *Adelphocoris* spp.

Species	Stage	Coefficients			P^*	Upper threshold (°C)	Optimum temperature (°C)
		P_1	P_2	P_3			
Adelphocoris suturalis	Egg	0.290	0.100	0.157	0.006	40.06	32.12
	Nymph	0.531	0.122	0.148	0.011	38.42	31.00
Adelphocoris fasciaticollis	Egg	0.206	0.083	0.233	0.021	38.95	32.08
	Nymph	0.459	0.104	0.118	0.010	41.89	32.85
Adelphocoris lineolatus	Egg	0.179	0.083	0.180	0.032	41.31	33.33
	Nymph	0.348	0.132	0.162	0.016	38.75	31.92

*P−value represents the statistical significance of the model.

The developmental rates of *Adelphocoris* spp. eggs and nymphs are related linearly to temperature over the range 15–30 °C and 10–30 °C, respectively. In general, the three *Adelphocoris* spp. have similar temperature requirements for immature (egg and nymphal) development (Ting, 1963). This is also reflected in a similar number of generations per year at some locations, as well as the co-occurrence of certain species under natural conditions (Lu & Wu, 2008). The thermal requirement of *A. suturalis* eggs is lower than that of *A. fasciaticollis* and *A. lineolatus*. This dissimilarity is consistent with their phenologies. The overwintering eggs of *A. suturalis* usually hatch earlier than eggs of the other two species (Lu & Wu, 2008). However, the estimated lower development thresholds and thermal constants of the three *Adelphocoris* spp. in the present study are different from those obtained by Ting (1963). These differences may be the result of the varying temperature range, dissimilar nutrition (i.e. host plant) and rearing conditions.

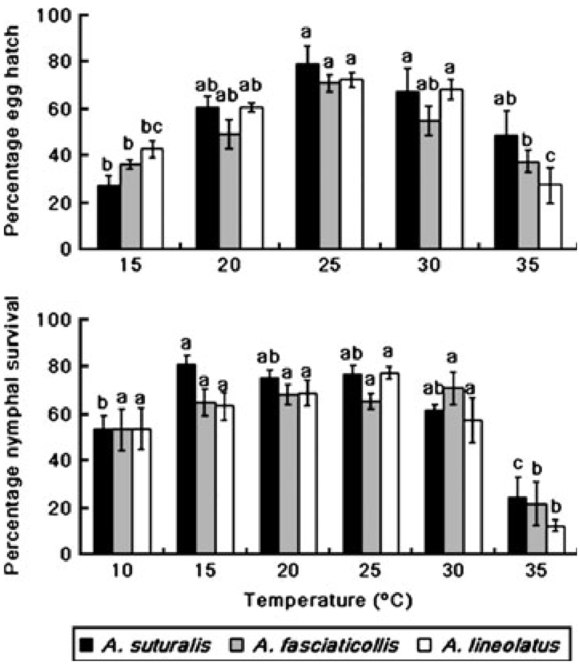

Fig. 2. Mean ± SEM survivorship of *Adelphocoris* spp. eggs and nymphs under constant temperatures. Different letters are significantly different (Tukey's honestly significant difference; *Adelphocoris suturalis* eggs: $F_{4,10} = 5.63$, $P < 0.011$; *A. suturalis* nymphs: $F_{5,12} = 14.49$, $P < 0.001$; *Adelphocoris fasciaticollis* eggs: $F_{4,10} = 8.50$, $P < 0.003$; *A. fasciaticollis* nymphs: $F_{5,12} = 7.32$, $P < 0.002$; *Adelphocoris lineolatus* eggs: $F_{4,10} = 14.85$, $P < 0.001$; *A. lineolatus* nymphs: $F_{5,12} = 13.78$, $P < 0.001$).

Unfavourable temperatures are detrimental to the development of *Adelphocoris* eggs and nymphs. Eggs fail to hatch at lowest temperatures (i.e. 10 °C), whereas immature stages develop slowly at the highest temperature (i.e. 35 °C). Predicted lethal and optimum temperatures are similar for the three *Adelphocoris* species, and are 40 and 32 °C for eggs and nymphs, respectively. In Chinese cotton fields, summer temperatures occasionally exceed upper development thresholds, and could therefore affect *Adelphocoris* development and survival. However, *Adelphocoris* species nymphs tend to avoid such negative effects by actively seeking favourable microclimates in the cotton canopy (Chu & Meng, 1958). Additionally, *Adelphocoris* eggs are drilled into tissues of living plants, and incubated under more stable temperature conditions than when exposed to open atmosphere or deposited in dead plant materials (Lu & Wu, 2008). Hence, further studies need to be conducted under natural conditions.

