

Effects of diapause duration on future reproduction in the cabbage beetle, *Colaphellus bowringi*: positive or negative?

XIAO-PING WANG^{1,3}, FANG-SEN XUE², AI HUA² and FENG GE¹

¹State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, ²Institute of Entomology, Jiangxi Agricultural University, Nanchang and ³College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, P. R. China.

Abstract. Cabbage beetles, *Colaphellus bowringi*, undergoing an imaginal summer and winter diapause in the soil, show a great difference in diapause duration (from several months to more than 3 years) under natural conditions. The effects of diapause duration on future reproduction in the beetle are investigated at 25 °C with an LD 14 : 10 h photoperiod and under natural conditions. The fecundity of postdiapause adults with a short diapause of 5 months and nondiapause adults is similar, showing that a short diapause has no effect on reproduction, whereas the longevity of postdiapause adults with a short diapause of 5 months is significantly shorter than nondiapause adults, showing that a short diapause has a negative effect on longevity. The mean total egg production per female and longevities of postdiapause adults with long diapause periods of 16, 22, 29 and 34 months are similar to nondiapause adults, but the mean daily egg production per female is significantly higher than nondiapause adults, showing that extended diapause has a positive effect on postdiapause reproduction. The offspring of postdiapause parents require a relatively shorter time for egg development compared with the offspring of nondiapause parents, showing that diapause has a positive effect on their offspring's performance. However, there are no significant differences among offspring performance in terms of survival, adult longevity, mean egg production per female and mean daily egg production per female.

Key words. *Colaphellus bowringi*, developmental time, diapause duration, fecundity, longevity, offspring.

Introduction

Diapause is defined as a neurohormonally mediated, dynamic state of low metabolic activity. Associated with diapause is reduced morphogenesis, increased resistance to environmental extremes, and altered or reduced behavioural activity (Tauber & Kyriacou, 2001). The benefits of diapause are a clear-cut-synchronization of the active stages with a

favourable season and survival of adverse conditions (Masaki, 1980; Tauber *et al.*, 1986; Danks, 1987). Diapause also permits the insects to breed dispersively at different times throughout a reproductive season so that their chances of survival are greatly enhanced (Xue & Kallenborn, 1993). However, in many species, individuals that pass a diapause are less fecund than nondiapause individuals and also may have a shorter adult life (Danks, 1987; Gebre-Amlak, 1989; Van Houten *et al.*, 1991; Ishihara & Shimada, 1995; Kroon & Veenendaal, 1998; Ellers & Van Alphen, 2002). Therefore, diapause is generally believed to be costly. Such costs are usually described in the form of the existence of trade-offs between diapause duration and other life-history traits (Bradshaw *et al.*, 1998; Saunders *et al.*, 1999).

Correspondence: Feng Ge, Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, People's Republic of China. Tel.: +86 10 6256 5689; fax.: +86 10 6256 5689; e-mail: gef@panda.ioz.ac.cn

The cabbage beetle, *Colaphellus bowringi* Baly, undergoes an imaginal summer and winter diapause in the soil. Temperature and photoperiod are two major diapause induction factors in this species. Its photoperiodic response is highly dependent upon temperature and all adults enter diapause at ≤ 20 °C regardless of day length. The diapause-averting influences of short day lengths are expressed only at high temperatures above 20 °C (Xue *et al.*, 2002a, b). Thermoperiod also has an important role in determination of diapause induction (Wang *et al.*, 2004). The life history of this beetle is complex. Adults that enter summer and winter diapause at the same time, or the same season, show a great inter-individual difference in diapause duration (from several months to more than 3 years). For example, in a group of 588 adults that began diapause in late November 1998, 78.7% emerged from the soil in the next spring and autumn; 12.8% in the third spring and autumn; 6.5% in the fourth spring and autumn; and 2.0% in the fifth spring and autumn (Xue *et al.*, 2002a). Thus, some individuals take more than 1 year to produce one generation; some are biovoltine (i.e. one generation in spring, another in autumn); and some are multivoltine (i.e. one generation in spring, two or three generation in autumn). Furthermore, postdiapause adults with different diapause durations can emerge from the soil at the same time. Accordingly, this species provides an excellent experimental model to examine the effects of diapause duration on future reproduction.

