Effect of Temperature and Photoperiod on the Development, Reproduction, and Predation of the Predatory Ladybird *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae)

Author(s): Su Wang , Xiao-Ling Tan , Xiao-Jun Guo , and Fan Zhang
Source: Journal of Economic Entomology, 106(6):2621-2629. 2013.
Published By: Entomological Society of America
URL: http://www.bioone.org/doi/full/10.1603/EC13095

Effect of Temperature and Photoperiod on the Development, Reproduction, and Predation of the Predatory Ladybird *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae)

SU WANG,[1] XIAO-LING TAN,[2] XIAO-JUN GUO,[1] AND FAN ZHANG[1,3]

J. Econ. Entomol. 106(6): 2621–2629 (2013); DOI: http://dx.doi.org/10.1603/EC13095

ABSTRACT The polyphagous predatory ladybird *Cheilomenes sexmaculata* (F.) (Coleoptera: Coccinellidae) is distributed throughout southern China and has been investigated as a potential biological control agent against herbivorous insects in various agroecosystems. In the current study, we evaluated the preimaginal development, eclosion rate, reproduction, fertility, adult longevity, and prey consumption of *C. sexmaculata* under five temperature and five photoperiod regimens. The results showed that preadult developmental duration decreased significantly with increasing temperature and amount of daylight. Adult eclosion rate was highest at 35°C and under conditions of complete darkness. Higher temperatures shortened the duration of copulation and preoviposition, prolonged the duration of oviposition, and increased the level of fecundity. Hatchability was highest at 30°C. By contrast, the shortest copulation and oviposition duration and lowest level of fecundity and hatchability occurred with a completely dark photoperiod. Temperature and the gender of *C. sexmaculata* influenced adult longevity. In addition, there was a significant interaction effect of photoperiod and gender on adult longevity. Furthermore, prey consumption by fourth instar larvae and adult females both increased with increasing temperature and photoperiod. Our results reveal the high thermal and light sensitivities of *C. sexmaculata*, which highlight the importance of environment regulation in the mass rearing of this natural enemy for application as a biological control in agroecosystems in China.

KEY WORDS *Cheilomenes sexmaculata* development, adult longevity, fertility, prey consumption

The use of predacious ladybirds as biological control agents could suppress outbreaks of and reduce the damage inflicted by herbivorous pests in agroecosystems worldwide (Obrycki and Kring 1998). Currently, >250 predatory ladybird species are documented as natural enemies that can be used to control aphids, whiteflies, scale insects, phytophagous mites, and other pests (Dreistadt and Flint 1996, Dixon et al. 1997, Sengonca et al. 2005, Ponsonby and Copland 2007, Britto et al. 2009). Predatory ladybirds are well suited for use as biological control agents, given their wide range of prey species, high rate of prey consumption, and adaptability in terms of their development and reproduction (Hodek and Honek 1996, Dixon et al. 1997, Koch 2003).

The predacious ladybird *Cheilomenes* (*Menochilus*) *sexmaculata* (F.) (Coleoptera: Coccinellidae) preys on several herbivorous arthropod species in its native habitats in Asia (Agarwala and Yasuda 2000, Rai et al. 2003, Duan and Zhang 2004, Pervez and Omkar 2005, Tank and Korat 2007). In southern China, *C. sexmaculata* produces six to seven generations per year but produces only three to four generations in northern China (Zhang et al. 1980). Owing to its high tolerance of high temperatures and humidity, *C. sexmaculata* has been considered to be an efficacious biological control agent in the high-temperature regions and agroecosystems in China, including greenhouses. A previous field survey determined the approximate length of the different developmental stages of *C. sexmaculata*, which differed significantly between seasons (Zhang et al. 1980). Laboratory experiments demonstrated that prey consumption by *C. sexmaculata* was limited simultaneously by prey density and environmental temperature (AliKhan and Yousuf 1986). Environmental temperature variation has been widely documented to influence the developmental and reproductive performances of predatory coccinellids (Hodek 1973). In terms of the thermal responses of insects, excessively low or high temperatures can restrict the biological and physiological activities of insects, whereas an optimal environmental temperature would benefit most biotic processes (Saltm 1961, Miller and Paustian 1992, Aksit et al. 2007, Bahşi and Tunç 2008, Kang et al. 2009). Some ladybird species were shown to reduce their developmental period, survival rate, and reproductive efficiency in cold en-

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[1] Institute of Plant & Environment Protection, Beijing Academy of Agriculture & Forestry Sciences, Beijing, 100097, China.

[2] State Key Laboratory of Crop Stress Biology on the Arid Areas, and Key Laboratory of Northwest Loess Plateau Crop Pest Management of Ministry of Agriculture, Northwest A&F University, Yangling, Shaanxi, 712100, China.