Although temperature effects on immature development rate are similar for various *Adelphocoris* species, the effects on egg and nymphal survival are different. High temperatures (i.e. 35 °C) adversely affect the egg incubation rate of *A. fasciaticollis* and *A. lineolatus*, but not *A. suturalis*. Low temperatures (i.e. 10 °C) interfere with nymphal survival rate for *A. suturalis*, but not that of *A. fasciaticollis* or *A. lineolatus*. The effect of temperatures on respective development and survival of the different *Adelphocoris* spp. may aid in an understanding of the geographic distribution of each species (e.g. Keena, 2006). The present study suggests that *A. suturalis* is not adapted to relatively cold climates, whereas *A. fasciaticollis* and *A. lineolatus* are not adapted to comparatively warmer conditions. This speculation is in good agreement with the geographic distribution of these species (Lu & Wu, 2008; Lu *et al.*, 2008a).

Table 3. Longevity (days) of *Adelphocoris suturalis*, *Adelphocoris lineolatus* and *Adelphocoris fasciaticollis* adults under constant temperatures ($60 \pm 5\%$ relative humidity and an LD 14 : 10 h photoperiod)

Species	Gender	Temperature (°C) 10	15	20	25	30	35	Kruskal–Wallis test statistic	Linear model	Statistic
Adelphocoris suturalis	Male	52.6 ± 3.3^{a}	50.0 ± 3.6^{a}	31.3 ± 2.3^{b}	24.6 ± 1.5^{b}	23.3 ± 1.4^{b}	13.6 ± 0.8^{c}	KW = 139.6, d.f. = 5,348, $P < 0.001$	$y = -1.61x + 68.74$	$r^2 = 0.93$, $F_{1,4} = 55.71$, $P < 0.002$
	Female	61.5 ± 4.0^{a}	56.6 ± 3.4^{a}	34.9 ± 2.5^{b}	24.6 ± 1.7^{bc}	20.0 ± 1.4^{cd}	14.9 ± 0.9^{d}	KW = 156.5, d.f. = 5,348, $P < 0.001$	$y = -2.02x + 80.78$	$r^2 = 0.94$, $F_{1,4} = 57.22$, $P < 0.002$
Adelphocoris fasciaticollis	Male	40.6 ± 4.9^{a}	36.2 ± 3.5^{a}	30.8 ± 3.8^{ab}	28.6 ± 2.9^{ab}	27.5 ± 2.7^{ab}	17.1 ± 1.9^{b}	KW = 24.3, d.f. = 5,110, $P < 0.001$	$y = -0.83x + 48.82$	$r^2 = 0.93$, $F_{1,4} = 53.09$, $P < 0.002$
	Female	43.5 ± 4.2^{a}	38.0 ± 3.6^{a}	36.9 ± 3.4^{a}	30.8 ± 3.7^{ab}	30.1 ± 2.5^{ab}	16.9 ± 1.6^{b}	KW = 30.8, d.f. = 5,110, $P < 0.001$	$y = -0.93x + 53.67$	$r^2 = 0.90$, $F_{1,4} = 34.76$, $P < 0.004$
Adelphocoris lineolatus	Male	47.5 ± 3.1^{a}	36.8 ± 3.2^{b}	27.4 ± 2.0^{bc}	27.2 ± 1.5^{c}	20.6 ± 1.5^{c}	17.0 ± 0.9^{c}	KW = 82.4, d.f. = 5,346, $P < 0.001$	$y = -1.19x + 55.07$	$r^2 = 0.90$, $F_{1,4} = 37.64$, $P < 0.004$
	Female	56.6 ± 4.2^{a}	49.7 ± 3.1^{a}	26.4 ± 1.7^{b}	25.5 ± 1.5^{b}	20.2 ± 1.3^{bc}	15.3 ± 0.9^{c}	KW = 126.0, d.f. = 5,346, $P < 0.001$	$y = -1.69x + 70.29$	$r^2 = 0.89$, $F_{1,4} = 31.72$, $P < 0.005$

Means ± SEM followed by different superscript letters within a row are significantly different [Kruskal–Wallis (KW) test, P¡0.05]. The linear model was used for analysing the relationship between longevity and temperature.