In the present study, the differences of fecundity and longevity between postdiapause adults with different diapause durations and nondiapause adults are compared, and their offspring's performance is also investigated.

Materials and methods

Life-history traits of postdiapause and nondiapause adults

All postdiapause adults came from those naturally diapausing adults that were collected in the field (29°1'N, 114°4'E) in different years (from November 1999 to April 2002) and were transferred to large glass bottles containing soil and kept under natural conditions. All the postdiapause adults chosen for this study emerged from the soil in late September 2002. Thus, the postdiapause adults had experienced a duration of diapause of approximately 5, 9, 16, 22, 29 and 34 months, respectively. The nondiapause adults (with a diapause duration of '0'), produced by the autumn generation, also emerged in late September 2002.

The postdiapause and nondiapause adults were paired in Petri dishes (9.0 cm diameter). One female-male pair as one replicate was reared in one Petri dish with a piece of wet filter paper and provided with fresh radish leaves, *Raphanus sativus*. These paired adults were divided into two groups. One group was kept in an illuminating incubator (LRH-250-GS; Guangzhou, China) at 25 ± 1 °C under an LD 14 : 10 h photoperiod (light intensity during the photophase was approximately 1.97 W m^{-2}). Another group

was kept under natural conditions (the daily mean temperature was approximately 18.9 °C from 18 September to 1 December). The numbers kept in incubator were 19 pairs for nondiapause adults, 43 pairs with a diapause duration of 5 months, 55 pairs with a diapause duration of 9 months, 10 pairs with a diapause duration of 16 months, 29 pairs with a diapause duration of 22 months, 13 pairs with a diapause duration of 29 months, and 23 pairs with a diapause duration of 34 months. The numbers kept under natural conditions were 35 pairs for nondiapause adults, 44 pairs with a diapause duration of 5 months, 46 pairs with a diapause duration of 9 months, 44 pairs with a diapause duration of 22 months, and 40 pairs with a diapause duration of 34 months. Date of the first egg(s), the total number of eggs per female and survival of males and females were recorded daily. After every observation, radish leaves were replaced with fresh leaves. The experiments were terminated when all of the males and females died.

Performance of offspring produced by non- and postdiapause adults

The performance of offspring produced by non- and postdiapause adults reared under natural conditions was investigated. The performance of offspring included egg hatch, developmental time in different stages, survival of larvae and pupae, and fecundity and longevity of nondiapause adults.

In the experiment for egg hatch, each treatment contained four replicates each with 100 eggs. For the observations of survival of larvae and pupae, each treatment contained three replicates each with at least 80 individuals. Approximately 15 pairs of nondiapause adults in each treatment were used to test for fecundity and longevity. The beetles were fed on fresh radish leaves.

Experiments were carried out in incubators at 25 °C under an LD 12 : 12 h photoperiod. Temperature variation and light intensity in the incubators was the same as described above.

Statistical analysis

Using SPSS (SPSS Inc., Chicago, Illinois), some of the data were analysed by one-way analysis of variance (ANOVA) and means were compared using a Tukey test at $P = 0.05$. Data with respect to egg hatching, survival of larvae and pupae were arcsine square-root transformed prior to analysis.

Results

Life-history traits of postdiapause and nondiapause adults

Pre-oviposition period The pre-oviposition period of nondiapause females was significantly longer than that of

postdiapause females at 25 °C under an LD 14 : 10 h photoperiod (Fig. 1a) and under natural conditions (the mean daily temperature of first 5 days was 24.3 °C) (Fig. 1b). The preoviposition periods among postdiapause females were similar except for a diapause duration of 34 months under natural conditions (Fig. 1b).