[3] Corresponding author, e-mail: zf6131@yahoo.com.cn.

vironments, whereas other ladybird species showed a reduction in the same variables at high temperatures (Naranjo et al. 1990). In addition, some species such as *Harmonia axyridis* (Pallas), have shown substantial adaption to variations in environmental temperature. *H. axyridis* is able to colonize multiple areas and this combined with its rapid dispersal during worldwide biological control release programs has resulted in nontarget prey being consumed with severe ecological impacts (Roy and Wajnberg 2008). A laboratory study showed a high efficiency of temperature-driven regulation in the mass rearing of the ladybird *Propylea dissecta* (Mulsant) for augmentative biological control release (Pervez and Omkar 2004). The presetting of optimal temperature during mass rearing could not only shorten the life cycle and reduce mortality but also increase the net fertility. Optimal temperature conditions could also enhance prey consumption and stimulate locomotory activity, which would benefit the colonization and dispersal of reared ladybirds in the field (Frazer and McGregor 1992, Berkvens et al. 2008).

Light conditions, especially photoperiod length, have a similar influence on ladybirds as environmental temperature (Hodek 1973). Unsuitable day length can induce diapause and impede the general process of development and reproduction in most insects (De Wilde 1962, Wolda 1988). Ladybirds have shown high sensitivity to photoperiod length; for example, few daylight hours prolonged the developmental period and induced reproductive diapause in *Coelophora saucia* (Mulsant) (Omkar and Pathak 2006). In addition, the widely dispersed ladybird *H. axyridis* showed low photoperiodic responses in terms of its development and reproduction in populations from its native and invasive regions (Berkvens et al. 2008, Reznik and Vaghina 2011). Thus, the use of an optimal light environment could also improve the mass rearing efficiency of ladybirds and ensure the efficiency of fertility by decreasing the likelihood of diapause. Daylight-dependent photoperiodism is considered to be one of the most important factors in the evaluation of the environmental suitability of predacious ladybird species for mass rearing and biological control application.

Clearly, there is a need for further studies of the effects of environmental conditions on the biotic characteristics of predacious ladybirds when considering their suitability for use as biological control agents. Our objectives were to determine the optimal temperature and photoperiod that could be used for the mass rearing of *C. sexmaculata* and to predict the environmental adaptability of this predator, helping to define conditions suitable for its release as a biological control agent.

Materials and Methods

Ladybird Colony. *C. sexmaculata* were collected from Wuhan Botanic Garden, Chinese Academy of Sciences (Wuhan city, Hubei province, China) during July–August, 2011. In total, 507 adults (207 females and 300 males) were transported to the lab of Natural Enemy Research, Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences (Beijing, China) and reared using the aphid *Megoura japonica* (Matsumura) as prey. The aphids were collected from a soybean field during spring 2011 and were maintained on cultured horse bean *Vicia faba* L. seedling as host plant in the lab at the same environmental conditions as *C. sexmaculata.* The ladybird beetles were reared in custom-made culturing cages (45.0 by 50.0 by 50.0 cm, made with aluminum alloy frames and 100-mesh plastic gauze) at a density of 80–100 adults or 130–150 larvae per cage. The culturing environment was regulated using an automatic environmental condition management system (Sunauto, Beijing, China) at 25 ± 1°C, 70% relative humidity (RH), a photoperiod of 16:8 (L:D) h, and 1200 l× illumination intensity.

Development Under Different Environmental Conditions. In total, 50 pairs of *C. sexmaculata* were maintained in culturing plastic boxes as mentioned above and provided with aphid prey and several broad-bean leaves as oviposition substrates. After oviposition, the leaves carrying eggs were transferred into a clean plastic petri dish (9.0 cm in diameter) with one cluster of eggs (15–40 eggs per cluster) per dish. The dishes were placed into artificial environment chambers (Sanyo, MH351, Japan), which were either set at a temperature (T) of either 15, 20, 25, 30, or 35°C (with the remaining environmental conditions being 60% RH, photoperiod of 16:8 (L:D) h, and 1200 l× illumination intensity) or set with a photoperiod of 0:24, 6:18, 12:12, 18:6, or 24:0 (L:D) h (with the remaining environmental conditions being T = 25°C,

Table 1. Durations (days) of different development stages (mean ± SE) of *C. sexmaculata* reared at different environmental temperatures, 60% RH, photoperiod of 16:8 (L:D) h, and 1200 l× illumination intensity

