Physiological Entomology (2005) **30**, 48–53

Thermal orientation of *Anthonomus pomorum* (Coleoptera: Curculionidae) in early spring

CLAUDIA HAUSMANN, JÖRG SAMIETZ and SILVIA DORN
Institute of Plant Sciences, Applied Entomology, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland

Abstract. The selection of habitats with favourable temperature by the apple blossom weevil *Anthonomus pomorum* (L.) is investigated in a temperature gradient arena with a range of approximately 0–15 °C. Single female and male weevils are tested in the arena 2, 4 and 6 days after termination of diapause, during photophase and during scotophase. During photophase, weevils of both sexes choose the warmest part of the temperature gradient arena, irrespective of the time elapsed after diapause. During scotophase, high temperature is favoured by male weevils, as well as by females 2 and 4 days after diapause. However, 6 days after termination of diapause, females show no thermal preference in the temperature gradient arena during scotophase, indicating that thermal choice of female *A. pomorum* in the scotophase changes with time after the termination of diapause. The results suggest that both sexes benefit from thermoregulation by habitat choice during photophase when the weevils are flight active and colonize apple trees.

Key words. *Anthonomus pomorum*, microhabitat, temperature choice, thermal orientation, thermoregulation.

Introduction

Due to their size and tendency to ectothermic control of body temperature, insects are highly sensitive to abiotic ambient conditions, including temperature (Digby, 1955). Ambient temperature plays an important role because it not only affects insect development, survival, abundance and reproduction (Lapointe, 2000; Stathas, 2000; Roy *et al.*, 2002), but also their activity (Heinrich, 1995; Duan *et al.*, 1996). Consequently, insects have evolved various means of regulating their body temperature to avoid specific physiologically unsuitable conditions caused by abiotic factors of the environment. In general, there are three possibilities: morphological, physiological and behavioural (Clench, 1966; Bursell, 1974; Casey & Hegel, 1981; Willmer, 1982; Schmitz, 1994; Kreuger & Potter, 2001). Insects from several taxa regulate their body temperature by behavioural adaptations (e.g. by orientation to sun and wind direction; Hamilton, 1975), by the position of their wings during basking (Clench, 1966) or by the exploitation of the thermal heterogeneity of their environment (Cloudsley-Thompson, 1962). Mobile insect stages are capable of avoiding unfavourable conditions by using different microhabitats, and choosing particular sites appropriate to their thermal balance (May, 1979; Casey, 1981). The behaviour of insects in relation to differences in temperature within the habitat may ensure their exposure to conditions far closer to the optimum than would be expected based on ambient air temperature (Bursell, 1974). Such thermoregulation by habitat choice could be demonstrated within temperature gradients for many insect species (Deal, 1941; Ferguson & Land, 1961; Cokendolpher & Francke, 1985; Flinn & Hagstrum, 1998; Jian *et al.*, 2003).

Benefits from thermoregulation by habitat selection are particularly important to insect species that are forced to be active under relatively low temperatures during the seasonal cycle. Individuals that choose thermally favourable microclimates should benefit from increased mobility, mating, oviposition and development (Willmer, 1982).

The apple blossom weevil, *Anthonomus pomorum* (L.), uses closed flower buds of apple trees, *Malus domestica* Borkh., for oviposition in early spring. The adults colonize

Correspondence: Dr Joerg Samietz, Agroscope FAW Waedenswil, Swiss Federal Research Station for Horticulture, PO Box 185, CH-8820 Waedenswil, Switzerland. Tel.: +41 1 7836193; fax: +41 1 7836434; e-mail: joerg.samietz@faw.admin.ch

the orchard from overwintering sites and have to mature and mate at a time when the blossom buds are still closed. Therefore, both sexes have to be active in early spring under still relatively low ambient temperatures (Central Europe: late February/beginning of March; Toepfer *et al.*, 1999; 2002). Their small body size of a few millimetres precludes endothermic regulation by metabolic heat production, which would at least allow for a partial independence of body temperature from environmental conditions (Heinrich, 1993). Behavioural studies demonstrate that the ambient temperature of the weevils indeed influences activity such as crawling, feeding and mating (Duan *et al.*, 1996; Toepfer *et al.*, 2002). Furthermore, the hiding behaviour of the apple blossom weevils in thermal shelters corresponds with the coldest periods of the diurnal cycle (Hausmann *et al.*, 2004).

In the present study, the hypothesis that adult *A. pomorum* weevils use thermoregulation by choosing microhabitats with different temperatures is tested. Benefits from higher body temperatures may differ between males and females (e.g. due to the need for egg maturation in females) and such benefits may change with age due to developmental processes. Consequently, experiments are performed in a temperature gradient arena to test the possible dependency of thermoregulation behaviour on sex and on time after termination of diapause. Furthermore, possible behavioural differences are compared between photophase (i.e. the period of highest activity of the weevils) and scotophase (i.e. when the lowest ambient temperatures during the diel cycle may trigger the thermoregulation behaviour).