Reproductive period The reproductive period of nondiapause females was significantly longer than that of postdiapause females with a short diapause duration (5 months), but not longer than that of postdiapause females with a longer diapause duration (16, 22, 29 and 34 months) at 25 °C under an LD 14 : 10 h photoperiod (Fig. 2a) with similar results under natural conditions (Fig. 2b). The reproductive period of females with a diapause duration of 5 months was significantly shorter than females with a longer diapause durations (22–34 months, except for 29 months at 25 °C under an LD 14 : 10 h photoperiod).

Fecundity The mean total egg production per female and mean daily egg production per female of non- and postdiapause female beetles differed significantly at 25 °C under an LD 14 : 10 h photoperiod (d.f. = 6,183, $F = 8.356$, $P < 0.001$, Fig. 3a; d.f. = 6,183, $F = 12.058$, $P < 0.001$, Fig. 4a) and under natural conditions (d.f. = 4,192, $F = 11.402$, $P < 0.001$, Fig. 3b; d.f. = 4,192, $F = 23.453$, $P < 0.001$, Fig. 4b). Trends in

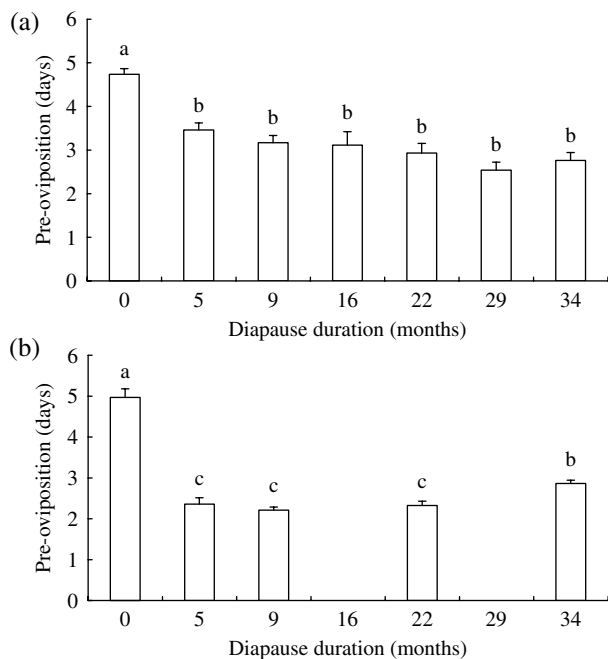


Fig. 1. Pre-oviposition of non- and postdiapause adult female cabbage beetles, *Colaphellus bowringi*, at 25 °C under (a) an LD 14 : 10 h photoperiod and (b) natural conditions. Error bars indicate the SE. Bars with same letter are not significantly different in a Tukey test ($P > 0.05$).

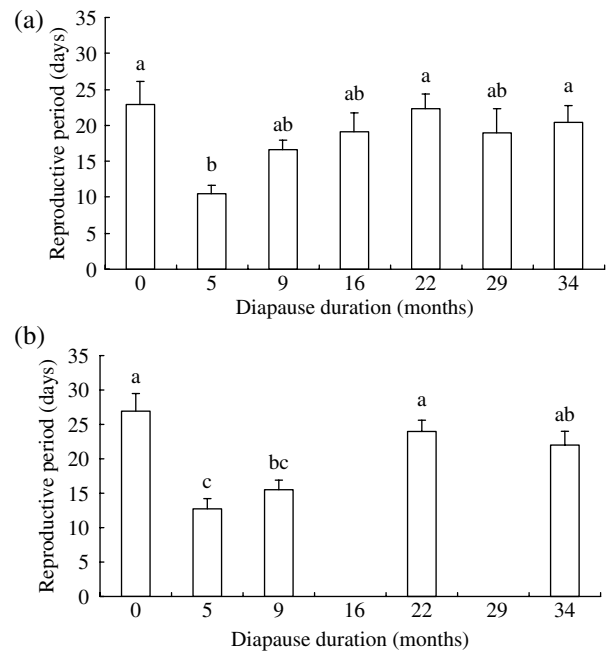


Fig. 2. Reproductive period of non- and postdiapause adult female cabbage beetles, *Colaphellus bowringi*, at 25 °C under (a) an LD 14 : 10 h photoperiod and (b) natural conditions. Error bars indicate the SE. Bars with same letter are not significantly different in a Tukey test ($P > 0.05$).

