

# Parental effect of diapause in relation to photoperiod and temperature in the cabbage beetle, *Colaphellus bowringi* (Coleoptera: Chrysomelidae)

H.-M. He, H.-J. Xiao and F.-S. Xue\*

Institute of Entomology, Jiangxi Agricultural University Nanchang, 330045, China

## Abstract

Increasing evidence has demonstrated that the environmental conditions experienced by parents can shape offspring phenotypes. Here, we examined the effects of the photoperiod and temperature experienced by parents on the incidence of diapause in their progeny in the cabbage beetle, *Colaphellus bowringi*, using three experiments. The first experiment examined parental diapause incidence under different photoperiods at 25°C and the incidence of diapause in progeny from both non-diapausing and diapausing parents under the same rearing conditions. The results revealed that the incidence of diapause among progeny was exactly opposite to that of their parents, i.e., higher parental diapause incidence led to lower progeny diapause incidence, showing a negative relationship in diapause incidence between the parental generation and the progeny generation. The incidence of diapause among progeny produced by diapausing parents was higher than that in progeny produced by non-diapausing parents. The second experiment examined parental diapause incidence at different temperatures under LD 12:12 and the incidence of diapause in progeny from both non-diapausing and diapausing parents under the same rearing conditions. Similarly, the incidence of diapause in progeny was also opposite to that of their parents. However, the incidence of diapause in progeny produced by non-diapausing parents was different from that in progeny produced by diapausing parents. In the third experiment, naturally diapausing adults were maintained at a constant temperature of 9, 28°C or the mean daily summer temperature of 27.84°C under continuous darkness for 3 months of dormancy. After dormancy, the progeny of these post-diapause parents were reared under different photoperiods at 25°C. The results showed that the incidence of diapause among progeny was higher when their parents experienced high temperatures than when they experienced low temperatures. All results demonstrate that the photoperiod and temperature experienced by parents may significantly affect the diapause incidence among progeny.

**Keywords:** *Colaphellus bowringi*, parental effects, diapause, photoperiod, temperature

(Accepted 11 December 2017; First published online 5 February 2018)

## Introduction

There is increasing evidence that the environmental conditions experienced by parents can influence the phenotype and

life-history traits of their progeny by affecting their physiological conditions (Mousseau & Dingle, 1991; Mousseau & Fox, 1998; Badyaev & Uller, 2009; Bonduriansky & Day, 2009; Valtonen *et al.*, 2012; Burgess & Marshall, 2014; Attisano & Kilner, 2015; Kilner *et al.*, 2015). These transgenerational effects can be viewed as plastic phenotypic responses of the progeny to parental environmental conditions, i.e., non-genetic parental effects.

Parental effects on reaction norms for morphological, behavioural and physiological traits have been investigated in a number of insects, such as the tobacco budworm

---

\*Author for correspondence

Phone: +867913813248

Fax: +8679183828081

E-mail: xue\_fangsen@hotmail.com

(*Heliothis virescens*) in terms of the effect of parental diet on progeny development time (Gould, 1988), the seed beetle *Stator limbatus* in terms of the effect of parental feeding on progeny body mass (Fox *et al.*, 1997), the desert locust (*Schistocerca gregaria*) in regard to the effect of parental rearing density on progeny morphology and behaviour (Simpson & Miller, 2007), the fly *Drosophila melanogaster* in terms of the effect of parental food quality on progeny development time (Valtonen *et al.*, 2012), the tobacco hornworm (*Manduca sexta*) in regard to the effect of immunochallenged parents on progeny larval development time and body mass (Trauer & Hilker, 2013) and the burying beetle *Nicrophorus vespilloides* in terms of the effect of the parental developmental environment on progeny reproduction and wing morphology (Kilner *et al.*, 2015; Attisano & Kilner, 2015).

Environmentally modulated transgenerational plasticity in progeny diapause has been examined in some insects that undergo facultative summer or winter diapause (Danks, 1987; Yang *et al.*, 2007; Lai *et al.*, 2008; Scharf *et al.*, 2010). In general, the photoperiod, temperature, host availability or density experienced by the parental generation will determine the probability of diapause in their offspring (Vinogradova, 1974; Mousseau & Dingle, 1991; Fox & Mousseau, 1998; Oku *et al.*, 2003; Tachibana & Numata, 2004; Huestis & Marshall, 2006; Yang *et al.*, 2007; Lai *et al.*, 2008; Scharf *et al.*, 2010).

Parental effects have been regarded as an important source of evolutionary diversification. Parental effects can alter the nature and pace of ecological and evolutionary change, potentially permitting organisms to adapt quickly in a rapidly changing environment (e.g., Räsänen & Kruuk, 2007; Badyaev & Uller, 2009; Kilner *et al.*, 2015).

