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Research

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Effects of Pre-Diapause Temperature and Body Weight on the Diapause Intensity of the Overwintering Generation of *Bactrocera minax* (Diptera: Tephritidae)

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Abstract

The Chinese citrus fruit fly, *Bactrocera minax* (Enderlein), is an economically important pest of citrus. The fly has an obligatory pupal diapause in soil from November to March. However, techniques for predicting or determining the emergence of the adult have, thus far, not been well documented. In this study, we investigated the effects of different pre-diapause temperatures (8, 12, 16, and 20°C) and pupal body weight (five groups according to pupal weight: G-58, 55.0–61.0 mg; G-68, 65–71 mg; G-78, 75–81 mg; G-88, 85–91 mg; G-95, 92–98 mg) on pupal period (the indicator of diapause intensity). The pupal period of *B. minax* larvae pupated at 8°C was 193.41 d, which was significantly shorter than that of larvae incubated at higher temperatures, suggesting that there was a lower diapause intensity for larvae pupated at lower pre-diapause temperatures. There were also significant differences in the pupal periods at different pupal body weights. The pupal period of G-58 was significantly shorter than that of the heavier groups (G-88 and G-95), and the pupal period increased with increasing pupal body weight in the five groups. Moreover, the pupal period of *B. minax* significantly and positively correlated to pupal body weight. These findings demonstrate that the pre-diapause temperature and pupal body weight are suitable indicators for predicting the pupal period of overwintering individuals, and the results of this study will contribute to the development of new and effective strategies for predicting the occurrence and population dynamics of *B. minax* adult.

Key words: *Bactrocera minax*, diapause intensity, pre-diapause temperature, body weight

The Chinese citrus fruit fly, *Bactrocera minax* (Enderlein), is an economically important pest of citrus in China, Bhutan, Nepal, and India (Wang and Luo 1995, Dorji et al. 2006, Drew et al. 2006). It is a univoltine species with an extended obligatory diapause during its soil-inhabiting pupal stage, which normally occurs from November to March to combat the harsh environmental conditions (Wang and Luo 1995). To date, the only available method for predicting or determining the emergence of adult flies in spring is monitoring by field observation. Considering the current lack of an effective strategy for predicting the emergence of adults in the upcoming growing seasons, it was deemed necessary to develop a new and effective strategy for predicting the timing of future adult emergence. As yet, the possible relationship between the number of overwintering individuals and pre-overwintering environmental temperatures have not been factored into models for predicting field dynamics (Zhou et al. 2012). Therefore, enhancing our understanding of the overwintering ecology of *B. minax* might be helpful in predicting the emergence of adults.

Diapause intensity is measured as the relative duration of developmental arrest (diapause) at a given moment and under particular environmental conditions (Vinogradova 1974). The initiation and maximum levels of diapause intensity between the same and different populations of a given species often differ because of the distinct conditions experienced during the diapause period (including pre-diapause, diapause, and post-diapause) (Danks 1987, Xu et al. 2011, Posledovich et al. 2015). Accordingly, the impact that various environmental conditions during the diapause induction phase may have on the diapause intensity of insects with an obligate diapause needs further investigation. Temperature and photoperiod are the most important factors affecting the diapause intensity of insects, and these have varying degrees of influence depending on the species or a population's geographic location (Hodek and Hodkova 1988). Exposure to different environmental conditions during diapause induction can enhance or reverse various diapause states, leading to induction via different pathways and thus affecting the duration of the diapause (Fujiyama and Takahashi 1973, 1977; Bodnaryk

1978; Pener and Orshan 1980; Sieber and Benz 1980; Tauber et al. 1986; Principi et al. 1990; Kalushkov et al. 2001). Therefore, understanding the possible influence environmental conditions during diapause induction have on the intensity of diapause may be helpful in predicting the timing and extent of the emergence of overwintering fly populations.

The diapausing insects generally either abstain from feeding or feed only rarely for an extended period of time, which is the major survival challenge for most insects during this period (Hahn and Denlinger 2007, 2011). The body weight of diapausing individuals greatly depends on the degree of food intake before entering diapause. Thus, individuals of different body weights are challenged differently during diapause. Previous studies have suggested that the diapause duration is closely related to body size (Saunders 1997, Danforth 1999, Menu and Desouhant 2002, Xu 2011). In China, the body weight of *B. minax* pupae varies within 50–100 mg in nature. This kind of overwintering pupal weight variation, and the implied variations in pupal energy reserves, may be related to the amount of food consumed before diapause. Thus, changes in body weight and the accumulation of energy reserves are among the most conspicuous alterations that occur during the pre-diapause period (Tauber et al. 1986, Danks 1987, Denlinger et al. 2005). Therefore, we hypothesize that the diapause intensities of *B. minax* pupae are related to their pupal body weight.