Temperatures	Developmental duration (d)							
	Egg	First instar	Second instar	Third instar	Fourth instar	Prepupae	Pupae	Total
15°C	5.5 ± 0.2a	1.4 ± 0.1a	2.2 ± 0.2a	2.8 ± 0.2	2.6 ± 0.2a	2.6 ± 0.2a	5.0 ± 0.3a	23.8 ± 0.5a
20°C	3.0 ± 0.1b	1.4 ± 0.1a	1.2 ± 0.1b	1.6 ± 0.1	1.8 ± 0.1b	1.0 ± 0.1b	4.9 ± 0.2a	14.9 ± 0.4b
25°C	2.5 ± 0.1c	1.4 ± 0.1a	0.9 ± 0.1c	1.1 ± 0.1	1.5 ± 0.1b	0.6 ± 0.1c	2.9 ± 0.1b	10.9 ± 0.3c
30°C	1.8 ± 0.1d	1.1 ± 0.1b	1.0 ± 0.1c	1.0 ± 0.1	1.6 ± 0.1b	0.6 ± 0.1c	2.2 ± 0.1c	9.4 ± 0.3d
35°C	1.7 ± 0.1d	1.1 ± 0.1b	1.1 ± 0.1c	0.9 ± 0.1	1.7 ± 0.1b	0.5 ± 0.1c	2.3 ± 0.1c	9.2 ± 0.3d
F	167.042	3.639	26.287	43.806	15.699	126.897	62.224	29.175
df	4,245	4,245	4,243	4,241	4,241	4,241	4,167	4,167

Different letters indicate significant differences ($P < 0.05$; Duncan test) across different temperatures per developmental stages.

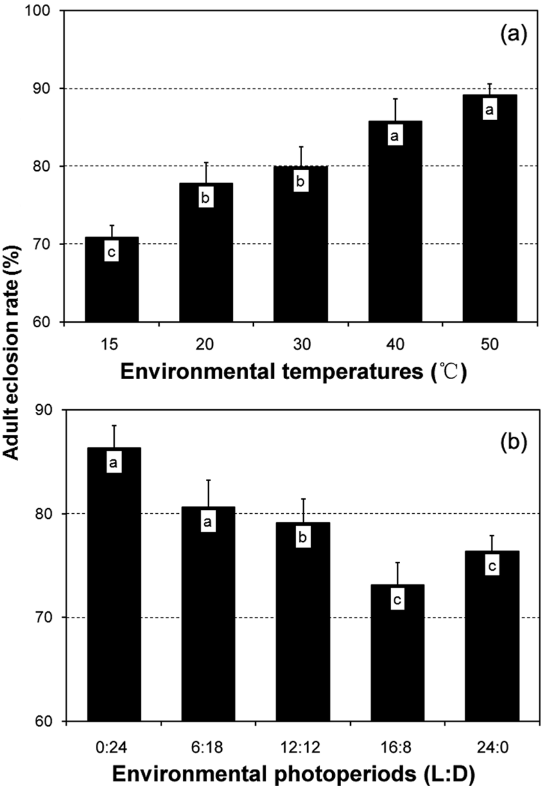

Fig. 1. The adult eclosion rate (%) of *C. sexmaculata* at different temperatures (15, 20, 25, 30, and 35°C [chart a]) or photoperiods (0:24, 6:18, 12:12, 18:6, and 24:0 [L:D] h [chart b]). The error bars correspond to SE. Different letters indicate a difference that is significant at the 5% level (Duncan test).

60% RH, and 1200 l× illumination intensity). Newly hatched first instar larvae were separated using a soft brush and removed to another plastic petri dish (4.5 cm in diameter, one larvae per dish), which was then placed in a chamber with the same conditions as its original chamber. Daily, 80 *M. japonica* nymphs were supplied as prey, which was increased to 120 when *C. sexmaculata* larvae had reached the third instar.

Observations were made every 8 h for the development of each individual until death. The developmental duration of each instar and pupal stages, adult eclosion rate, and adult longevity (unmated males and females) were recorded. The observations for each set of environmental treatments were repeated five times with 10 samples per time.

Reproduction Under Different Environmental Conditions. Pairs of matured *C. sexmaculata* adults (10-d-old) were placed in one clean plastic petri dish (9.0 cm in diameter, one pair per dish) with 80 *M. japonica* nymphs as prey. The dishes were placed into the environmental chambers with the different environmental conditions as described above. The reproductive parameters of *C. sexmaculata* were recorded from each chamber every 30 min. When copulation was terminated (i.e., the male and female had completely separated), the males were removed and the female was kept in the chamber until death. Data relating to copulation duration, preoviposition and oviposition durations, cumulative fecundity, egg hatchability, and mated female longevity were recorded. The observations for each set of environmental treatments were repeated five times, with 10 samples per time.