The cabbage beetle, *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae), is a serious pest of crucifers in the mountainous areas of Jiangxi Province. In the field, there are two distinct infestation peaks: the single spring generation between March and April and the three autumn generations between September and November, which undergo aestivating and hibernating imaginal diapause in the soil, respectively (Xue *et al.*, 2002a). This cabbage beetle shows a short-day response (develops in response to short day length and enters diapause in response to long day length) when the mean daily temperature is  $\geq 20^{\circ}\text{C}$ . All individuals enter diapause when the mean daily temperature is  $\leq 20^{\circ}\text{C}$  regardless of the photoperiod. High temperatures strongly weaken the diapause-inducing effects of long day lengths (Xue *et al.*, 2002b). The female parent exhibits a greater effect on diapause initiation than the male parent (Chen *et al.*, 2014). Previous studies of *C. bowringi* have revealed that parental physiological age, mating pattern, diapause duration, geographical origin and host plant had a significant influence on the incidence of diapause in their progeny (Yang *et al.*, 2007; Lai *et al.*, 2008). The present study aimed to detect how the photoperiod and temperature experienced by parents of *C. bowringi* influence the incidence of diapause in their progeny.

## Materials and methods

### Experimental animal

Diapausing adults of *C. bowringi* were collected from the field in autumn in Xiu-Shui County, Jiangxi Province, PR China ( $29^{\circ}1' \text{N}$ ,  $114^{\circ}4' \text{E}$ ) and then transferred to large glass bottles (diameter: 50 cm; height: 180 cm) containing soil to burrow for dormancy. The bottles were placed outdoors at Jiangxi Agricultural University, Nanchang, Jiangxi Province

( $28^{\circ}46' \text{N}$ ,  $115^{\circ}59' \text{E}$ ). When post-diapause adults emerged from the soil, they were transferred in pairs to Petri dishes for mating and oviposition. The eggs were collected every day at approximately 5:00 pm, and newly hatched larvae were transferred to plastic rearing boxes ( $17.5 \times 12.5 \times 6.5 \text{ cm}^3$ ). Each box contained at least 60 individuals. In all experiments, each treatment was replicated three to five times. Larvae were fed with mature leaves of radish (*Raphanus sativus* var. *longipinnatus*) until the adults entered diapause. The diapausing adults were transferred to large glass bottles containing soil to burrow for dormancy.

### Experimental designs

To examine the effects of the photoperiod and temperature experienced by parents on the incidence of diapause in their progeny, three experiments were conducted. The first experiment spanned 2 years. The parental larval generation produced by post-diapause adults was reared under different photoperiods (LD 10:14, LD 11:13, LD 12:12, LD 13:11, LD 14:10, LD 15:9 and LD 16:8 h) at  $25^{\circ}\text{C}$  (a diapause-preventing temperature) and produced non-diapausing and diapausing parents. The incidence of diapause in the progeny from non-diapausing and diapausing parents was evaluated under LD 12:12 at  $25^{\circ}\text{C}$  both in the current spring and in the next spring (fig. 1a).

The second experiment also spanned 2 years. The parental larval generation produced by post-diapause adults was reared under LD 12:12 at 22, 25, 28 and  $30^{\circ}\text{C}$  and produced non-diapausing and diapausing parents. Similar to the first experiment, the incidence of diapause in the progeny from non-diapausing and diapausing parents was evaluated under LD 12:12 at  $25^{\circ}\text{C}$  both in the current spring and in the following spring (fig. 1b).

In the third experiment, naturally diapausing adults (parental generation) were maintained at a constant temperature of  $9^{\circ}\text{C}$  (an overwintering temperature),  $28^{\circ}\text{C}$  (an aestivating temperature) or the mean daily summer temperature of  $27.84^{\circ}\text{C}$  for 90 days under continuous darkness conditions. Then, the incidence of diapause in the progeny from these post-diapause parents was evaluated under different photoperiods (LD 10:14, LD 11:13, LD 12:12, LD 13:11, LD 14:10 and LD 15:9 h) at  $25^{\circ}\text{C}$  (fig. 1c).

It should be mentioned that diapausing parents that experienced different photoperiods and temperatures emerged from the soil the following spring (early March) at the same time.

### Diapause identification

All diapausing adults show a digging behaviour and burrow into the soil after 4–6 days at 25 or  $30^{\circ}\text{C}$  and after 7–9 days at  $20^{\circ}\text{C}$  (Xue *et al.*, 2002b).

### Statistical analyses

Data on parental diapause incidence under different photoperiods and temperatures and diapause incidence data for progeny from non-diapausing and diapausing parents were analysed using analysis of variance (ANOVA) followed by a Bonferroni multiple comparisons test (STATA 9.0 software). The percentage data for diapause incidence were arcsine square root transformed before analysis. Data on the incidence of diapause in progeny were compared by two-way ANOVA with the photoperiod or temperature experienced by parents,