In the suburbs of Jingzhou, Hubei Province, P.R. China, temperatures in the areas in which *B. minax* larval pupate vary greatly. In this study, the effects of pre-diapause temperatures and the body weights of fruit fly pupae in relation to the pupal period were investigated. We aimed to may provide a better understanding of the factors affecting adult emergence and population dynamics following overwintering in this species.

Materials and Methods

Insect Rearing

Bactrocera minax larvae were collected from infested fallen fruit in a citrus orchard located in Songzi, Jingzhou Country (E 111°39′41.43″, N 30°17′04.57″), Hubei Province, P.R. China, in October 2015. All collected larvae were placed into plastic containers (20 cm diameter, 16 cm height) contain pre-moistened sand (approximately 15–20% absolute humidity), and 300 larvae were placed into each container for use in the following experimental treatments.

Pre-Diapause Temperature Treatment

The range of daily air temperatures in the citrus orchard in October for the 3 yr previous to 2015 is shown in Fig. 1. We selected experimental pupation temperatures according to this range. Then, 2,400 *B.minax* larvae were segregated into eight individual containers (20 cm diameter, 16 cm height), and two containers were placed in each of the four tested temperatures (8, 12, 16, and 20°C) (RH: 70 ± 5%; 14:10 (L:D) h) for continuous rearing, and the larvae were allowed to pupate. The stages of the individual larvae were observed and recorded every 2 d until pupation. The pupation time of every larva was recorded until no larvae had pupated for an entire week. In addition, the body weight of each pupa was determined using an analytical balance.

Body Weight Group Treatment

A further 1,000 *B. minax* larvae were allowed to pupate at a constant temperature (18°C). Afterward, pupae were weight and divided into five groups, 55–61 mg (G-58), 65–71 mg (G-68), 75–81 mg (G-78), 85–91 mg (G-88), and 92–98 mg (G-95), to investigate the effects of body weights on diapause intensity.

Overwintering Treatment

After pupation, every *B. minax* pupa from the above experiments was placed individually into separate plastic cups (6.5 cm diameter, 7.5 cm height) filled with sand (approximately 15–20% absolute humidity) and overwintered at 15°C, ca. 75 ± 5% relative humidity, and a photoperiod of 14:10 (L: D) h in climate cabinets (GZX-400BS-III, Shanghai CIMO Medical Instrument Manufacturing Co., LTD, Shanghai). We observing emergence of the adults from March of the following year, and the time, date, and sex of each emergence fly were recorded. The experiment was run until all of the adults had undergone eclosion or the pupae had died.

Diapause Intensity Analysis

We defined the length of time between pupation and emergence as the pupal period. In this study, the intensity of diapause was defined as the average number of days required to complete eclosion after the pupated *B. minax* larvae had been transferred to the plastic cups (Xiao et al. 2010).

Statistical Analysis

All statistical analyses were performed using IBM SPSS Statistical Version 18 (SPSS Inc., Chicago, IL). Differences in diapause intensity were compared using a one-way analysis of variance (ANOVA), followed by Tukey's test for multiple comparisons with $P < 0.05$ and *t*-test for two samples with $P < 0.05$. Curve fit was also used to detect the relationship between the body weight of *B.minax* pupae and the diapause intensity.

Results

Effects of Pre-Diapause Temperature on Pupal Period of *B. minax*

All pupae were incubated at 15°C for overwintering after they have pupated under the different temperature regimes. The pupal period of each pupa is shown in Fig. 2. The pre-diapause temperature was shown to have a significant effect on the pupal period of *B. minax* ($F = 238.017$, df = 3, 459, $P < 0.001$) (Fig. 3A). The mean pupal period extended from approximately 193 d at 8°C to approximately 230 d at 20°C, revealing that a low pre-diapause temperature significantly shortened the length of the pupal period.