the data suggest that mean egg production per female of nondiapause females was similar to that of females after 9 months of diapause, and higher than that of females after 5 months of diapause, but was lower than that of females with longer diapause durations (22, 29 and 34 months) (significant only for 22 months under natural conditions; Fig. 3b). Mean daily egg production per female of nondiapause females was significantly lower than that of postdiapause females (except for 5 months at 25 °C under an LD 14 : 10 h photoperiod, Fig. 4a). Among the postdiapause females, mean daily egg production per female of the females with a diapause duration of 5 months was significant lower than that of females with a longer diapause duration of 16, 22, 29 and 34 months (Fig. 4).

Longevity The longevity of non- and postdiapause adults differed significantly at 25 °C under an LD 14 : 10 h photoperiod (d.f. = 6,190, $F = 5.783$, $P < 0.001$ for females; d.f. = 6,190, $F = 11.675$, $P < 0.001$ for males; Fig. 5a) and under natural conditions (d.f. = 4,207, $F = 13.446$, $P < 0.001$ for females; d.f. = 4,204, $F = 36.701$, $P < 0.001$ for males; Fig. 5b). The longevity of nondiapause adults was significantly higher than adults with a shorter diapause duration (5 and 9 months), except for the females with a diapause duration of 9 months at 25 °C under an LD 14 : 10 h photoperiod (Fig. 5a), but similar to adults with a longer diapause duration (16, 22,

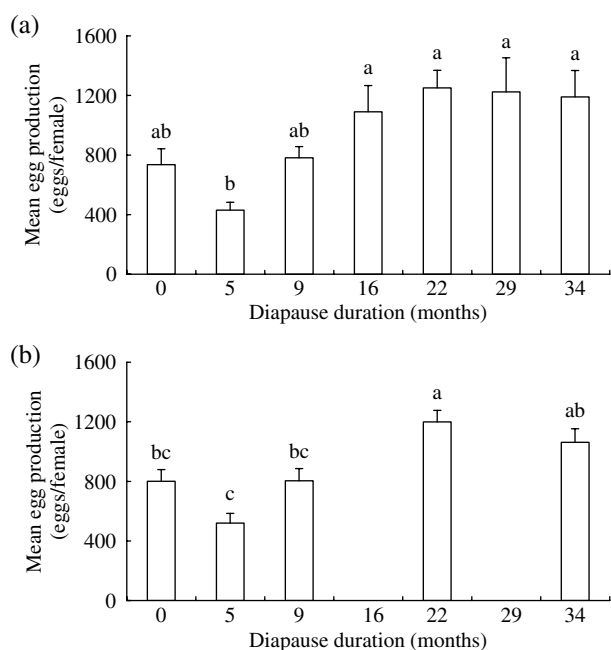


Fig. 3. Mean egg production per female of non- and postdiapause adult female cabbage beetles, *Colaphellus bowringi*, at 25 °C under (a) an LD 14 : 10 h photoperiod and (b) natural conditions. Error bars indicate the SE. Bars with same letter are not significantly different in a Tukey test ($P > 0.05$).

29 and 34 months), except for the males with a diapause duration of approximately 29 months at 25 °C under an LD 14 : 10 h photoperiod (Fig. 5a). Among postdiapause adults, a longer diapause duration was followed by a greater postdiapause longevity, but this plateaued after approximately 22 months.

Performance of offspring produced by non- and postdiapause adults

The performance of offspring produced by the beetles reared under natural conditions was investigated at 25 °C under an LD 12 : 12 h photoperiod. The number of eggs hatching from non- and postdiapause beetles did not differ (d.f. = 4,24, $F = 1.863$, $P = 0.156$ for first replicate; d.f. = 4,24, $F = 1.338$, $P = 0.29$ for second replicate; d.f. = 4,9, $F = 0.591$, $P = 0.685$ for third replicate; and d.f. = 4,11, $F = 1.647$, $P = 0.265$ for fourth replicate) and the percentages ranged from 80.6–98.8% in the four replicates. There was a significant difference in the developmental time of eggs, larvae and pupae produced by different parents. The offspring of nondiapause parents require more time for egg development (Table 1). There was no difference in the survival of larvae (81.7–95.1%; d.f. = 4,14, $F = 3.792$, $P = 0.04$) or pupae (92.5–99.4%; d.f. = 4,14, $F = 0.76$, $P = 0.575$), the female adult longevity of the offspring (39.7–52.9 days; d.f. = 4,68, $F = 1.270$,