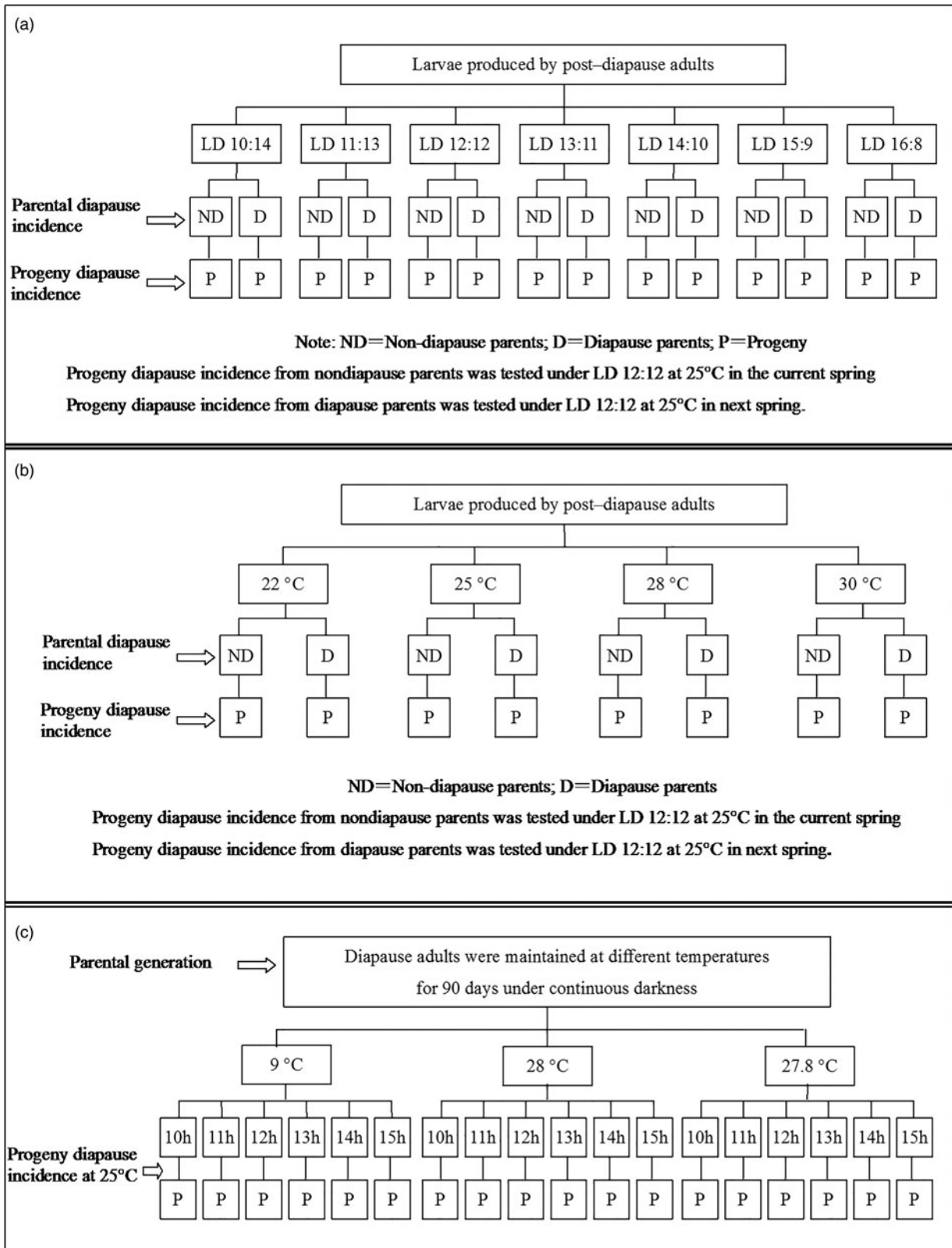


Fig. 1. Experimental design used to test the effects of photoperiod and temperature experienced by *Colaphellus bowringi* parents on the incidence of diapause among their progeny. (a) Effect of photoperiod experienced by parents on diapause incidence in their progeny; (b) effect of temperature experienced by parents on diapause incidence in their progeny; (c) effect of temperature experienced by diapausing parents during diapause period on diapause incidence among their progeny.

parent status (diapausing or non-diapausing) and their interaction as explanatory variables. Different treatment effects were compared using a Bonferroni test after ANOVA with a significance level of  $P = 0.05$  for all comparisons.

## Results

### *Effect of photoperiod experienced by parents on diapause incidence among progeny*

The incidence of diapause among progeny was significantly affected by the photoperiod experienced by parents ( $F = 29.71$ ,  $df = 6$ ,  $P = 0.0000$ ), parental status (diapausing or

non-diapausing) ( $F = 28.12$ ,  $df = 1$ ,  $P = 0.0000$ ) and their interaction ( $F = 2.85$ ,  $df = 6$ ,  $P = 0.0272$ ) (fig. 2, Table S1).

When parents were exposed to different photoperiods, the parental diapause incidence gradually decreased from LD 10:14 to LD 12:12 (from 50.7 to 43.8%) and gradually increased from LD 12:12 to LD 16:8 (from 49.6 to 82.6%) (fig. 2a). There were significant differences among photoperiods in parental diapause incidence ( $F = 53.03$ ,  $df = 6, 14$ ,  $P < 0.001$ ). However, the incidence of diapause among the progeny from both non-diapausing and diapausing parents showed a gradual increase when the parental rearing photoperiod changed from LD 10:14 to LD 12:12 (from 26.7 to 36.4% when produced by non-diapausing parents and from 35.6 to 46.3% when produced by

