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Authors: Tian, Zhenqi, Wang, Suji, Bai, Bing, Gao, Bo, and Liu, Jian

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Effects of temperature on survival, development, and reproduction of *Aphis glycines* (Hemiptera: Aphididae) autumnal morphs

Zhenqi Tian¹, Suji Wang¹, Bing Bai¹, Bo Gao¹, and Jian Liu^{1,*}

Abstract

Aphis glycines Matsumura (Hemiptera: Aphididae) is a common pest in soybeans in China. Though the pest has been studied extensively for many yr, there is little information regarding life history traits of *A. glycines* autumnal morphs on buckthorn in autumn. Life tables were constructed of *A. glycines* gynoparae, males, and oviparae reared at 13, 18, 23, 28, and 33 °C with a photoperiod of 12:12 h (L:D). Our results showed that gynoparae nymphs of *A. glycines* could survive well at temperatures from 13 to 33 °C, but male and oviparae nymphs could not develop into adults at 33 °C. Development time of nymphal gynoparae, males, and oviparae all gradually decreased when temperatures increased from 13 to 28 °C. Adult longevity of gynoparae and virgin males also decreased gradually when temperatures increased from 13 to 28 °C. Fecundity of *A. glycines* gynoparae was the greatest at 23 °C, with a value of 15.87 ± 0.33 oviparae per gynoparae. Males and oviparae of *A. glycines* mated only at 13 and 18 °C in the laboratory. Oviparae fecundity at 18 °C was greater than at 13 °C. This study provides important information on survival, development, and reproduction of *A. glycines* autumnal morphs, which is useful for understanding the population dynamics and life cycle of *A. glycines* in autumn, and to study the ecological adaptability of *A. glycines* in autumn.

Key Words: *Aphis glycines*; autumnal morphs; temperature; life table

Resumen

Aphis glycines Matsumura (Hemiptera: Aphididae) es una plaga común en la soja en China. Aunque la plaga ha sido ampliamente estudiada durante muchos años, hay poca información sobre los rasgos de la historia de vida de las formas otoñales de *A. glycines* en espinoso amarillo en el otoño. Se construyeron tablas de vida de los ginoparae, machos y ovíparas de *A. glycines* criados a 13, 18, 23, 28, y 33 °C con un fotoperíodo de 12:12 (L:D). Nuestros resultados mostraron que las ninfas ginoparae de *A. glycines* podrían sobrevivir bien a temperaturas de 13 a los 33 °C, pero las ninfas masculinas y ovíparas no podrían desarrollarse en adultos a los 33 °C. El tiempo de desarrollo de la ninfa ginoparae, los machos y las ovíparas disminuyó gradualmente cuando las temperaturas aumentaron de 13 a 28 °C. La longevidad adulta de gynoparae y machos vírgenes también disminuyó gradualmente cuando las temperaturas aumentaron de 13 a 28 °C. La fecundidad del ginoparae de *A. glycines* fue la mayor a 23 °C, con un valor de 15.83 ± 0.33 ovíparas por ginoparae. Los machos y las ovíparas de *A. glycines* se aparearon solo a 13 y 18 °C en el laboratorio. La fecundidad de las ovíparas a 18 °C fue mayor que la de 13 °C. Este estudio proporciona información importante sobre la sobrevivencia, el desarrollo y la reproducción de las formas otoñales de *A. glycines*, lo que es útil para comprender la dinámica de la población y el ciclo de vida de *A. glycines* y para estudiar la adaptabilidad ecológica de *A. glycines* en otoño.

Palabras Claves: *Aphis glycines*; morfos otoñales; formas otoñales temperatura; tabla de vida

Aphis glycines Matsumura (Hemiptera: Aphididae) is an important pest in soybeans and is native to Asia (Liu & Zhao 2007). Since *A. glycines* invaded North America in 2000 (Hartman et al. 2001; Ragsdale et al. 2004), they have spread throughout the main soybean planting regions (Venette & Ragsdale 2004). They can damage soybean plants directly by feeding in addition to transmission of plant viruses (Hill et al. 2001). Additionally, black sooty mold fungus growing on honeydew produced by *A. glycines* may lead to inhibition of soybean photosynthesis (Liu & Zhao 2007).