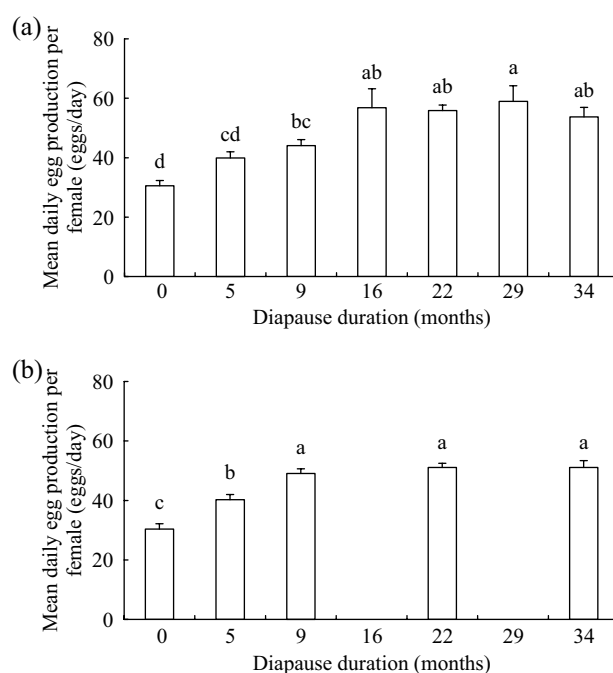


Fig. 4. Mean daily egg production per female of non- and postdiapause adult female cabbage beetles, *Colaphellus bowringi*, at 25 °C under (a) an LD 14 : 10 h photoperiod and (b) natural conditions. Error bars indicate the SE. Bars with same letter are not significantly different in a Tukey test ($P > 0.05$).

$P = 0.291$), the male adult longevity of the offspring (33.5–53.0 days; d.f. = 4,68, $F = 1.744$, $P = 0.151$), and the fecundity of the female adults produced by different parents in terms of mean egg production per female or mean daily egg production per female (Table 1). However, the survival of larvae from nondiapause beetles (81.7%) was lower than that of larvae from the postdiapause beetles (87.2–95.1%).

Discussion

In many insects, there is a negative phenotypic correlation between diapause duration and postdiapause life-history traits. Individuals experiencing diapause have lower fecundity and shorter adult longevity compared with nondiapause individuals for the sawfly *Neodiprion sertifer* (Sullivan & Wallace, 1967); for the sawfly *N. swainei* (Lyons, 1970); for the flesh fly *Sarcophaga bullata* (Denlinger, 1981); for the maize stalk borer *Busseola fusca* (Gebre-Amlak, 1989); for the predatory mite *Amblyseius andersoni* (Van Houten *et al.*, 1991); for the bruchid *Kytorhinus sharpianus* (Ishihara & Shimada, 1995); for the spider mite *Tetranychus urticae* (Kroon & Veenendaal, 1998); for the blow fly *Calliphora vicina* (Saunders, 2000); and for the parasitoid *Asobara tabida* (Ellers & Van Alphen, 2002). In the flesh fly, *S. bullata*, and the sawflies, *N. sertifer* and *N. swainei*, fecundity may be most reduced