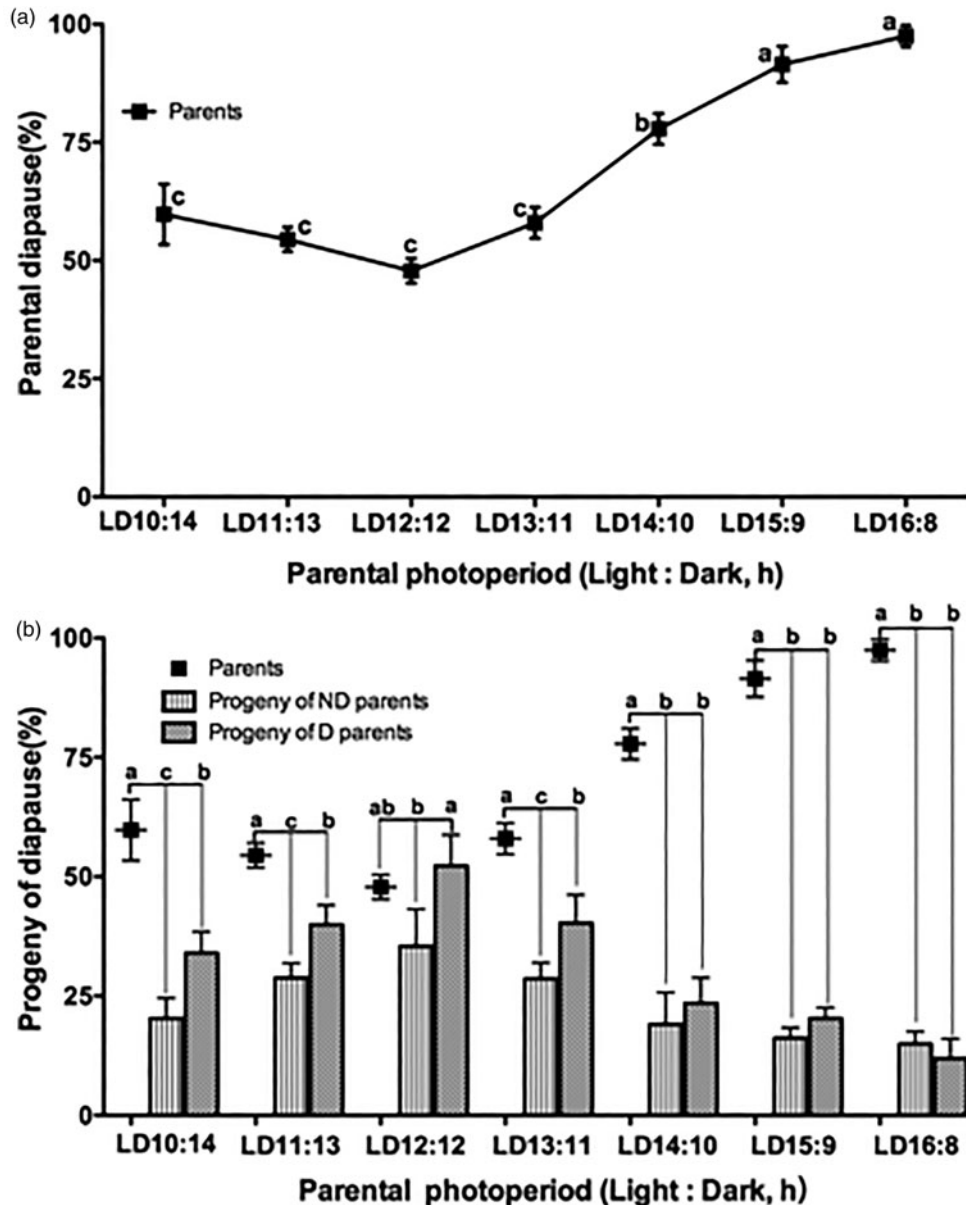


Fig. 2. Parental diapause incidence in *Colaphellus bowringi* when parental larvae were reared under different photoperiods at 25°C (a). Diapause incidence in progeny under LD 12:12 at 25°C (b) when their non-diapausing (ND) and diapausing (D) parents experienced different photoperiods. Error bars indicate SD. Values with different lowercase letters are significantly different for different photoperiods and types at the 0.05 level ( $n = 205\text{--}235$  for each treatment).