In China, the life cycle of *A. glycines* is characterized as heteroecious and holocyclic (Wang et al. 1962). During spring, overwintering eggs on buckthorn (*Rhamnus* spp. [Rhamnaceae], the primary host) hatch and become fundatrices (wingless females). Their offspring undergo several generations, then winged viviparous females are pro-

duced which migrate to soybeans *Glycine max* (L.) Merr. (Fabaceae) where they reproduce parthenogenetically on this host throughout the summer. When temperatures decrease, d-lengths shorten and plants become senescent in autumn. At this time, winged gynoparae are produced on soybean plants and then migrate to *Rhamnus* spp. where they produce oviparae. Similarly, winged males develop in soybean and migrate to *Rhamnus* spp. (buckthorn) where they mate with oviparae, which lay overwintering eggs (Wang et al. 1962; Ragsdale et al. 2004; Wu et al. 2004).

Summer morphs of *A. glycines* (virginoparae) have been extensively studied with a wealth of research articles on their population dynamics (Liu et al. 2004; Fan et al. 2017), natural enemies (Costamagna & Landis 2006; Desneux et al. 2006; Dieckhoff & Heimpel 2010; Liu et al. 2012), host plants (Sun et al. 2015; Chen et al. 2017; Wang et al. 2019),

¹Department of Entomology, Northeast Agricultural University, Harbin, 150030, China; E-mail: tzq152519@163.com (Z. T.), 304879494@qq.com (S. W.), 1770063297@qq.com (B. B.), 13045148976@163.com (B. G.), jliu@neau.edu.cn (J. L.)

*Corresponding author; E-mail: jliu@neau.edu.cn

economic thresholds (Ragsdale et al. 2007; McCarville et al. 2011), etc. However, there is only a limited number of studies dealing with autumnal morphs of *A. glycines*. Thus far, morphological characteristics of gynoparae, males, and oviparae have been identified (Takahashi et al. 1993; Voegtlin et al. 2004; Tian et al. 2018); gynoparae and males may also be induced in the laboratory (Wang et al. 2014; Xu et al. 2015; Oka et al. 2018). Temperature is one of the most important factors that can affect development and reproduction of herbivorous insects. Effects of temperature on morphological traits, development, and reproduction of *A. glycines* virginoparae on *G. max* have been studied (Hirano et al. 1996; McCornack et al. 2004; Richardson et al. 2011; Xu et al. 2011). In the Harbin region, northeast China, virginoparae of *A. glycines* disappear gradually on soybeans in Sep (Fan et al. 2017), whereas gynoparae, males, and oviparae occur on buckthorn at that time. In this region, environmental temperatures fluctuate usually from daily lowest to highest (-10.4°C to 31.4°C) during Sep to Oct (2007–2014, Heilongjiang Meteorological Bureau, China). Many questions remain unanswered regarding their survival, development and reproduction on primary hosts when gynoparae, males and oviparae of *A. glycines* are subject to these fluctuating temperatures in autumn.

The life table is an important tool for the study of insect population dynamics. It can provide crucial information on life traits, including survivability, growth, development, and reproduction of insects (Chi 1988). The life table also is beneficial for studying the influence of different temperatures on ecological fitness of pests (Gao et al. 2013). Here we report on life table studies of survival, development, and reproduction of *A. glycines* autumnal morphs on their primary host, *Rhamnus davurica* Pallus (Rhamnaceae). This information is important for understanding the seasonal ecological adaptability of this pest in northeast China.

Materials and Methods

APHID SOURCE AND ITS PRIMARY HOST

In our study, 20 wingless virginoparae *A. glycines* were collected from a soybean field at Northeast Agricultural University, Harbin, Heilongjiang Province, northeast China (1.445333°E , $45.740000^{\circ}\text{N}$) in 2014. Only 1 individual adult was retained as the mother aphid to build a monoclonal population resulting in greater fecundity and body size. The only aphids used in our study were the offspring of this single mother aphid. In this way, we could ensure the homology of individuals used in experiments. The colony was maintained on *G. max* (variety 'Heinong 51') in a growth chamber at $25 \pm 1^{\circ}\text{C}$, $70 \pm 5\%$ RH, and a 14:10 h (L:D) photoperiod with artificial light of 12,000 lx. Primary host leaves of *A. glycines* were collected from *R. davurica* in a garden at Northeast Agricultural University, where no insecticides were used.