There were also significant differences between the pupal period of females and males (Female: $F = 122.566$, df = 3, 220, $P < 0.001$, Male: $F = 133.37$, df = 3, 235, $P < 0.001$) (Fig. 3B), with the average pupal period increasing in proportion to the increase in pre-diapause temperature. The shortest pupal periods occurred in female and male adults emerging from *B. minax* pupae that had been induced to diapause at 8°C, while the longest pupal periods occurred in individuals induced to diapause at 20°C (Fig. 3B). No significant differences were found between females and males within the different pre-diapause temperature groups except for those pupating at 16°C (8°C: $F = 0.573$, df = 1, 109, $P = 0.4507$, 12°C: $F = 3.196$, df = 1, 57, $P = 0.0791$, 16°C: $F = 9.83$, df = 1, 171, $P = 0.002 < 0.05$, 20°C: $F = 3.553$, df = 1, 118, $P = 0.0619$) (Fig. 3C). The results showed that larvae pupated at lower pre-diapause temperature had shorter pupal period.

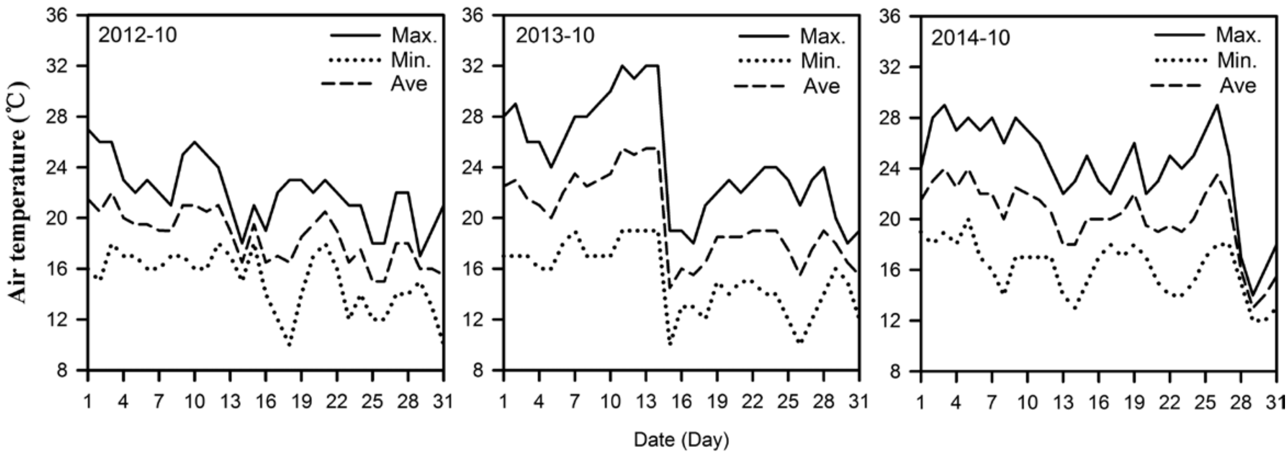

Fig. 1. Daily maximal, minimal and average air temperatures detected during October at a local meteorological station in Songzi, Hubei, China.