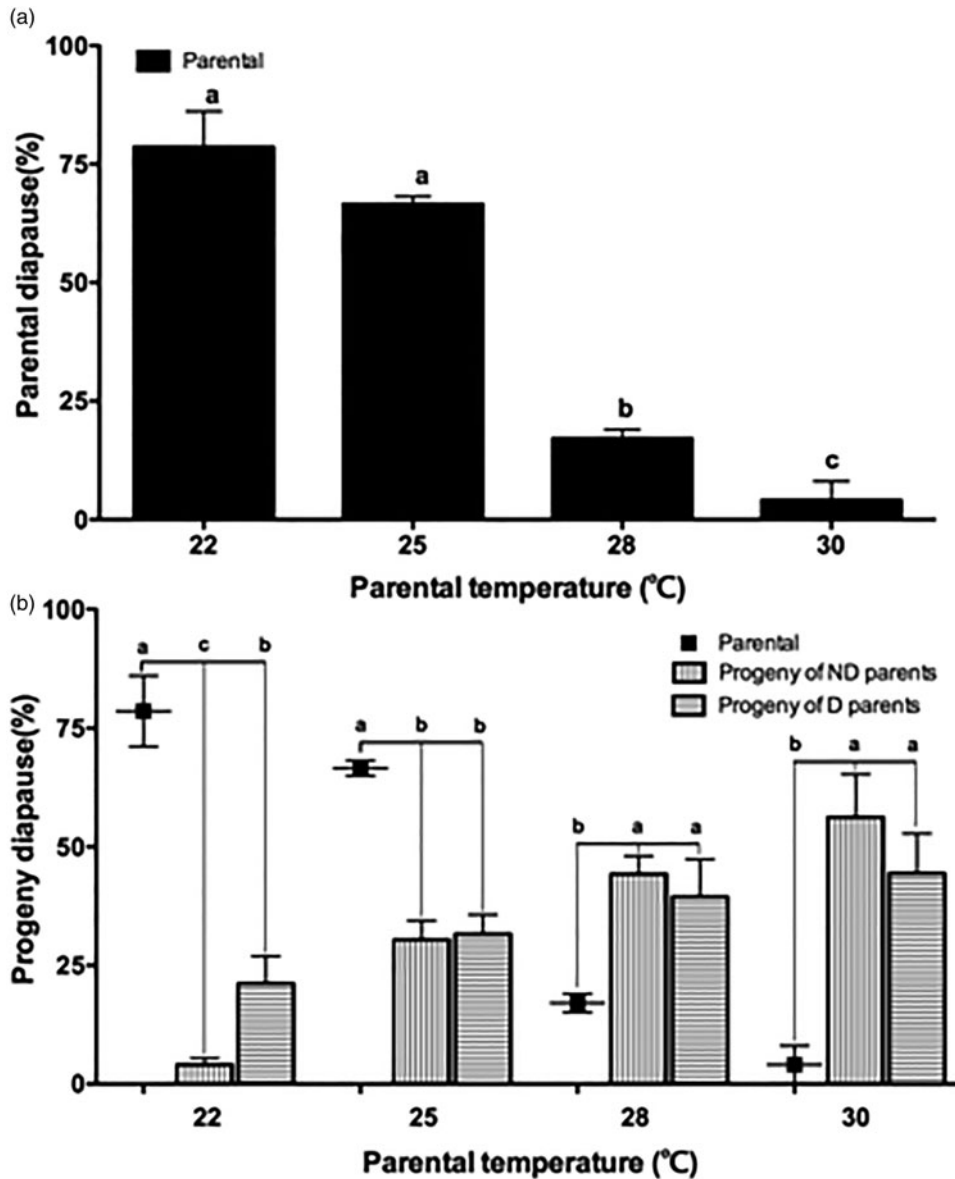


Fig. 3. Parental diapause incidence of *Colaphellus bowringi* when parental larvae were reared under LD 12:12 at 22, 25, 28, and 30°C (a). Diapause incidence among under LD 12:12 at 25°C when their non-diapausing (ND) and diapausing (D) parents experienced different temperatures (b). Error bars indicate SD. Values with different lowercase letters are significantly different at the 0.05 level ( $n = 198$ – $225$  for each treatment).

diapausing parents) and a gradual decrease when the parental rearing photoperiod changed from LD 12:12 to LD 16:8 (from 32.3 to 22.7% when produced by non-diapausing parents and from 29.3.3 to 20.0% when produced by diapausing parents) (fig. 2b). This result shows that the incidence of diapause among progeny was exactly opposite to that of their parents, i.e., the higher the parental diapause incidence, the lower the diapause incidence among their progeny. There were significant differences in diapause incidence among progeny (for non-diapausing progeny:  $F = 8.04$ ,  $df = 6,14$ ,  $P < 0.001$ ; for diapausing progeny:  $F = 24.69$ ,  $df = 6,14$ ,  $P < 0.001$ ) (fig. 2b). The incidence of diapause among progeny from diapausing parents was generally higher than that among progeny from non-

diapausing parents, with significant differences when their parents experienced the shorter photoperiods from LD 10:14 to LD 13:11 ( $P < 0.05$ ).

#### Effect of temperature experienced by parents on the incidence of diapause among progeny

The diapause incidence among progeny was significantly affected by the temperature experienced by parents ( $F = 54.36$ ,  $df = 5$ ,  $P = 0.0000$ ) and by the interaction between the temperature experienced by parents and parental status (diapausing or non-diapausing) ( $F = 10.50$ ,  $df = 3$ ,  $P = 0.0005$ ) (fig. 3, Table S2).