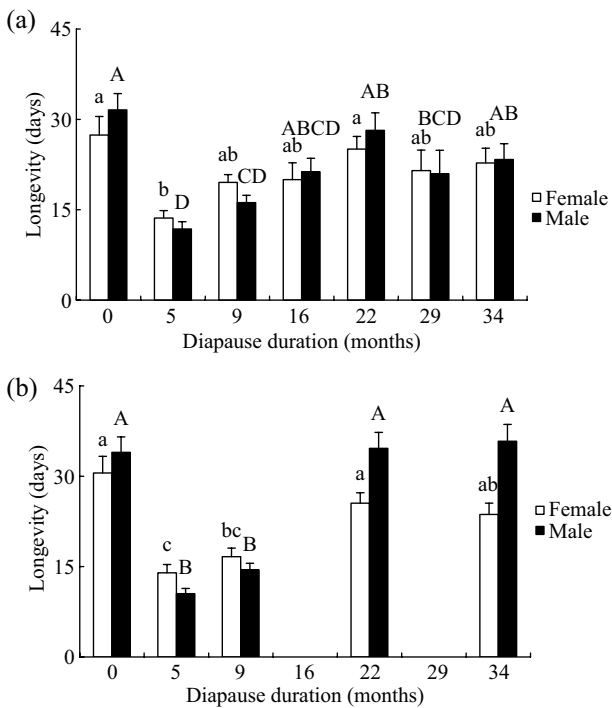


Fig. 5. Mean longevity of non- and postdiapause adult cabbage beetles, *Colaphellus bowringi*, at 25 °C under (a) an LD 14 : 10 h photoperiod and (b) natural conditions. Error bars indicate the SE. Bars with same letter (Capital letter for male and lower-case letter for female, respectively) are not significantly different in a Tukey test ($P > 0.05$).

when they experience longer diapause. Many of these effects are attributed to the use of stored metabolic reserves during the diapause period. However, in a few species, diapause has positive effects on postdiapause reproduction. In four pond skater species, *Gerris buenoi*, *Gerris comatus*, *Gerris pingreensis* and *Limnoporus dissortis*, individuals that have experienced diapause are more fecund than those that develop directly (Spence, 1989). In the grasshopper, *Tetrix undulata*, fecundity of overwintered postdiapause females is higher than that of females that oviposit without overwintering (Poras, 1976). In the corn stalk borer, *Sesamia non-agrioides*, the larval diapause duration is positively correlated with fecundity of the adults (Fantinou *et al.*, 2004). In the Colorado potato beetle, *Leptinotarsa decemlineata*, diapause has no or little effect on total fecundity (Peferoen *et al.*, 1981; Jansson *et al.*, 1989).

The correlations between diapause and postdiapause life-history traits in *C. bowringi* are surprising complicated. The fecundity of the postdiapause adults with a short diapause of 5 months and nondiapause adults is similar, except mean daily egg production per female under natural conditions, showing that a short length diapause has no effect on postdiapause reproduction, whereas the longevity of postdiapause adults with a short diapause period of 5 months is significantly shorter than nondiapause adults, showing that

Table 1. Developmental time of immature stage and fecundity of the offspring produced by non- and postdiapause parents of the cabbage beetles, *Colaphellus bowringi*, at 25 °C under an LD 12 : 12 h photoperiod.

Diapause duration of parents (months)	Egg (days)	Larva (days)	Pupa (days)	Mean total egg production per female (eggs female ⁻¹)	Mean daily egg production per female (eggs female ⁻¹ day ⁻¹)
0	4.58 ± 0.05 (37) ^a	9.00 ± 0.07 (28) ^a	4.07 ± 0.04 (28) ^a	1252.00 ± 136.63 (12) ^a	49.45 ± 3.83 (12) ^b
5	4.31 ± 0.05 (57) ^b	9.02 ± 0.09 (16) ^a	4.02 ± 0.06 (16) ^a	946.72 ± 217.71 (11) ^a	41.10 ± 2.99 (11) ^{a,b}
9	4.26 ± 0.04 (41) ^b	8.87 ± 0.05 (32) ^{a,b}	3.81 ± 0.05 (29) ^b	1532.20 ± 310.52 (10) ^a	46.29 ± 4.93 (10) ^{a,b}
22	4.30 ± 0.04 (30) ^b	8.97 ± 0.06 (29) ^a	4.08 ± 0.04 (29) ^a	1441.55 ± 162.19 (11) ^a	44.44 ± 3.08 (11) ^{a,b}
34	4.14 ± 0.07 (68) ^b	8.68 ± 0.04 (38) ^b	4.12 ± 0.04 (36) ^a	1082.11 ± 235.35 (9) ^a	35.76 ± 5.69 (9) ^b
Results of ANOVA	d.f. = 4,232, $F = 7.201$, $P < 0.001$	d.f. = 4,142, $F = 6.086$, $P < 0.001$	d.f. = 4,137, $F = 7.814$, $P < 0.001$	d.f. = 4,52, $F = 1.273$, $P = 0.294$	d.f. = 4,52, $F = 1.571$, $P = 0.197$