Predation Under Different Environmental Conditions. Newly emerged fourth instar larvae were placed into clean petri dishes (9.0 cm in diameter, one larva per dish) with 200 *M. japonica* nymphs as food. The dishes were placed into the environmental chambers under the same environmental conditions and treatments as described above. After 12 h, the number of prey consumed was recorded (ignoring the number of aphids that died naturally) for each chamber.

The experiment was repeated with newly emerged adult female *C. sexmaculata* to test the effects of variable environmental conditions on prey consumption by adult ladybirds. The observations for each set of environmental treatments were repeated five times, with 10 samples per time.

Statistical Analysis. The influence of temperature and photoperiod on the developmental duration, eclosion, reproductive performance, prey consumption, and respiratory quotient of *C. sexmaculata* was analyzed using a one-way analysis of variance (ANOVA). The data of adult eclosion rate (%) was transformed by arcsine square-root transformation before ANOVA. The multiple comparisons were conducted using the Duncan test ($P < 0.05$) when significant differences were detected by ANOVA. A mixed factorial ANOVA was used to analyze the variation in adult ladybird lon-

Table 2. **Durations (days) of different development stages (mean ± SE) of *C. sexmaculata* reared at different environmental photoperiods, 25°C, 60% RH, and 1200 l× illumination intensity**

Photoperiod	Developmental duration (d)							
	Egg	First instar	Second instar	Third instar	Fourth instar	Prepupae	Pupae	Total
0:24 (L:D) h	3.6 ± 0.2a	1.6 ± 0.1a	1.3 ± 0.1a	1.7 ± 0.2a	2.1 ± 0.1a	1.2 ± 0.1a	2.6 ± 0.1a	14.2 ± 0.3a
6:18 (L:D) h	2.9 ± 0.1b	1.3 ± 0.1b	1.1 ± 0.1ab	1.2 ± 0.1b	1.3 ± 0.1b	1.0 ± 0.2ab	2.4 ± 0.1ab	11.2 ± 0.3b
12:12 (L:D) h	2.8 ± 0.1b	1.3 ± 0.1b	1.1 ± 0.1ab	1.2 ± 0.1b	1.3 ± 0.1b	0.9 ± 0.1b	2.3 ± 0.1b	10.9 ± 0.2b
18:6 (L:D) h	2.2 ± 0.1c	1.2 ± 0.1b	0.9 ± 0.1b	1.1 ± 0.1b	1.2 ± 0.2b	0.7 ± 0.1b	2.3 ± 0.2b	9.6 ± 0.2c
24:0 (L:D) h	1.9 ± 0.1c	1.1 ± 0.1b	0.9 ± 0.1b	1.1 ± 0.1b	1.3 ± 0.1b	0.7 ± 0.1b	2.2 ± 0.1b	9.1 ± 0.2c
F	30.416	3.683	3.937	6.437	14.718	2.527	3.507	68.135
df	4,425	4,245	4,245	4,245	4,245	4,245	4,245	4,245

Different letters indicate significant differences ($P < 0.05$; Duncan test) across different photoperiods per developmental stages.

Table 3. Reproductive performances (mean ± SE) of *C. sexmaculata* reared at different environmental temperatures, 60% RH, photoperiod of 16:8 (L:D) h, and 1200 l× illumination intensity

Temperatures	Copulation (h)	Preoviposition (d)	Oviposition (d)	Fecundity	Hatchability (%)
15°C	5.8 ± 0.2a	8.1 ± 0.4a	18.0 ± 0.7c	371.6 ± 11.2c	61.2 ± 2.0c
20°C	4.5 ± 0.2b	6.9 ± 0.2b	20.2 ± 0.7bc	542.7 ± 27.4b	69.8 ± 1.8b
25°C	4.6 ± 0.4b	6.3 ± 0.2b	20.5 ± 1.1b	532.4 ± 18.5b	75.7 ± 1.3a
30°C	3.7 ± 0.4bc	6.4 ± 0.3b	23.3 ± 0.8a	510.7 ± 23.9a	79.2 ± 1.2a
35°C	3.3 ± 0.5c	5.2 ± 0.3c	24.2 ± 1.0a	609.1 ± 22.0a	69.1 ± 2.7b
F	13.777	14.139	9.034	21.133	14.139
df	4,425	4,425	4,425	4,425	4,425

Different letters indicate significant differences ($P < 0.05$; Duncan test) across different temperatures per reproductive characteristics.

gevity using environmental temperature, photoperiod, and gender as fixed independent factors. All statistical analyses were calculated using SPSS 18.0 (Allen and Bennett 2010).