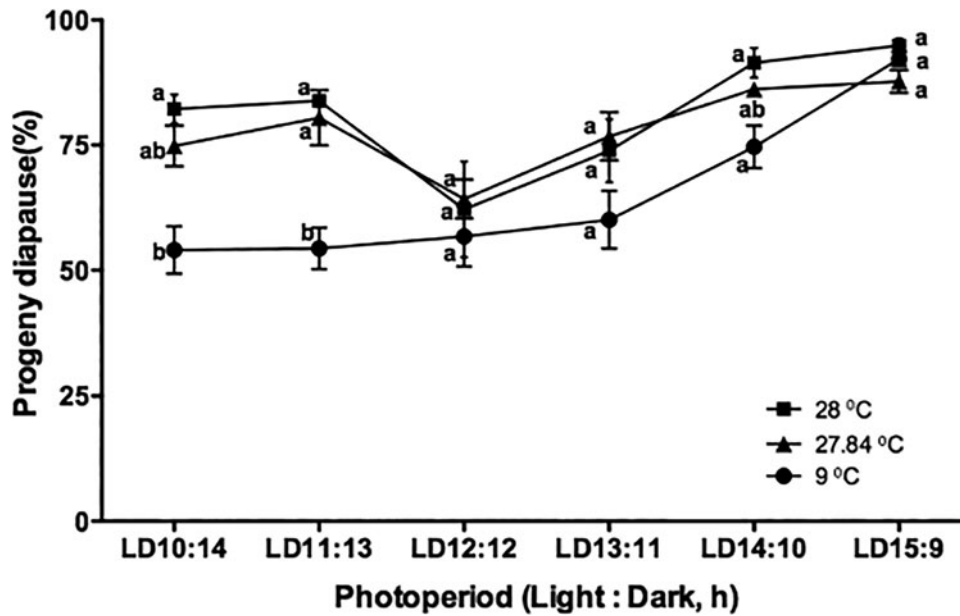


Fig. 4. Diapause incidence of *Colophellus bowringi* progeny under different photoperiods at 25°C when their diapausing parents were maintained at the constant temperatures of 9 and 28°C and under natural conditions, with a daily mean temperature of 27.84°C, under continuous darkness for 90 days. Error bars indicate SD. Values with different lowercase letters are significantly different for the same photoperiod at the 0.05 level ( $n = 178\text{--}347$  for each point).

The rearing temperature had a significant influence on parental diapause incidence ( $F = 74.35$ ,  $df = 3,8$ ,  $P < 0.001$ ), which decreased gradually (from 62.7 to 9.5%) with increasing rearing temperature from 22 to 30°C (fig. 3a). However, the diapause incidence in progeny from both non-diapausing and diapausing parents showed a significant increase (from 11.6 to 48.6% when produced by non-diapause parents and from 27.3 to 41.7% when produced by diapause parents) with increasing parental rearing temperature (for non-diapausing progeny:  $F = 74.02$ ,  $df = 3,8$ ,  $P < 0.001$ ; for diapausing progeny:  $F = 7.01$ ,  $df = 3,8$ ,  $P < 0.001$ ) (fig. 3b). This indicates that the incidence of diapause among progeny was exactly opposite to that of their parents (fig. 3b). The incidence of diapause in progeny from diapausing parents was significantly higher than that in progeny from non-diapausing parents when their parents were reared at 22°C ( $P < 0.05$ ) but lower when their parents were reared at the higher temperatures of 28 and 30°C without showing significant differences ( $P > 0.05$ ).

#### Effect of temperature experienced by diapausing parents on diapause incidence among progeny

The incidence of diapause among progeny was significantly affected by photoperiod ( $F = 21.10$ ,  $df = 5$ ,  $P = 0.0000$ ), temperature experienced by parents ( $F = 22.53$ ,  $df = 2$ ,  $P = 0.0000$ ) and their interaction ( $F = 2.24$ ,  $df = 10$ ,  $P = 0.0353$ ) (fig. 4, Table S3).

By maintaining the diapausing adults at different temperatures and then exposing their progeny to different photoperiods, the incidence of diapause among their progeny significantly changed with increasing photoperiod under all temperatures experienced by the parents (for the constant temperature of 9°C:  $F = 14.98$ ,  $df = 5,12$ ,  $P < 0.001$ ; for the constant temperature of 28°C:  $F = 5.72$ ,  $df = 5,12$ ,  $P < 0.05$ ; for the daily mean temperature of 27.84°C:  $F = 4.76$ ,  $df = 5,12$ ,  $P < 0.05$ )

(fig. 4). The incidence of diapause among progeny was higher when their parents experienced high temperatures (28 and 27.84°C) than when they experienced low temperatures (9°C), with significant differences for the short day lengths of 10 and 11 h ( $P < 0.05$ ). However, the diapause incidence among progeny did not significantly differ between 28 and 27.84°C ( $P > 0.05$ ).

## Discussion

To our knowledge, few studies have tested parental effects on diapause under a wide range of photoperiodic and temperature conditions, likely because of the difficulty and time required to collect the data. The results we present here reveal how the photoperiod and temperature experienced by parents affect the incidence of diapause in their progeny.