Sample numbers are given in the parentheses. Values (means ± SE) followed by different superscript letters within a column are significantly different in a Tukey test at $P < 0.05$.

a short period diapause has a negative effect on postdiapause longevity. The mean total egg production per female and the longevity of postdiapause adults with a long diapause periods of 16, 22, 29 and 34 months is similar to nondiapause adults, but the mean daily egg production per female is significantly higher than nondiapause adults, showing that a long diapause has a positive effect on reproduction. The results suggest that a short period of diapause has a negative or no affect on reproduction compared with development directly, whereas a longer period of diapause has positive effects.

In a few insect species, diapause can also affect the performance of the offspring (Tauber *et al.*, 1986). For example, in the cotton bollworm, *Heliothis zea*, the offspring of postdiapause parents require more time for egg and larval development than the offspring of nondiapause parents (Akkawi & Scott, 1984). Unlike the cotton bollworm, the offspring of nondiapause parents in the beetle *C. bowringi* require more time for egg development compared with the offspring of postdiapause parents. These results suggest that diapause has positive effects on the performance of offspring, but further studies are needed to verify this.

Although diapause typically slows down the metabolic rate, when the state of diapause is maintained over an extended period, even a low metabolism can draw heavily on energy reserves (Tauber *et al.*, 1986; Ellers & Van Alphen, 2002). However, in a few species, a nutrient effective for reproduction can be accumulated during diapause. For example, the corn stalk borer *S. nonagrioides*, the larval diapause duration is positively correlated with fecundity of the adults. These responses appear to be related to the prolonged dormant period of larvae, which produces heavier larvae (Fantinou *et al.*, 2004). In the cabbage beetle, *C. bowringi*, long diapause may lay down greater metabolic reserves for future reproduction (i.e. long diapause duration has positive effects on the future reproduction). Uptake of a nutrient effective for reproduction is not possible in this beetle during diapause, because the beetles undergo diapause in the soil (Xue *et al.*, 2002a), but accumulation is possible. It is also possible that there is a genetic correlation between diapause duration and postdiapause reproduction. The naturally selected long-diapausing individuals might be the fittest individuals of a population with the ability to accumulate and compensate for the use of stored metabolic reserves during the diapause period.

Acknowledgements

We thank Mr Haijun Xiao and Fujin Liu for assistance with the experiments. The research was partially supported by grants from National Natural Science Foundation of China (30460074), Jiangxi Provincial Key Research Program (20031B0200500), and Innovation Program of Chinese Academy of Sciences (KSCX3-Ioz-04).