ARTIFICIAL INDUCTION OF *APHIS GLYCINES* AUTUMNAL MORPHS

In this study, autumnal morphs of *A. glycines* gynoparae, males, and oviparae were successfully induced in the laboratory under low temperatures and a reduced photoperiod. Detached leaves of *G. max* (variety 'Heinong 51') were cut into 2.0 cm diam leaf discs using a hole-punch. Solid agar media were prepared in 45 mL, 4 cm \times 4.5 cm (diam \times height) glass beakers. Twenty wingless adult aphids (denoted as the G_0 cohort) were transferred from the stock colony onto soybean leaf discs with 1 aphid per disc and were reared at $20 \pm 1^{\circ}\text{C}$, a 10:14 h (L:D) photoperiod, and $70 \pm 5\%$ RH. Each adult was placed on the reverse side of a leaf disc adhered to the surface of the medium.

The beaker was then placed upside-down on a 5 cm diam Petri dish (Chen et al. 2017). Adults were checked daily and newly deposited nymphs were removed individually from beakers with a small brush. Nymphs deposited by generation G_0 aphids on d 1, 6, and 11 were denoted as G_1 , and reared to adults using the leaf disc method above. Nymphs deposited by G_1 aphids on d 1, 6, and 11 were denoted as G_2 , and also reared to adults using the same methods. Leaves and media were replaced every 5 to 7 d when old leaves became yellowish or upon observation of fungal growth (Tian et al. 2018). The first instar of *A. glycines* gynoparae were used for trials on nymphal development as mentioned in the following section, which were produced on d 6 by G_1 from that produced on the first d by G_0 . The first instar of males were produced on day 11 by G_1 from that produced on d 11 by G_0 . The first instar of oviparae produced by gynoparae adults also were used for the following trial.

NYMPHAL DEVELOPMENT OF *APHIS GLYCINES* AUTUMNAL MORPHS

Life tables were constructed of autumnal morphs on their primary host, *R. davurica*, at 13 , 18 , 23 , 28 , and $33 \pm 1^{\circ}\text{C}$, $70 \pm 5\%$ RH, and a photoperiod of 12:12 h (L:D). The first instar of *A. glycines* gynoparae, males, and oviparae were placed in growth chambers using the aforementioned leaf disc method (Chen et al. 2017). Gynoparae and males were fed on soybean leaf discs, whereas oviparae were fed on *R. davurica* leaf discs. For each different temperature treatment, 23 to 50 nymphs were tested. Individual aphids were checked daily for ecdysis and survivorship. Leaves and media were replaced every 5 to 7 d when old leaves became yellowish or the media showed fungal growth.

ADULT LONGEVITY AND FECUNDITY OF *APHIS GLYCINES* AUTUMNAL MORPHS

Adults of *A. glycines* gynoparae, males, and oviparae, reared from nymphs at 13 to $33 \pm 1^{\circ}\text{C}$ were maintained in the same conditions as the immature aphids. All adults of the 3 autumnal morphs were reared on *R. davurica* leaves. Adult longevity was recorded daily until the death of each adult. Nymphs deposited by gynoparae were counted and removed daily.

Another group of artificially induced males and oviparae of *A. glycines* adult also were used in this trial. Each couple, males and oviparae, were placed together into 1 beaker to mate. Couples were maintained together until they mated for the first time. Once mated, males and oviparae were moved into separate beakers and reared individually. Longevity of these mated morphs were recorded daily. Eggs deposited by mated oviparae were counted and removed daily. Males and oviparae were reared on *R. davurica* leaves that also served as egg-laying substrate. Leaves and media were replaced every 5 to 7 d as mentioned earlier.

LIFE TABLE PARAMETERS OF *APHIS GLYCINES* GYNOPARAE AND OVIPARAE

The age-stage-specific survival rate (S_{xj}) and age-stage-specific fecundity (f_{xj}) of gynoparae and mated oviparae were calculated from raw recording data. Intrinsic rate of increase (r) was calculated by bisecting method from the Euler-Lotka equation: $\sum_{x=0}^{\infty} (e^{-rx} \sum_{j=1}^m f_{xj} S_{xj}) = 1$, with age indexed from 0 (Goodman 1982). Finite rate of increase (λ) was calculated as $\lambda = e^r$. Net reproductive rate (R_0) was calculated as $R_0 = \sum_{x=0}^{\infty} \sum_{j=1}^m f_{xj} S_{xj}$. Mean generation time (T) was calculated as $T = (\ln R_0)/r$, and defines the time necessary for a population size to increase to R_0 -fold at the stable stage distribution (Chi & Liu 1985; Chi 1988).