In the parental photoperiodic experiment, the parental generation of *C. bowringi* exhibited a short-day response (fig. 2a), in support of previous research findings (Xue *et al.*, 2002b). In the parental temperature experiment, we observed that parental diapause incidence significantly decreased with increasing rearing temperature (fig. 3a), which is consistent with previous research findings showing that the higher the temperature, the stronger the influence of short days (Xue *et al.*, 2002b). Interestingly, in both experiments, the incidence of diapause among progeny was exactly opposite to that of their parents, i.e., the higher the parental diapause incidence, the lower the progeny diapause incidence (figs 2b and 3b). We believe this to be the first report on the negative relationship of diapause incidence between the parental generation and the progeny generation. This phenomenon may be explained as follows. When exposed to a diapause-preventing photoperiod or temperature, only a small proportion of individuals in the parental generation that have a genetically strong tendency to enter diapause become diapausing adults. Therefore, the

incidence of diapause among their progeny should be accordingly high when they are reared under the same conditions. When exposed to a diapause-inducing photoperiod or temperature, most individuals in the parental generation that have a genetically weak tendency to enter diapause become diapausing adults. Therefore, the incidence of diapause among their progeny should be accordingly low when they are reared under the same conditions. This case may demonstrate frequency-dependent selection. This negative relationship in diapause incidence between the parental generation and the progeny generation in *C. bowringi* may provide useful information for analysing field population dynamics.

In the two experiments, the post-diapause adults produced both non-diapausing and diapausing parents under different photoperiods and different temperatures. We found that the diapause incidence among progeny produced by non-diapausing parents was significantly lower than that among progeny produced by diapausing parents when the parents were reared under the day lengths of 10, 11, 12 and 13 h (diapause-preventing day lengths), whereas the incidence of diapause among progeny produced by non-diapausing parents was higher than that among progeny produced by diapausing parents when the parents were reared at the higher temperatures of 28 and 30°C (diapause-preventing temperatures). This suggests that the photoperiodic and temperature controls of diapause inductions in *C. bowringi* may have different genetic bases (Xue *et al.*, 2002b).

In the third experiment, it is notable that the diapause-maintaining temperatures that diapausing parents experienced had a significant effect on the incidence of diapause in progeny, with the incidence of diapause in progeny being higher when their parents experienced high temperatures than when their parents experienced the lower temperature. Therefore, exposure to diapause-maintaining temperatures in the parental generation is the principal factor that may induce distinct physiological preparations (Danks, 1991; Denlinger, 1991) and result in differences in diapause incidence in the parental generation and progeny generation. Further study of the physiology of this beetle may aid in the understanding of these phenomena.

Previous studies have demonstrated that *C. bowringi* is a species composed of several types of individuals with different diapause potentials, showing distinct variation in diapause induction and diapause duration among individuals (Xue & Kallenborn, 1993; Xue *et al.*, 2002a; Wei *et al.*, 2010). In the three present experiments related to diapause induction, total emergence was never achieved (figs 2a and 3a and 4), and some individuals always entered diapause regardless of the rearing photoperiod and temperature, further suggesting that the onset of diapause in these individuals is independent of the environment. The adaptive advantage of such a reproductive strategy is that it prevents the situation in which individuals have 'placed all their eggs into one basket' and subjects them all simultaneously to the possibility of meeting unfavourable environmental conditions (Waldbauer, 1978; Wise, 1980; Xue & Kallenborn, 1993). Thus, their chances of survival are increased.

### Supplementary material

The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485318000019>

### Acknowledgements

The authors thank Dr Shaohui Wu from the Department of Entomology at Rutgers University (New Brunswick, NJ) for providing critical comments and polishing the language of the manuscript. The research was supported by a grant from the National Natural Science Foundation of the People's Republic of China (31560608).

### References

- Attisano, A. & Kilner, R.M. (2015) Parental effects and flight behaviour in the burying beetle *Nicrophorus vespilloides*. *Animal Behaviour* **108**, 91–100.
- Badyaev, A.V. & Uller, T. (2009) Parental effects in ecology and evolution: mechanisms, processes and implications. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1169–1177.
- Bonduriansky, R. & Day, T. (2009) Nongenetic inheritance and its evolutionary implications. *Annual Review of Ecology, Evolution, and Systematics* **40**, 103–125.
- Burgess, S.C. & Marshall, D.J. (2014) Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately. *Oikos* **123**, 769–776.
- Chen, C., Xiao, L., He, H.M., Xu, J. & Xue, F.S. (2014) A genetic analysis of diapause in crosses of a southern and a northern strain of the cabbage beetle *Colaphellus bowringi* (Coleoptera: chrysomelidae). *Bulletin of Entomological Research* **104**, 586–591.
- Danks, H.V. (1987) Insect dormancy: an ecological perspective. Biological survey of Canada (Terrestrial Arthropods), Monograph Series No. 1.
- Danks, H.V. (1991) Winter habitats and ecological adaptations for winter survival. pp. 231–259 in Lee, R.E. Jr., Denlinger, D.L. (Eds) *Insects at Low Temperature*. New York, Chapman & Hall.
- Denlinger, D.L. (1991) Relationship between cold hardiness and diapause. pp. 174–189 in Lee, R.E. Jr., Denlinger, D.L. (Eds) *Insects at Low Temperature*. New York, Chapman & Hall.
- Fox, C.W. & Mousseau, T.A. (1998) Maternal effects as adaptations for transgenerational plasticity in insects. pp. 159–177 in Mousseau, T.A. and Fox, C.W. (Eds) *Maternal Effects as Adaptations*. New York, Oxford University Press.
- Fox, C.W., Thakar, M.S. & Mousseau, T.A. (1997) Egg size plasticity in a seed beetle: an adaptive maternal effect. *American Naturalist* **149**, 149–163.
- Gould, F. (1988) Stress specificity of maternal effects in *Heliothis virescens* (Boddie) (Lepidoptera: Noctuidae) larvae. *Memoirs of the Entomological Society of Canada* **146**, 191–197.
- Huestis, D.L. & Marshall, J.L. (2006) Interaction between maternal effects and temperature affects diapause occurrence in the cricket *Allonemobius socius*. *Oecologia* **146**, 513–520.
- Kilner, R.M., Boncoraglio, G., Henshaw, J.M., Benjamin, J.M., Jarrett, B.J.M., Gasperin, O.D., Attisano, A. & Kokko, H. (2015) Parental effects alter the adaptive value of an adult behavioural trait. *eLife* **4**, e07340.
- Lai, X.T., Yang, D., Wu, S.H., Zhu, X.F. & Xue, F.S. (2008) Diapause incidence of progeny in relation to parental geographic origin, host plants, and rearing density in the cabbage beetle, *Colaphellus bowringi*. *Entomologia Experimentalis et Applicata* **129**, 117–123.
- Mousseau, T.A. & Dingle, H. (1991) Maternal effects in insects: examples, constraints, and geographic variation. *The Unity of Evolutionary Biology: Proceedings of the ICSEB IV Meeting, Portland 1991*, 745–761.
- Mousseau, T.A. & Fox, C.W. (1998) The adaptive significance of maternal effects. *Trends in Ecology & Evolution* **13**, 403–407.