References

- Akkawi, M.M. & Scott, D.R. (1984) The effect of age of parents on the progeny of diapaused and nondiapaused *Heliothis zea*. *Entomologia Experimentalis et Applicata*, **35**, 235–239.
- Bradshaw, W.E., Armbruster, P.A. & Holzapfel, C.M. (1998) Fitness consequences of hibernal diapause in the pitcher-plant mosquito, *Wyeomyia smithii*. *Ecology*, **79**, 1458–1462.
- Danks, H.V. (1987) *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada (Terrestrial Arthropods), Canada.
- Denlinger, D.L. (1981) Basis for a skewed sex ratio in diapause-destined flesh flies. *Evolution*, **35**, 1247–1248.
- Ellers, J. & Van Alphen, J.J.M. (2002) A trade-off between diapause duration and fitness in female parasitoids. *Ecological Entomology*, **27**, 279–284.
- Fantinou, A.A., Perdikis, D.C.H. & Zota, K.F. (2004) Reproductive responses to photoperiod and temperature by diapausing and nondiapausing populations of *Sesamia nonagrioides* Lef. (Lepidoptera-Noctuidae). *Physiological Entomology*, **29**, 169–175.
- Gebre-Amlak, A. (1989) Phenology and fecundity of maize stalk borer *Busseola fusca* (Fuller) in Awassa, southern Ethiopia. *Insect Science and its Application*, **10**, 131–137.
- Ishihara, M. & Shimada, M. (1995) Trade-off in allocation of metabolic reserves: effects of diapause on eggs production and adult longevity in a multivoltine bruchid, *Kytorhinus sharpianus*. *Functional Ecology*, **9**, 618–624.
- Jansson, R.K., Zitzman, A.E. Jr & Lashomb, J.H. (1989) Effects of food plant and diapause on adult survival and fecundity of Colorado potato beetle (Coleoptera: Chrysomelidae). *Environmental Entomology*, **18**, 291–297.
- Kroon, A. & Veenendaal, R.L. (1998) Trade-off between diapause and other life-history traits in the spider mite *Tetranychus urticae*. *Ecological Entomology*, **23**, 298–304.
- Lyons, L.A. (1970) Some population features of reproductive capacity in *Neodiprion swainei* (Hymenoptera: Diprionidae). *Canadian Entomologist*, **102**, 68–84.
- Masaki, S. (1980) Summer diapause. *Annual Review of Entomology*, **25**, 1–25.
- Peferoen, M., Huybrechts, R. & De Loof, A. (1981) Longevity and fecundity in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata*, **29**, 321–329.
- Poras, M. (1976) Influence de la photoperiode et de la temperature sur quelques aspects de la diapause imaginaire chez les femelles de *Tetrix undulata* (Sow.) (Orthoptère, Tetrigidae). *Annales de Zoologie Ecologie Animale Genus*, **8**, 373–380.
- Saunders, D.S. (2000) Larval diapause duration and fat metabolism in three geographical strains of the blow fly, *Calliphora vicina*. *Journal of Insect Physiology*, **46**, 509–517.
- Saunders, D.S., Wheeler, I. & Kerr, A. (1999) Survival and reproduction of small blow flies (*Calliphora vicina*; Diptera: Calliphoridae) produced in severely overcrowded short-day larval cultures. *European Journal of Entomology*, **96**, 19–22.
- Spence, J.R. (1989) The habitat templet and life history strategies of pond skaters (Heteroptera: Gerridae): reproductive potential, phenology, and wing dimorphism. *Canadian Journal of Zoology*, **67**, 2432–2447.
- Sullivan, C.R. & Wallace, D.R. (1967) Interaction of temperature and photoperiod in the induction of prolonged diapause in *Neodiprion sertifer*. *Canadian Entomologist*, **99**, 834–850.
- Tauber, E. & Kyriacou, B.P. (2001) Insect photoperiodism and circadian clock models and mechanisms. *Journal of Biology Rhythms*, **16**, 381–390.

- Tauber, M.J., Tauber, C.A. & Masaki, S. (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York, New York.
- Van Houten, Y.M., Bruin, J. & Veerman, A. (1991) Repeated induction and termination of diapause in the predacious mite, *Amblyseius potentillae* (Garman) (Phytoseiidae). *The Acari. Reproduction, Development and Life-History Strategies* (ed. by R. Schuster and P. W. Murphy), pp. 267–275. Chapman & Hall, U.K.
- Wang, X.-P., Xue, F.-S., Ge, F. *et al.* (2004) Effects of thermoperiods on the diapause induction in the cabbage beetle, *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae). *Physiological Entomology*, **29**, 419–425.
- 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. *et al.* (2002a) Diversity in life history of the leaf beetle, *Colaphellus bowringi* Baly. *Acta Entomologica Sinica*, **45**, 494–498 (in Chinese with English abstract).
- 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.

Accepted 12 December 2005

First published online 27 March 2006