DATA ANALYSIS

Raw data of nymph duration, adult longevity, and fecundity of gynoparae and oviparae at different temperatures were calculated according to age-stage, Two-Sex Life Table Theory (Chi 1988). Differences in nymph duration and adult longevity of gynoparae, males, and oviparae, and gynoparae fecundity among temperatures were analyzed using PROC general linear model (GLM) and Tukey's honest significant difference (HSD) tests. Differences in adult longevity of mated males and oviparae and fecundity of mated oviparae between 13 and 18 °C were analyzed using a *t*-test with SAS 8.1 software (SAS 2000). To estimate the lower developmental temperature threshold and effective cumulative temperature for nymph development of *A. glycines* gynoparae, males, and oviparae, linear regression of the mean developmental rate *y* (the reciprocal of development time to adult) on temperature *x* was applied to each temperature from 13 °C to 28 °C (Murai 2000), and was performed with a general linear model.

Intrinsic rate of increase and finite rate of increase, mean generation time, and net reproduction rate of gynoparae and oviparae were calculated using the bootstrap technique (Efron & Tibshirani 1993) in the computer program TWSEX-MSChart (Chi 2017). Because bootstrap analysis uses random resampling, a small number of replications will generate variable means and standard errors; thus, 200,000 bootstrap iterations were used to reduce the variability of the results. The differences among parameters at each temperature were analyzed by the paired bootstrap test (Efron & Tibshirani 1993).

Results

NYMPHAL DEVELOPMENT OF *APHIS GLYCINES* AUTUMNAL MORPHS

There were significant differences in development time of nymphal *A. glycines* among different temperatures (gynoparae: *F* = 1,696.73; *df* = 4,157; *P* < 0.05; males: *F* = 1,100.07; *df* = 3,191; *P* < 0.05; oviparae: *F* = 191.70; *df* = 3,136; *P* < 0.05). Generally nymphal

gynoparae, males, and oviparae decreased gradually when temperatures increased from 13 to 28 °C (Table 1). At 33 °C, only nymphs of *A. glycines* gynoparae could develop into adults. At this temperature, nymphal development time was 6.96 ± 0.14 d. Lower temperature thresholds for nymphal development of gynoparae, males, and oviparae were estimated as 6.24, 2.85, and 3.87 °C, respectively; based on those temperatures, the effective cumulative developmental times of gynoparae, males, and oviparae from first instar to adult were estimated at 117.64, 185.19, and 212.77 degree-d, respectively (Table 2).

ADULT LONGEVITY AND FECUNDITY OF *APHIS GLYCINES* AUTUMNAL MORPHS

Survival time of gynoparae, males, and oviparae of *A. glycines* decreased gradually when temperatures increased from 13 to 33 °C. At 13 °C, survival time of gynoparae was the longest whereas a similar pattern was observed for autumnal morphs at 18 °C. At 23 and 28 °C, survival time of oviparae was the greatest, followed by gynoparae and males. However, at 33 °C, no autumnal morphs could survive more than 14 d (Fig. 1).

There were significant differences in adult longevity of *A. glycines* among different temperatures (gynoparae: *F* = 76.58; *df* = 4,157; *P* < 0.05; virgin males: *F* = 206.78; *df* = 3,191; *P* < 0.05; virgin oviparae: *F* = 9.21; *df* = 3,136; *P* < 0.05). Adult longevity of gynoparae decreased gradually when temperatures increased from 13 to 33 °C (Table 3). Adult longevity of virgin males also decreased gradually when temperatures increased from 13 to 28 °C. There were no significant differences in adult longevity of virgin oviparae among 13, 18, and 23 °C, which were all longer than at 28 °C (Table 3). Males of *A. glycines* only mated with oviparae at 13 °C and 18 °C. Adult longevity of mated males and mated oviparae at 13 °C were significantly greater than at 18 °C (males: *t* = 2.79; *P* < 0.05; oviparae: *t* = 2.43; *P* < 0.05) (Table 3).