- Oku, K., Yano, S. & Takafuji, A.** (2003) Different maternal effects on diapause induction of tetranychid mites, *Tetranychus urticae* and *T. kanzawai* (Acari: Tetranychidae). *Applied Entomology and Zoology* **38**, 267–270.
- Räsänen, K. & Kruuk, L.E.B.** (2007) Maternal effects and evolution at ecological time-scales. *Functional Ecology* **21**, 408–421.
- Scharf, I., Bauerfeind, S.S., Wolf U. Blanckenhorn, W.U. & Schäfer, M.A.** (2010) Effects of maternal and offspring environmental conditions on growth, development and diapause in latitudinal yellow dung fly populations. *Climate Research* **43**, 115–125.
- Simpson, S.J. & Miller, G.A.** (2007) Maternal effects on phase characteristics in the desert locust, *Schistocerca gregaria*: a review of current understanding. *Journal of Insect Physiology* **53**, 869–876.
- Tachibana, S.I. & Numata, H.** (2004) Parental and direct effects of photoperiod and temperature on the induction of larval diapause in the blow fly *Lucilia sericata*. *Physiological Entomology* **29**, 39–44.
- Trauer, U. & Hilker, M.** (2013) Parental legacy in insects: variation of transgenerational immune priming during offspring development. *PLoS ONE* **8**, e63392.
- Valtonen, T.M., Kangassalo, K., Pälkki, M. & Rantala, M.J.** (2012) Transgenerational effects of parental larval diet on offspring development time, adult body size and pathogen resistance in *Drosophila melanogaster*. *PLoS ONE* **7**, e31611.
- Vinogradova, E.B.** (1974) The pattern of reactivation of diapausing larvae in the blowfly *Calliphora vicina*. *Journal of Insect Physiology* **20**, 2487–2496.
- Waldbauer, G.P.** (1978) Phonological adaptation and the poly-modal emergence patterns of insects. pp. 127–144 in Dingle, H. (Ed.) *Evolution of Insect Migration and Diapause*. New York, Heidelberg, Berlin, Springer.
- Wei, X.T., Zhou, Y.C., Xiao, H.J., Wang, X.P. & Xue, F.S.** (2010) Relationship between the natural duration of diapause and post-diapause reproduction in the cabbage beetle, *Colaphellus bowringi* (Coleoptera: Chrysomelidae). *European Journal of Entomology* **107**, 337–340.
- Wise, E.J.** (1980) Seasonality distribution and life histories of Ephemeroptera in a Northumbrian river. *Freshwater Biology* **10**, 101–111.
- Xue, F.S. & Kallenborn, H.G.** (1993) Dispersive breeding in agricultural pest insects and its adaptive significance. *Journal of Applied Entomology* **116**, 170–177.
- Xue, F.S., Li, A.Q., Zhu, X.F., Gui, A.L., Jiang, P.L. & Liu, X.F.** (2002a) Diversity in life history of the leaf beetle, *Colaphellus bowringi* Baly. *Acta Entomologica Sinica* **45**, 494–498, (in Chinese).
- Xue, F.S., Spieth, H.R., Li, A.Q. & Hua, A.** (2002b) The role of photoperiod and temperature in determination of summer and winter diapause in the cabbage beetle, *Colaphellus bowringi* (Coleoptera: Chrysomelidae). *Journal of Insect Physiology* **48**, 279–286.
- Yang, D., Lai, X.T., Sun, L. & Xue, F.S.** (2007) Parental effects: physiological age, mating pattern, and diapause duration on diapause incidence of progeny in the cabbage beetle, *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae). *Journal of Insect Physiology* **53**, 900–908.