Results

Development Under Different Environmental Conditions. As shown in Table 1, environmental temperature significantly influenced the developmental duration of *C. sexmaculata* at the egg stage ($P < 0.01$), first–fourth larval stages ($P_{first\text{-}fourth} < 0.01$), prepupal stage ($P < 0.01$), pupal stage ($P < 0.01$), and overall developmental period ($P < 0.01$). Furthermore, the adult eclosion rate was significantly higher at warmer temperatures (Fig. 1a; $P < 0.01$).

In *C. sexmaculata,* the developmental periods of the egg stage ($P < 0.01$), first–fourth larval stages ($P_{first\text{-}fourth} < 0.01$), prepupal ($P = 0.046$) and pupal ($P < 0.01$) stages, and overall developmental period ($P < 0.01$) were significantly influenced by photoperiod length (Table 2). Adult eclosion rate also showed significant differences among photoperiodic treatments (Fig. 1b; $P < 0.01$)

Reproduction Under Different Environmental Conditions. The mean duration of copulation ($P < 0.01$), preoviposition ($P < 0.01$), and oviposition ($P < 0.01$) of *C. sexmaculata* varied significantly among different environmental temperatures (Table 3). Likewise, the fecundity ($P < 0.01$) and egg hatchability ($P < 0.01$) were also significantly influenced by environmental temperature (Table 3). As shown in Fig. 2, the results of the mixed factorial ANOVA showed that the longevity of *C. sexmaculata* was significantly affected not only by temperature ($P < 0.01$) but also among unmated males and females, and mated females of *C. sexmaculata* ($P < 0.01$). However, longevity was not influenced by the interaction of temperature and gender ($P = 0.125$).

Photoperiod length had a significant effect on the duration of copulation ($P < 0.01$), preoviposition ($P < 0.01$), and oviposition ($P < 0.01$; Table 4). Observations showed that photoperiod also significantly influenced fecundity ($P < 0.01$) and egg hatchability ($P < 0.01$; Table 4). As shown in Fig. 3, photoperiod and gender significantly affected *C. sexmaculata* longevity individually (photoperiod and ladybird status $P < 0.01$) and interactively ($P < 0.01$).

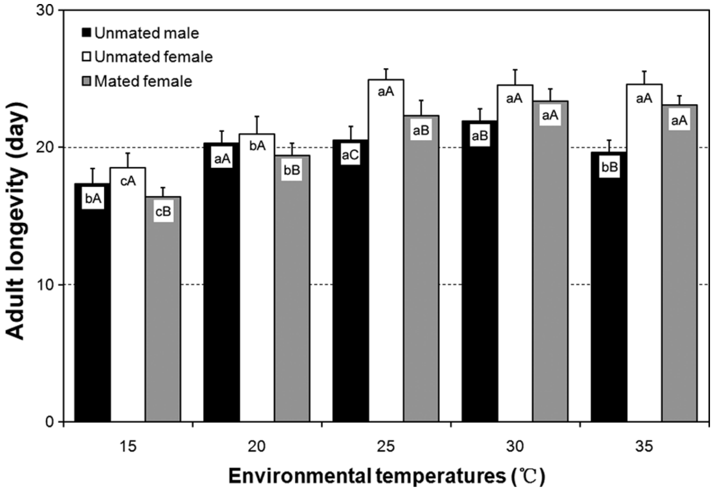

Fig. 2. Adult longevity of adult *C. sexmaculata* at different temperatures (15, 20, 25, 30, and 35°C). The error bars correspond to SE. Different lower-case letters across different temperatures per unmated male, unmated female, or mated female indicate significant differences t at $P < 0.05$ and after Duncan's test; and different upper-case letters within each temperature indicate adult longevity differences for unmated male, unmated female, or mated female by Duncan's test as above.

Table 4. Reproductive performances (mean ± SE) of *C. sexmaculata* reared at different environmental photoperiods, 25°C, 60% RH, and 1200 l× illumination intensity

Photoperiod	Copulation (h)	Preoviposition (d)	Oviposition (d)	Fecundity	Hatchability (%)
0:24 (L:D) h	3.4 ± 0.1c	9.2 ± 0.2a	16.9 ± 0.9c	377.7 ± 19.6c	62.6 ± 0.8b
6:18 (L:D) h	4.2 ± 0.1b	7.5 ± 0.1b	18.7 ± 0.9b	457.8 ± 27.2b	72.8 ± 1.7a
12:12 (L:D) h	4.5 ± 0.1a	7.1 ± 0.3b	21.5 ± 1.2a	538.7 ± 19.8a	72.3 ± 2.1a
18:6 (L:D) h	4.6 ± 0.2a	6.1 ± 0.2c	21.5 ± 0.8a	554.5 ± 16.9a	76.2 ± 2.7a
24:0 (L:D) h	4.8 ± 0.2a	4.9 ± 0.2d	22.4 ± 0.8a	598.9 ± 19.7a	76.2 ± 2.2a
F	13.619	55.605	10.558	12.794	6.753
df	4,425	4,425	4,425	4,425	4,425

Different letters indicate significant differences ($P < 0.05$; Duncan test) across different photoperiods per reproductive characteristics.