Materials and methods

Insects

Capped brown blossoms bearing *A. pomorum* pupae were collected in May 2002 in northern Switzerland. After emergence, weevils were kept in plastic boxes (28 × 20 × 24 cm) and were fed with fresh apple leaves and pieces of apple fruit until the onset of aestivo-hibernation (3–4 months after emergence). The adults were sexed by the characteristic differences in the dorsal part of the last abdominal plates (Duan *et al.*, 1999). Weevils were overwintered in a cooling chamber (SR Kältetechnik, Winterthur, Switzerland) at 4 ± 1 °C in plastic boxes (19 × 9 × 8 cm). Strips of corrugated cardboard were offered as shelter. During aestivo-hibernation, weevils were still provided with fresh pieces of apples and sprayed with water at weekly intervals. Weevils were kept in diapause for a minimum of 20 weeks because Ctvrtecka & Zdarek (1992) previously demonstrated that 65% of *A. pomorum* females showed initiation of ovarian development after a period of cold treatment (3–4 °C) of 5 months.

The weevils were transferred to a climate chamber (Heraeus, BK 6160, Germany) with a temperature of 10 °C during photophase (light period) and 5 °C during scotophase [LD 12 : 12 h, fluorescent light, approximately 50 W m^{-2}, 60–80% relative humidity (RH)] 2, 4, or 6 days before the experiments as needed. This photoperiod corresponds to the field conditions in Central Europe when weevils start activity in early spring (beginning of March). Adults were provided with apple fruit and water.

Test arena

The arena consisted of a transparent plastic tube (diameter 10 cm, length 30 cm, thickness 0.25 mm) that was closed with a plastic lid at one end and with fine gauze at the other end. Inside the tube was a piece of corrugated cardboard (5 × 29 cm) for the weevils to crawl on. The cardboard was suspended horizontally in the centre of the tube away from the walls by two triangles of 0.8-mm steel wire. In the experiments during scotophase, the corrugated side of the cardboard was covered with a plastic transparency film to provide the weevils with shelters because weevils tend to shelter during this time of the diel cycle (Hausmann *et al.*, 2004). The arena was placed in a climate chamber (E15, Conviron, Canada) at a temperature of −5 °C (80% RH) and illumination or darkness. To obtain a temperature gradient, an infrared lamp (PAR 38 IR 100 W, Royal Philips Electronics, Holland) was installed in front of the end of the tube with the plastic lid. The resulting linear temperature gradients on the surface of the cardboard, where the weevils rest and move, ranged from 0.7 to 15.4 °C (60 ± 10% RH, fluorescent light, 100 W m^{-2}) in the experiment during photophase and from 0.2 to 15.2 °C (60 ± 10% RH, no light) in the experiment during scotophase. Temperatures were measured with a shaded type-T thermocouple probe of 0.5 mm diameter (Physitemp Instruments, Clifton, New Jersey). Within the diel cycle of the weevils, the experiments were carried out approximately 5–8 h after the onset of photophase and approximately 4–1 h before the end of scotophase. These two periods correspond to the main activity of the weevils during the day and to the resting peak of the weevils at night in the field (Hausmann *et al.*, 2004). During each trial, one weevil at a time was placed at a randomly chosen position on the cardboard and its location was assessed again after 60 min. Each weevil was only tested once and the cardboard was exchanged for a new one after each trial. A control experiment was conducted in the same test arena with a constant temperature of 10 °C (80% RH, photophase: fluorescent light, 100 W m^{-2}). Thirty male and 30 female weevils per light treatment (photophase/scotophase) were tested for each time treatment after diapause (2, 4 and 6 days). Two full replications (Rep. 1, Rep. 2) of the entire experiment and of the control were performed.

Statistical analysis

For analysis of the distribution of the weevils in the temperature gradient, the cardboard was divided into five sectors of equal size (mean temperature in photophase: sector 1 = 14.3 °C, sector 2 = 8.5 °C, sector 3 = 6.4 °C, sector

4 = 5.3 °C, sector 5 = 2.1 °C; in scotophase: sector 1 = 13.4 °C, sector 2 = 6.5 °C, sector 3 = 5.9 °C, sector 4 = 5.0 °C, sector 5 = 2.7 °C). The distribution of the weevils in the temperature gradient (five sectors) after 60 min was analysed against an equal distribution by χ^2 for each of the three times after diapause (Zar, 1998). For each location, a temperature was attributed according to the gradient. Thus, individual temperatures could be assigned to the weevils after scoring their position. From these temperatures, the median and mean temperature of the weevil's choice was calculated. A Kruskal–Wallis test was performed to test for differences between the temperature choice of weevils 2, 4 and 6 days after termination of diapause. Possible differences in temperature choice between females and males were analysed with a Mann–Whitney *U*-test including all time treatments.

Data were analysed using the statistical software STATVIEW 5.0.1 for Apple Macintosh (SAS Institute Inc., Cary, North Carolina).