There were significant differences in fecundity of gynoparae at different temperatures (*F* = 203.49; *df* = 4,157; *P* < 0.05). Gynoparae fecundity increased gradually when temperature increased from 13 to 23 °C, with the highest value of 15.87 ± 0.33 oviparae per gynoparae at 23 °C. Gynoparae fecundity decreased gradually when temperature increased from 28 to 33 °C (Table 4). Oviparae fecundity at 18 °C was

Table 1. Nymphal development time (mean ± SE) of *Aphis glycines* gynoparae, males, and oviparae at different temperatures.

Temperature (°C)	Gynoparae		Male		Oviparae	
	<i>N</i>	<i>D</i>	<i>N</i>	<i>D</i>	<i>N</i>	<i>D</i>
13	50	17.50 ± 0.12 a	47	18.55 ± 0.24 a	23	24.78 ± 0.87 a
18	28	10.00 ± 0.16 b	49	12.63 ± 0.10 b	48	13.73 ± 0.32 b
23	31	7.03 ± 0.11 c	49	8.80 ± 0.11 c	25	11.96 ± 0.52 c
28	26	5.42 ± 0.13 d	50	7.58 ± 0.10 d	44	8.70 ± 0.30 d
33	27	6.96 ± 0.14 c	50	0	50	0

Means within the same column followed by different letters were significantly different (*P* < 0.05; HSD test).

Table 2. Lower threshold temperature and effective accumulated temperature for nymphal *Aphis glycines* gynoparae, males, and oviparae.

Autumnal morph	Linear regression equations	Coefficient of determination (<i>R</i> ²)	Lower threshold temperature (°C)	Effective accumulated temperature (degree-d)
Gynoparae	<i>y</i> = 0.0085 <i>x</i> – 0.0530	1.00*	6.24	117.65
Male	<i>y</i> = 0.0054 <i>x</i> – 0.0154	0.99*	2.85	185.19
Oviparae	<i>y</i> = 0.0047 <i>x</i> – 0.0182	0.97*	3.87	212.77

y = developmental rates, *x* = temperatures. An asterisk (*) denotes a significant difference at *P* < 0.05.