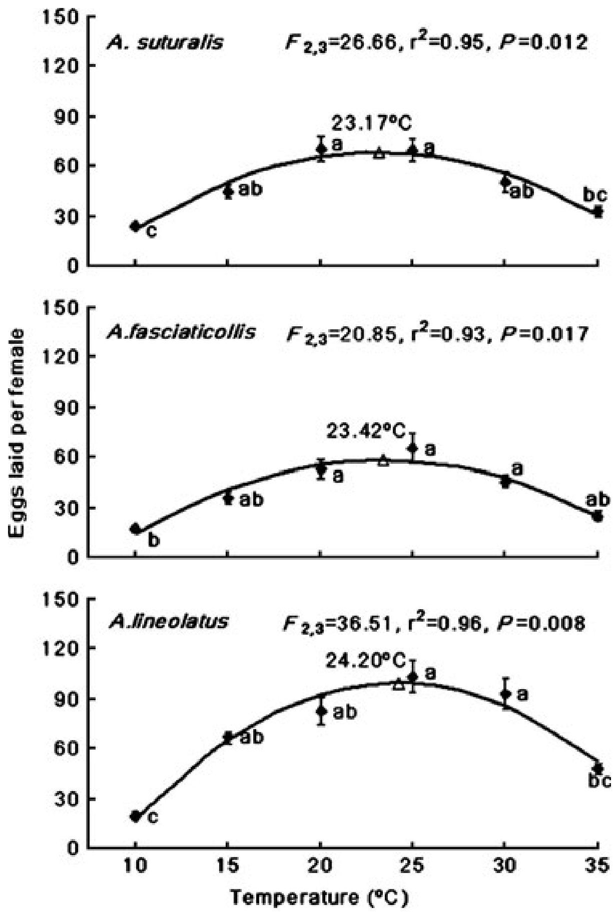

Fig. 3. Mean ± SEM fecundity of *Adelphocoris suturalis*, *Adelphocoris lineolatus* and *Adelphocoris fasciaticollis* adult females reared under different constant temperatures. Different letters indicate significantly different values [Kruskal–Wallis (KW) test; *A. suturalis*, KW = 43.03, d.f. = 5, 248, $P < 0.001$; *A. fasciaticollis*, KW = 39.28, d.f. = 5, 86, $P < 0.001$; *A. lineolatus*, KW = 42.72, d.f. = 5,225, $P < 0.001$]. Parameter estimates (F, R^2, d.f. and P) of the nonlinear model are labeled above the curve. The open triangles show the optimal temperature for adult fecundity predicted by the model.

Temperature also affects adult longevity and fecundity of *Adelphocoris* spp. Adult longevity declines with increasing temperature. Higher temperatures generally increase metabolism and, as a consequence, reduce life span proportionally (Slansky & Scriber, 1985). Temperature extremes affected fecundity adversely, with adult fecundity being greatest at 24 °C. On the basis of the effects of temperature on immature development and survival, as well as adult fecundity, the optimal temperature range for rearing *Adelphocoris* spp. under laboratory conditions is 25–28 °C (Lu *et al.*, 2009).

In addition to temperature, host plant species and various other biotic or abiotic factors are likely to affect *Adelphocoris* spp. development and, indirectly, its distribution and phenology. The three *Adelphocoris* spp. are considered polyphagous: *A. suturalis* has been reported to feed on > 100 plant species and overwinter on 90 species (Lu & Wu, 2008), *A. lineolatus* is found on approximately 125 host plants (Ting, 1963; Lu & Wu, 2008) and *A. fasciaticollis* feeds on 30 plant species and overwinters on several other plants (Chu & Meng, 1958; Lu & Wu, 2008). Among the variety of host plants for each *Adelphocoris* spp., there are several major crops and other common, widely-distributed plants. Hence, *A. suturalis* has usually a wide geographic distribution, *A. lineolatus* is found mainly in the principal alfalfa growing areas, whereas *A. fasciaticollis* is restricted to areas where overwintering plants (i.e. poplar, elm, and black locust) are present. Other abiotic factors, such as rainfall, can lead to substantial increases in mirid population numbers (Ting, 1964; Wu *et al.*, 2002), and rainfall patterns may therefore also have an effect in determining geographic distribution and phenology. However, much remains to be investigated on the effect of rainfall and RH on development, survival, fecundity and population dynamics in *Adelphocoris* spp.

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