Predation Under Different Environmental Conditions. The results showed that the predatory capacity of fourth-instar *C. sexmaculata* larvae was significantly influenced by temperature ($P < 0.01$) and photoperiod ($P < 0.01$; Fig. 4a and b). Figure 5 shows that mean prey consumption by *C. sexmaculata* adult females was significantly affected by temperature ($P < 0.01$) and photoperiod ($P < 0.01$).

Discussion

Despite its potential as a candidate for use in biological control, there are few published studies on the reproductive and physiological performance of the ladybird *C. sexmaculata* under variable environmental conditions, even though these have an important role in the successful mass rearing and releasing of coccinellids. The current study revealed that *C. sexmaculata* is highly sensitive to different temperatures and photoperiodic lengths in terms of its development, reproduction, and predation. Increasing temperature and daylight length positively affected the biological and physiological performance of *C. sexmaculata.*

The results showed that the length of each developmental stage decreased with increasing environmental temperature (Table 1). These results are in accordance with those of previous studies, which show that ladybird development can be positively affected by high temperatures (Mori et al. 2005, Aksit et al. 2007). *C. sexmaculata* is found mainly in the middle and lower reaches of the Yangtze River, including most provinces of southern China (Pang et al. 2004). Field studies showed that the developmental period of *C. sexmaculata* was significantly longer in colder years compared with warmer years (Zhang et al. 1980). In the current study, the prepupal stage was most susceptible to temperature in terms of its developmental duration. However, the process of metamorphosis is generally ensured by a highly efficient metabolic rate, which depends on a sufficient energy supply (Truman and Riddiford 2002). The lower developmental efficiencies of the prepupal and pupal stages at present could also be partially attributed to insufficient food, given that prey consumption was lowest at the coldest condition (Fig. 4). Low temperature is known to negatively influence the mobility and efficiency of foraging in predatory insects. Chiverton (1988) evaluated the locomotory performance and foraging behavior of two carabids, *Bembidion lampros* Herbst and *Pterostichus cupreus* L., feeding on the

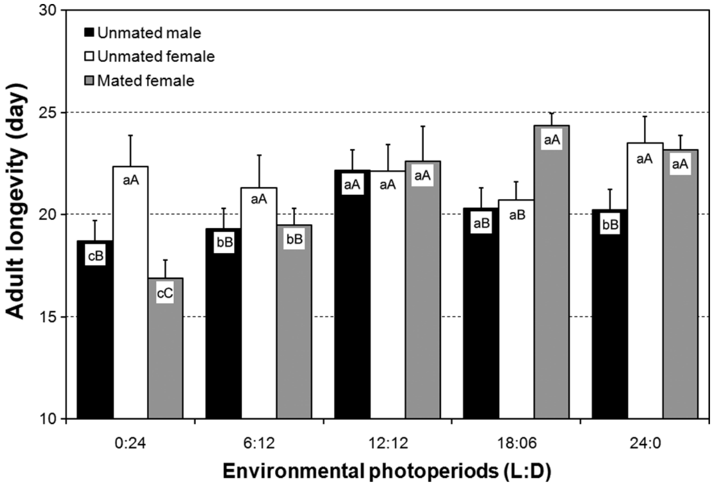

Fig. 3. Adult longevity of *C. sexmaculata* at different photoperiods (0:24, 6:18, 12:12, 18:6, and 24:0 [L:D] h). The error bars correspond to SE. Different lower-case letters across different temperatures per unmated male, unmated female, or mated female indicate significant differences at $P < 0.05$ and after Duncan's test, and different upper-case letters within each temperature indicate adult longevity differences for unmated male, unmated female, or mated female by Duncan's test as above.