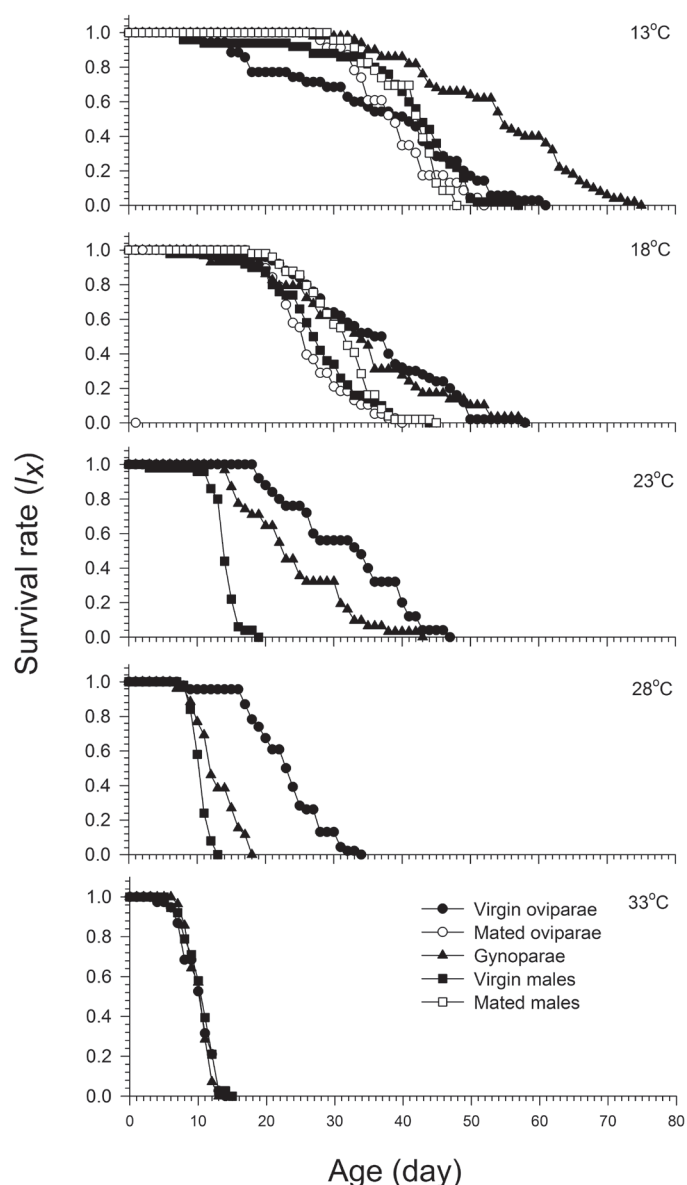


Fig. 1. Age-specific survival rates (l_x) of *Aphis glycines* gynoparae, males, and oviparae at 13, 18, 23, 28, and 33 °C.

higher than at 13 °C ($t = 2.51$; $P < 0.05$). At 23, 28, and 33 °C, no males mated with oviparae (Table 4).

Gynoparae adults of *A. glycines* started to produce oviparae on d 5, 6, 9, and 17 at 28, 23, 18, and 13 °C, respectively (Fig. 2). Peak gynoparae reproduction occurred at d 1, 2, and 3, as well as the first d during

reproductive periods at 23, 18, 13, and 28 °C, respectively. Oviparae adults of *A. glycines* started to produce eggs on d 14 and 19 at 18 °C and 13 °C, respectively (Fig. 2).

LIFE TABLE PARAMETERS OF *APHIS GLYCINES* GYNOPARAE AND OVIPARAE

When temperatures increased from 13 to 28 °C, intrinsic rate of increase and finite rate of increase of *A. glycines* gynoparae increased gradually (Table 5). Mean generation time of gynoparae decreased gradually when temperatures increased from 13 to 28 °C. The net reproduction rate of these individuals at 23 °C was greater than those at 18 and 28 °C, which were all greater than at 13 °C (Table 5). The intrinsic rate of increase, finite rate of increase, and net reproduction rate of *A. glycines* oviparae at 13 °C were lower than at 18 °C (Table 6). Mean generation time of oviparae at 13 °C was greater than at 18 °C.

Discussion

Temperature is an important abiotic factor that can affect survival, development, and fecundity of insects (Bale et al. 2002; Hoffmann et al. 2003). In the Harbin region of northeastern China, the average environmental temperature has been rising in recent yr at a rate of 0.37 °C per 10 yr (Yu et al. 2009; Zhou et al. 2013). Autumnal morphs of *A. glycines* are assumed capable of adapting to these increasing temperatures. Our results showed that nymphs and adults of *A. glycines* gynoparae, males, and oviparae could all survive at temperatures from 13 to 28 °C. Thus, it is likely that these morphs can survive in autumnal northeastern China. Moreover, gynoparae of *A. glycines* could develop into adults and survive at 33 °C. Even if only a few gynoparae could survive under high temperatures in early autumn in Harbin region, large numbers of oviparae would be produced due to their high reproductive potential. Oviparae of *A. glycines* are well adapted to low temperatures. We found when temperatures decreased from 23 to 13 °C, *A. glycines* oviparae longevity did not vary significantly. So when environmental temperatures become lower in late autumn in Harbin, oviparae of *A. glycines* could likely survive and overwintering eggs would be deposited.

Several workers have reported that longevity of *A. glycines* virginoparae decreased gradually when temperatures increased (Hirano et al. 1996; McCornack et al. 2004; Richardson et al. 2011; Xu et al. 2011). We found similar results regarding the temperature effects on development of *A. glycines* autumnal morphs. When temperatures increased from 13 to 28 °C, nymphal developmental times of gynoparae, males, and oviparae as well as adult longevity of gynoparae and virgin males decreased gradually. At 33 °C, nymphs of males and oviparae could not survive, and gynoparae adults could not produce oviparae. Males of *A. glycines* mated with oviparae only at 13 and 18 °C. However,

Table 3. Adult longevity (mean \pm SE) of *Aphis glycines* gynoparae, males, and oviparae at different temperatures.