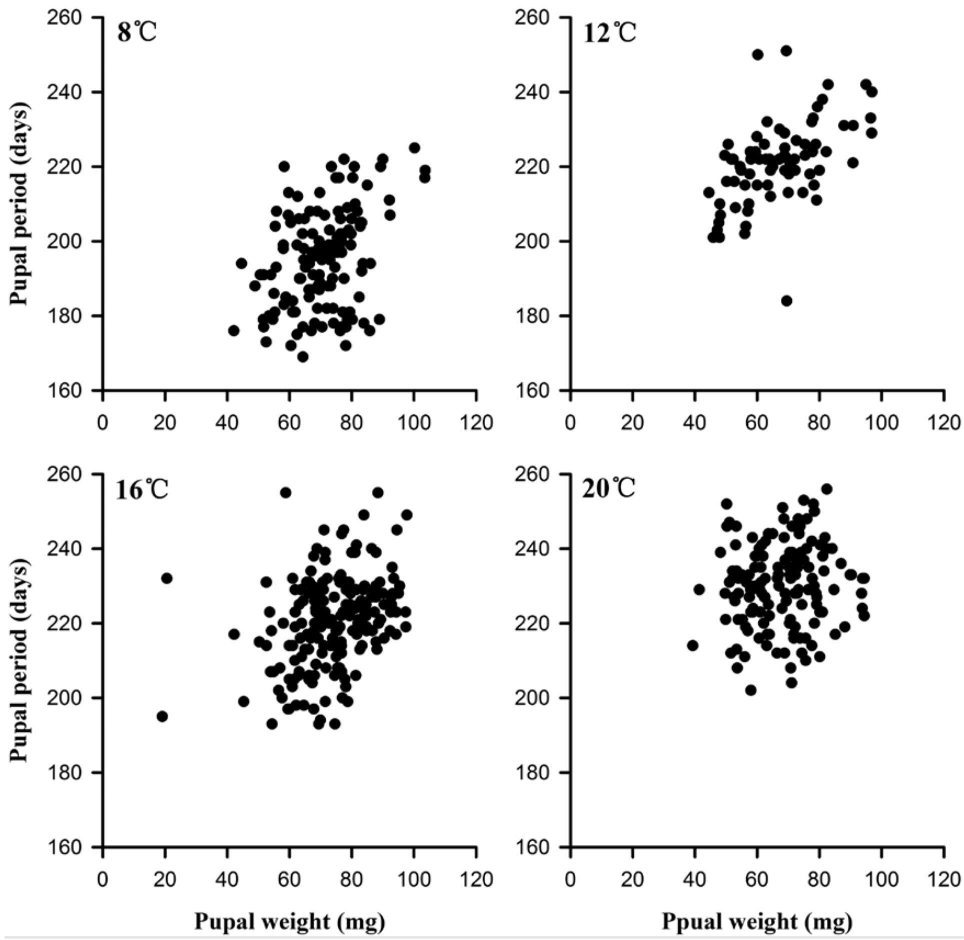

Fig. 2. The pupal period of *Bactrocera minax* larvae pupated at different temperatures. All larvae were divided into four groups and incubated at 8, 12, 16, and 20°C until pupation, and all pupae were incubated at 15°C after pupation.

Effect of Body Weight on Diapause Intensity of *B. minax*

The mean pupal period of every group is shown in Fig. 4A, significant differences occurred between several of the five body weight groups ($F = 1216.378$, df = 4, 116, $P < 0.001$), so five groups pupae were used as the basis for investigating the effect of body weight on pupal period. Separate pupae from each of the five weight groups were maintained at 15°C for overwintering. Significant differences were found among the pupal period of several groups ($F = 4.395$, df = 4, 116, $P = 0.0024 < 0.05$). G-58 had a shorter pupal period than G-88 and G-95. No significant differences, however, were found among G-58, G-68, and G-78, and no significant differences

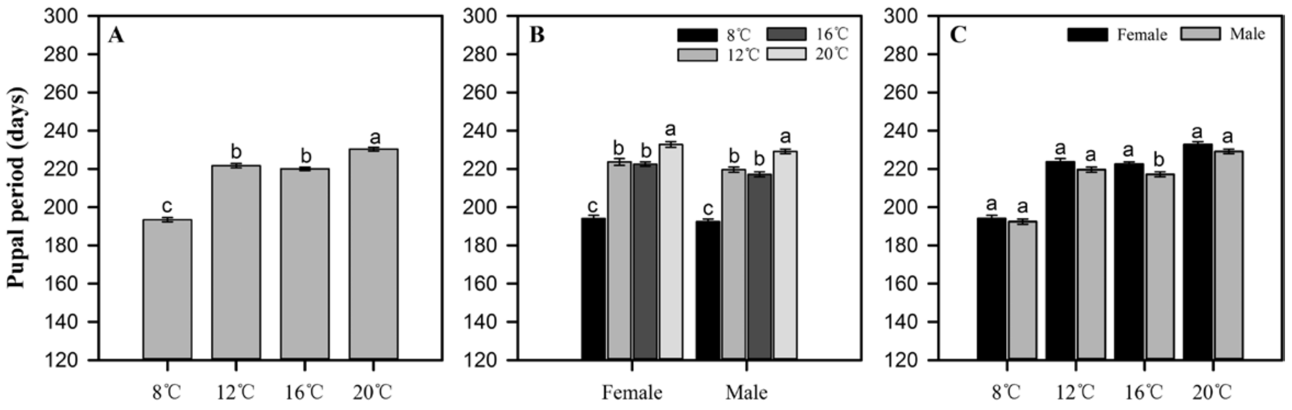

Fig. 3. Effect of pre-diapause temperature on pupal period of *Bactrocera minax* (A), female and male (B), between female and male (C). Larvae were reared at 8, 12, 16, and 20°C, and pupae were incubated at 15°C for overwintering. Values (means ± SE) labeled with the same letters are not significantly different (Tukey's test for multiple comparisons with $P < 0.05$, and *t*-test for two samples with $P < 0.05$).