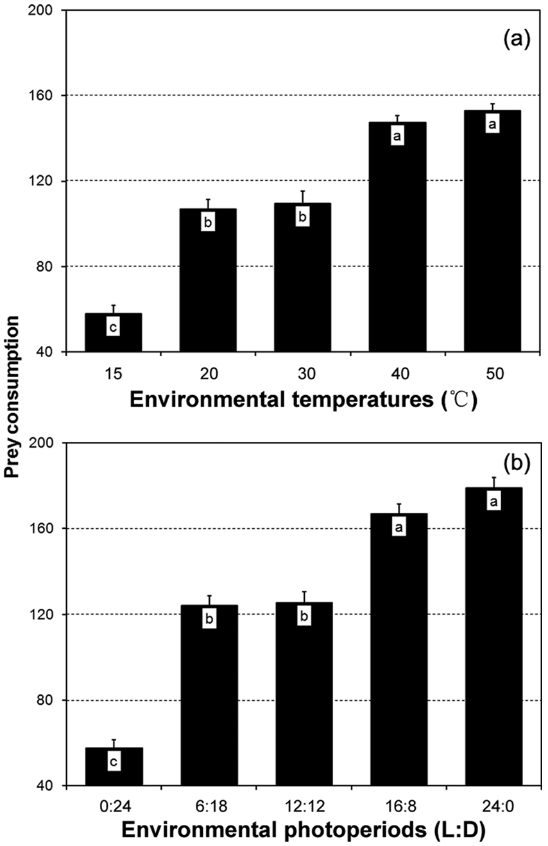

Fig. 4. Mean numbers (±SEM) of *M. japonica* nymphs preyed by fourth instar *C. sexmaculata* larva at different (a) temperatures and (b) photoperiods. Different letters across temperatures or photoperiods indicate significant differences at $P < 0.05$ and after Duncan's test.

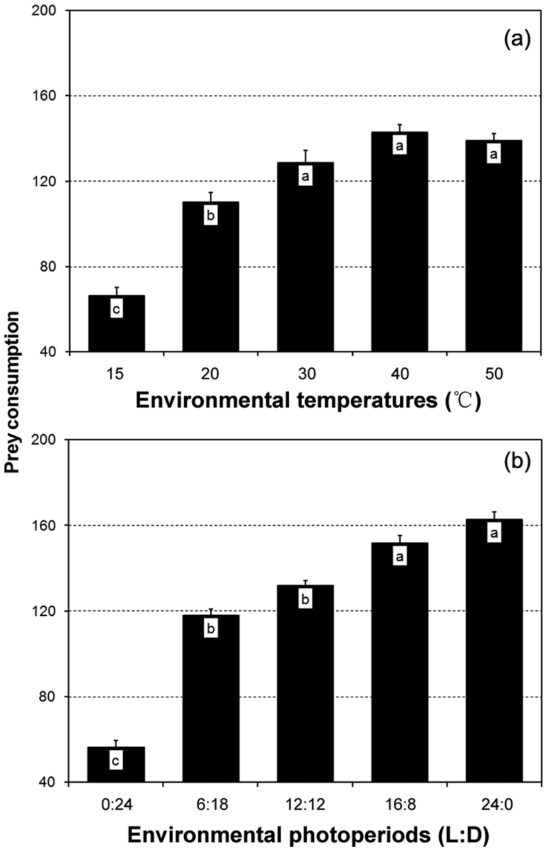

Fig. 5. Mean numbers (±SEM) of *M. japonica* nymphs preyed by female *C. sexmaculata* at different (a) temperatures and (b) photoperiods. Different letters across temperatures or photoperiods indicate significant differences at $P <$ 0.05 and after Duncan's test.

cereal aphid *Rhopalosiphum padi* L. at different temperatures and found that a cold environment severely inhibited the movement of beetles and decreased their prey consumption.

The temperature variation could have influenced the reproductive characters of *C. sexmaculata* in the current study. Colder environment could substantially extend the duration of copulation and preoviposition. Generally, a longer copulation period could be related to higher transmission rates of sperm or spermatophores in insects (Suter and Parkhill 1990, Mazzi et al. 2009). However, the lowest fecundity and hatchability of *C. sexmaculata,* which was recorded in the 15°C chamber, indicate that longer copulation did not benefit in terms of fertility and was probably the result of inhibition of motivation instead of increased sexual receptiveness. The current study also suggests that high temperature significantly increases the rate of prey consumption by adult females. A sufficient food supply could satisfy the requirements of insects to reach sexual maturity (House 1961), coincident with our observations. Although a shorter mating duration was found at high temperatures, we still observed a significant increase in the duration of the oviposition period and related higher fecundity. It is clear that higher temperatures increased the reproductive net efficiency by producing more viable offspring.