Temperature (°C)	Gynoparae ^a		Virgin males ^a		Virgin oviparae ^a		Mated males		Mated oviparae	
	N	D	N	D	N	D	N	D	N	D
13	50	36.4 \pm 1.8 a	47	24.3 \pm 0.9 a	23	20.4 \pm 1.8 a	23	22.7 \pm 1.0*	23	17.6 \pm 1.3*
18	28	24.5 \pm 2.1 b	49	15.3 \pm 0.9 b	48	23.0 \pm 1.3 a	49	19.0 \pm 0.8	38	14.4 \pm 0.7
23	31	17.4 \pm 1.4 c	49	5.7 \pm 0.2 c	25	20.2 \pm 1.5 a	0	0	0	0
28	26	7.6 \pm 0.6 d	50	3.1 \pm 0.2 d	44	15.0 \pm 0.7 b	0	0	0	0
33	27	3.5 \pm 0.3 d	0	0	0	0	0	0	0	0

^aMean adult longevity of gynoparae, virgin males, and virgin oviparae within the same column followed by different letters were significantly different ($P < 0.05$; HSD test). Differences in adult longevity only for each column group between 13 and 18 °C rows are marked with an asterisk (*) ($P < 0.05$; t-test).

Table 4. Mean fecundity ± SE of *Aphis glycines* gynoparae and oviparae on overwintering host, *Rhamnus davurica*, at different temperatures.

Temperature °C	Gynoparae		Mated oviparae	
	N	Fecundity* (oviparae/gynoparae)	N	Fecundity (eggs/oviparae)
13	50	9.14 ± 0.15 c	23	1.30 ± 0.25*
18	28	12.79 ± 0.41 b	38	2.16 ± 0.22
23	31	15.87 ± 0.33 a	0	0
28	26	11.81 ± 0.89 b	0	0
33	27	0 d	0	0

Mean gynoparae fecundity (column) followed by different letters were significantly different ($P < 0.05$; HSD test). Differences in mean fecundity of mated oviparae between 13 and 18 °C are marked with an asterisk () ($P < 0.05$; t-test).