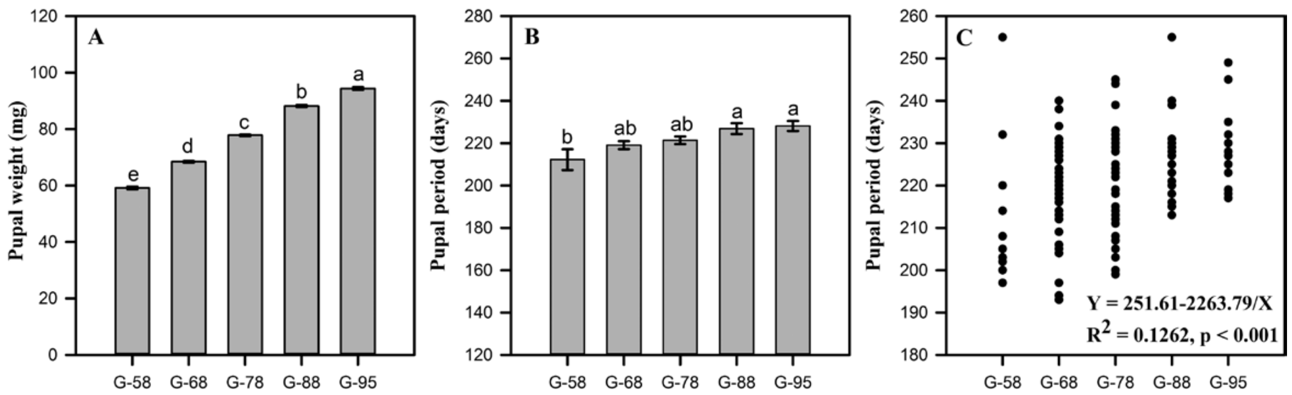

Fig. 4. The pupal weight (A) and pupal period (B, C) of *Bactrocera minax*. Larvae were pupated in the same condition and divided into five groups according to pupal weight (G-58: 55–61 mg; G-68: 65–71 mg; G-78: 75–81 mg; G-88: 85–91 mg; G-95: 92–98 mg). Values (means ± SE) labeled with the same letters are not significantly different (Tukey's test for multiple comparisons with $P < 0.05$).

were noted among G-68, G-78, G-88, and G-95 groups (Fig. 4B). These results represented that smaller individuals have less intense in diapause intensity, and significantly weaker than those of larger individuals. In addition, there was a strong ($R^2 = 0.1261$, $P < 0.001$) association between pupal period and pupal weight (Fig. 4C). The disparity of individual pupal periods in the G-58 group was more pronounced than in other groups, with only a few individuals in this group successfully emerging into adults.

There were no significant differences in the pupal periods within or between females and males (Female, $F = 1.932$, df = 4, 71, $P = 0.1145$; Male, $F = 1.234$, df = 3, 39, $P = 0.3105$; G-58, $F = 0.205$, df = 1, 10, $P = 0.6607$, G-68, $F = 2.196$, df = 1, 36, $P = 0.1471$, G-78, $F = 0.043$, df = 1, 37, $P = 0.8362$) (Table 1). Because of an insufficient sample size, only males were analyzed for differences in pupal period for G-58, G-68, and G-78. Although the body weight of *B. minax* had no significant effect on the pupal period of females and males, the pupal period of *B. minax* gradually increased with body weight.

Discussion

Pre-diapause temperature plays an important role in insect diapause, enhancing or reversing various diapause states during the diapause induction period, and, thereby, affecting the intensity of diapause in several diapause insects (Fujiyama and Takahashi 1973, 1977; Principi et al. 1990; Kalushkov et al. 2001; Nikos and Michael 2001). Moreover, Braune (1973) pointed out that only the duration and time of termination of the obligatory diapause periods of arrested growth are controlled and influenced by temperature. In addition, Xue et al. (2001) noted that a lower temperature at the pre-diapause stage could play an important role in the normal termination of insect obligatory diapause. In the present study, the pupal period of *B. minax* decreased in response to lower pre-diapause temperatures (Fig. 3A), indicating that the diapause intensity of *B. minax* weakened as the pre-diapause temperature decreased. Similar patterns have been reported previously in two other diverse taxa, *Mamestra configurata* (Bodnaryk 1978) and *Mallada flavifrons* (Principi et al. 1990). In addition, these results are similar to previous studies that found that with low temperatures were requirement for diapause termination, especially for *B. minax* (Dong et al. 2013), and other tephritids (Vankirk and Aliniazee 1982; Teixeira and Polavarapu 2005a,b,c,d; Dambroski and Feder 2007). Therefore, pupation at a lower temperature might induce overwintering pupa to enter the diapause stage prematurely or to begin entering post-diapause development earlier.