Temperature-dependent biological and physiological characters vary among predatory coccinellid species (Majerus 1994). Similar results were recorded for some coccinellids as for *C. sexmaculata,* in that they were more temperature sensitive and showed poor adaptation to temperature variation. For instance, the twospotted ladybird *Adalia bipunctata* L. failed to develop to the adult stage, despite the fact that their developmental rate showed a positive linear relation with temperature (Jalali et al. 2010). By contrast, the worldwide invasive predatory ladybird, *H. axyridis,* exhibited a higher cold tolerance and wider suitable temperature range (Berkvens et al. 2010). The great thermal adaptability of natural enemies can have both positive and negative influences on colonization efforts for biological control. On one hand, broad environmental adaptability of the released species could enhance its successful colonization to meet the requirements of biological control (Obrycki and Kring 1998, Symondson et al. 2002). However, broad environmental adaptability could weaken the limits to dispersal of polyphagous predators, resulting in potential ecological risks from their imported release (Koch 2003, Louda et al. 2003). Therefore, premeasurement of the environmental adaptability of a candidate predatory species is a necessary requirement of quarantine evaluation before field release. *C. sexmaculata* has been introduced into vegetable greenhouses in northern China to suppress pest outbreaks during the summer, with good effect (H. P. Zan, unpublished results). In addition, the population density should decrease during autumn because of the substantial difference in temperature between day and night, which could also limit the development and dispersal of the predatory species when their target prey are in short supply.

The current study showed that all of the recorded biotic characteristics of *C. sexmaculata* were significantly influenced by photoperiod length. It is well known that the photoperiodicity of organisms can be viewed as an anticipatory response to day length cues and seasonal events (De Wilde 1962, Bradshaw and Holzapfel 2007). In agroecosystems, the different number of generations recorded in different geographical populations of same arthropod species could be attributed to the responses to different environmental conditions (Beck and Apple 1961). *C. sexmaculata* showed decreased rates of copulation and oviposition and reproductive efficiency under shorter days and all-dark photoperiodic conditions. In fact, a long dark period has always been viewed as a signal to trigger initial dormancy or diapause in most arthropods, when combined with colder temperature (Tauber et al. 1986). Similarly with the temperature experiments, significantly lower prey consumption by both fourth instar larvae and adult females was observed under short-day and all-dark photoperiodic conditions. Coccinellid species have been widely described as predators that hunt primarily based on visual searching (Hodek et al. 2012). Therefore, shortage of light might decrease their nutritional intake, which could negatively influence sexual performance of mature *C. sexmaculata*, as seen in the current study. Some species are highly sensitive to day length but only in specific developmental stages or responses in successive stages (Sauders 2002). However, no delayed photoperiodic effects in *C. sexmaculata* were recorded in the current study. Other coccinellids, such as the acariphagous ladybird beetle *Stethorus gilvifrons* (Mulsant), showed different results in terms of variation in their total developmental period, indicating that sensitivity to the photoperiod does not extend to all life stages (De Wilde 1962, Aksit et al. 2007). By contrast, and similar to the current observations, high sensitivity to the photoperiod of the aphidophagous ladybird *Co. saucia* (Mulsant) was found across all life stages (Omkar and Pathak 2006). Field studies of *C. sexmaculata* showed substantial differences in the time at which population density peaked between northern and southern geographic populations in China and compared with populations in middle Gujarat, India (Zhang et al. 1980, Tank and Korat 2007). Day length was confirmed as one of the key factors in determining the induction and termination of diapause in ladybirds. Studies of *H. axyridis* showed that a decreasing photoperiod can induce imaginal diapause (Iperti and Bertrand 2001) and that the female adult was restored to general activity at a photoperiod of >12 h of daylight (Ongagna and Iperti 1994). A short daylight environment could inhibit the performance of *C. sexmaculata* in terms of its ability for population colonization and expansion. A long-day environment could not only increase the success rate of population colonization but also ensure the efficiency of pest control. The high photoperiodic sensitivity of *C. sexmaculata* might help to limit the potential risks surrounding its release as a biological control agent in different geographical areas, although this kind of sensitivity could be seen as an ecological disadvantage to the ladybird. Potentially, daylength may be managed in greenhouse environments to favor *C. sexmaculata.*

Environmental regulation could help promote the efficiency of the mass rearing of natural enemy agents. The results of the current study indicate that the periodic adjustment of temperature and light supplement could optimize the developmental and reproductive performance in the mass rearing of *C. sexmaculata.* The production of this ladybird in intensively regulated conditions based on the current results was approximately three times that of ladybirds reared under natural conditions (H.P., unpublished results).Thus, there is a need for more studies on the influence of environmental factors on the mass rearing and application of *C. sexmaculata* as potential agents for biological control.

Acknowledgments

We thank Shize Zhang (College of Plant Protection, Northwest A&F University, China) for his critical reviews and suggestions. The current study was supported by the funds from the State Key Development Program for Basic Research of China (973 plan, No. 2013CB127605) and the Special Fund for Agro-scientific Research in the Public Interest (No. 201303024 and No. 201303108)

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Received 22 February 2013; accepted 28 September 2013.