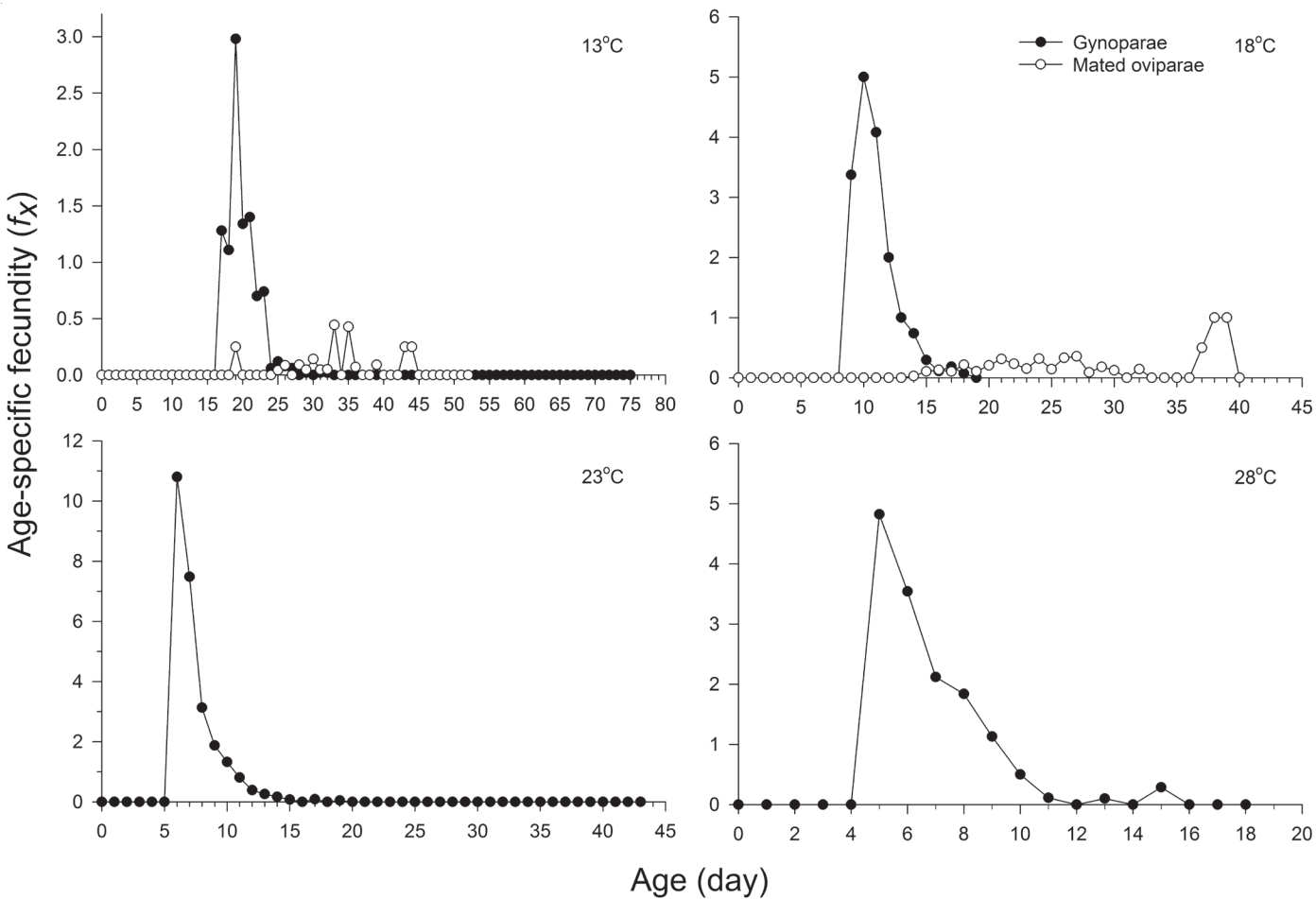


Fig. 2. Age-specific fecundity (f_x) of *Aphis glycines* gynoparae and oviparae on overwintering host, *Rhamnus davurica* at 13, 18, 23, and 28 °C.

Table 5. Life table parameters (mean ± SE) of *Aphis glycines* gynoparae at different temperatures.

Temperature °C	Intrinsic rate of increase r (d^{-1})	Mean generation time T (d)	Finite rate of increase λ (d^{-1})	Net reproductive rate R_0 (offspring)
13	0.1061 ± 0.0010 c	20.85 ± 0.17 a	1.1112 ± 0.0011 c	9.14 ± 0.15 c
18	0.2093 ± 0.0046 b	12.01 ± 0.15 b	1.2328 ± 0.0057 b	12.34 ± 0.58 b
23	0.3165 ± 0.0060 a	8.73 ± 0.16 c	1.3723 ± 0.0082 a	15.87 ± 0.33 a
28	0.3363 ± 0.0135 a	7.34 ± 0.14 d	1.4000 ± 0.0189 a	11.81 ± 0.87 b
33	0	0	0	0

Means followed by different letters within the same column were significantly different ($P < 0.05$; paired bootstrap test).

Table 6. Life table parameters (mean \pm SE) of *Aphis glycines* oviparae at 13 and 18 °C.

Temperature °C	Intrinsic rate of increase r (d ⁻¹)	Mean generation time T (d)	Finite rate of increase λ (d ⁻¹)	Net reproductive rate R_0 (egg)
13	0.0080 \pm 0.0059 b	33.24 \pm 3.31 a	1.0080 \pm 0.0059 b	1.30 \pm 0.24 b
18	0.0340 \pm 0.0044 a	22.64 \pm 0.77 b	1.0345 \pm 0.0045 a	2.16 \pm 0.22 a

Means followed by different letters within the same column were significantly different ($P < 0.05$; paired bootstrap test).

the question remains whether lower temperatures are required for sexual maturation of *A. glycines* oviparae and males. Yoo et al. (2005) reported that oviparae could deposit 4.2 and 0.8 eggs on *Rhamnus cathartica* L. and *Rhamnus alnifolia* L'Her (both Rhamnaceae) at 20 °C, respectively. In our study, only 1 and 2 eggs were deposited by oviparae on *R. davurica* at 13 and 18 °C, respectively. But differences in egg deposition likely could be attributed to differences in hosts as well as experimental temperatures.

To avoid underestimating the value of life history traits in our study, further investigations should be conducted on autumnal morphs of *A. glycines* that are group-reared or reared on living plants with clip cages in the field. Our experiments focused on constant temperature in the laboratory, though environmental temperatures fluctuate sharply between d and night in the Harbin region. If such experiments could be conducted they would provide additional insight into actual circumstances that occur under field conditions.

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