Most studies have shown that the amount of energy accumulated prior to diapause is reflected in the intensity of diapause. In general, smaller diapausing individuals tend to terminate diapause earlier and the diapause intensity is obviously weaker (Matsuo 2006). This has been demonstrated in a variety of insects, including the moths *Laspeyresia strobilella* (Bakke 1971, Nesin 1985), *Prodoxus*

Table 1. Female and male pupal periods of different body weight groups of *Bactrocera minax*

Group	Female	Male	Female vs Male		
			df	*F*	*P*
G-58	215.5 ± 7.7(4)a	210.6 ± 6.8(8)a	1	0.205	0.6607
G-68	221.9 ± 2.3(18)a	216.5 ± 2.8(20)a	1	2.196	0.1471
G-78	221.7 ± 2.3(26)a	220.8 ± 2.9(13)a	1	0.043	0.8362
G-88	226.3 ± 3.0(14)a	-	-	-	-
G-95	228.9 ± 2.4(14)a	-	-	-	-

All pupae were divided into five groups according to pupal weight (G-58: 55–61 mg; G-68: 65–71 mg; G-78: 75–81 mg; G-88: 85–91 mg; G-95: 92–98 mg). Values (mean ± SE) labeled with different letters in each group are significantly different by Tukey's test with $P < 0.05$, and *t*-test for two samples with $P < 0.05$. Sample numbers are given in parenthesis and '-' represents data absence for insufficient samples.

y-inversus (Powell 1989) and *Barbara colfaxiana* (Sahota and Ibaraki 1991); the desert bee *Perduta portalis* (Danforth 1999); and the chestnut weevil *Curculio elephas* (Menu and Desouhant 2002); their diapause intensity directly and positively correlated with their body weight. The results from this study confirm that body weight correlates closely with the intensity of diapause in overwintering individuals (Fig. 4), with smaller overwintering individuals emerging prior to larger individuals. In addition, body weight is also affected by the moisture levels of overwintering individuals; however, there were no significant changes in individual moisture levels during the overwintering period (unpublished data). Therefore, body weight affects the diapause intensity, which can be explained by the amount of energy resources available for metabolization by individuals during diapause. A longer diapause duration requires additional energy reserves, even though energy metabolism is substantially reduced during the diapause period. In essence, the diapause longevity and development of fitness of diapausing individuals depend on the energy reserves acquired before diapause initiation (Hahn and Denlinger 2007). Thus, further systematic studies are needed to explore differences in the energy metabolism of individuals with various body weights during the pupal period.

Some life history models predict that the temperature-size rule is a form of adaptive plasticity that optimizes fitness in a seasonal context (Atkinson 1995, Angilletta and Dunham 2003, Angilletta et al. 2004, Kingsolver et al. 2007, Stillwell et al. 2008, Chown and Gaston 2010). Seasonal dormancy typically includes long periods where feeding is restricted or eliminated. For this reason, upon receiving environmental cues that prompt them to enter dormancy, animals often prepare by altering their growth and resource-allocation patterns to increase nutrient reserves (Hahn and Denlinger 2007, 2011; Clemmensen and Hahn 2015). However, with regards to diapause insects, whether the pre-diapause temperature has a direct effect on the body weight of overwintering pupae and leads to differences in diapause intensity requires further study. Thus, the environmental temperature before diapause and its relationship to metabolic characteristics of the species during diapause, might be an important determining factor a new prediction method for the emergence of *B. minax* adults.

In addition, some other factors such as food resource, and the larval density, can also affect the body weight (Koyama and Mirth 2018). For *B. minax*, food resource and the larval density of each fruit are the same factors that lead to the differences in body weight. In the natural, the number of larvae in a fruit ranges from a few to nearly a hundred. Therefore, differences in the number of larval result in uneven food distribution, which affects the body weight. Thus, energy metablism of *B. minax* during diapause period needs more investigated.

In conclusion, our results provide an overview of the relationships among *B. minax* pre-diapause temperature, diapause intensity, and individual body weight. Pre-diapause environmental temperatures and overwintering individuals' body weights are important considerations when modeling the diapause duration. The period of *B. minax* adult emergence is a significant time for the effective control of this pest. Therefore, our study may be useful for more accurate estimations of adult emergence times in the field and in developing efficient pest control management for subsequent years.

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