Results

Photophase

Males 2, 4 and 6 days after termination of diapause chose the warm part of the temperature gradient arena with proportions between 46.7 and 79.3% (Table 1, Fig. 1a,b). The warm part of the temperature gradient arena was also chosen by the females 2, 4 and 6 days after diapause with proportions between 43.3 and 73.3% (Table 1, Fig. 1c,d).

In the control arena with a temperature of 10 °C in all five sectors, distribution of males and females in all treatments (2, 4 and 6 days after diapause) did not deviate significantly from an equal distribution (χ^2, $P > 0.05$; data not shown).

There was no difference between the actual temperatures chosen by males 2, 4 and 6 days after termination of diapause (Table 1, Kruskal–Wallis test, Rep. 1: $H = 4.28$, d.f. = 2, $P = 0.118$; Rep. 2: $H = 0.95$, d.f. = 2, $P = 0.622$) and by females 2, 4 and 6 days after termination of diapause (Table 1, Kruskal–Wallis test, Rep. 1: $H = 3.05$, d.f. = 2, $P = 0.217$; Rep. 2: $H = 1.45$, d.f. = 2, $P = 0.485$). No significant difference was found between the temperatures chosen by males and females (Table 1, Mann–Whitney *U*-test, Rep. 1: $U = 3704.00$, $P = 0.322$; Rep. 2: $U = 3553.00$, $P = 0.155$).

Scotophase

Males 2, 4 and 6 days after diapause termination, chose the warm part of the temperature gradient arena with proportions between 40.0 and 73.3% (Table 1, Fig. 2a,b). The warm part of the temperature gradient arena was also preferred by the females 2 and 4 days after termination of diapause with proportions between 46.7 and 56.7%. Females showed no thermal preference 6 days after diapause (Table 1, Fig. 2c,d).

In the control arena with a temperature of 10 °C in all sectors, distribution of males and females in all treatments (2, 4 and 6 days after diapause), did not deviate significantly from an equal distribution (χ^2, $P > 0.05$; data not shown).

In males, there was no difference between the actual temperatures chosen 2, 4 and 6 days after termination of diapause (Table 1, Kruskal–Wallis test, Rep. 1: $H = 1.84$, d.f. = 2, $P = 0.398$; Rep. 2: $H = 2.45$, d.f. = 2, $P = 0.293$). In females, there was a significant difference between the temperatures chosen 2, 4 and 6 days after termination of diapause in one replication (Table 1, Kruskal–Wallis test, Rep. 1: $H = 6.39$, d.f. = 2, $P = 0.041$; Rep. 2: $H = 1.84$, d.f. = 2, $P = 0.398$). No significant difference was found between the behaviour of males and females (Table 1, Mann–Whitney *U*-test, Rep. 1: $U = 3697.00$, $P = 0.313$; Rep. 2: $U = 3927.00$, $P = 0.725$).

Table 1. Temperature chosen by the apple blossom weevils in the temperature gradient arena after 60 min during photophase and during scotophase.

		Temperature chosen (°C)				
	Days after diapause	Median	Mean	SD	χ^2	*P*
Photophase						
Males						
Rep. 1	2	7.8	9.4	5.82	15.67	< 0.005
	4	15.4	12.5	4.69	54.67	< 0.001
	6	10.6	9.2	6.51	21.67	< 0.001
Rep. 2	2	15.4	10.8	6.06	37.00	< 0.001
	4	15.4	12.3	4.99	41.67	< 0.001
	6	15.4	11.5	4.50	35.33	< 0.001
Females						
Rep. 1	2	13.4	10.9	5.22	30.67	< 0.001
	4	12.5	10.7	5.14	21.33	< 0.001
	6	15.4	12.7	4.82	56.00	< 0.001
Rep. 2	2	13.4	11.4	4.70	30.67	< 0.001
	4	13.9	11.0	5.50	33.33	< 0.001
	6	9.4	9.5	5.56	11.33	< 0.05
Scotophase						
Males						
Rep. 1	2	15.0	11.6	5.24	55.00	< 0.001
	4	13.6	10.2	5.89	40.00	< 0.001
	6	12.9	9.8	5.74	24.00	< 0.001
Rep. 2	2	12.4	10.3	5.32	37.67	< 0.001
	4	8.6	8.5	4.46	9.67	< 0.05
	6	8.1	8.9	5.59	19.00	< 0.001
Females						
Rep. 1	2	11.8	10.3	5.14	26.67	< 0.001
	4	14.7	10.9	5.30	30.33	< 0.001
	6	5.9	7.4	5.23	6.00	NS
Rep. 2	2	8.6	8.9	5.34	15.00	0.005
	4	11.8	9.8	5.31	22.33	< 0.001
	6	6.0	8.1	5.23	7.67	NS

A χ^2 test was performed to compare the number of weevils in each sector of the arena with an equal distribution ($n = 30$, d.f. = 4). NS, Not significant; Rep., replication.

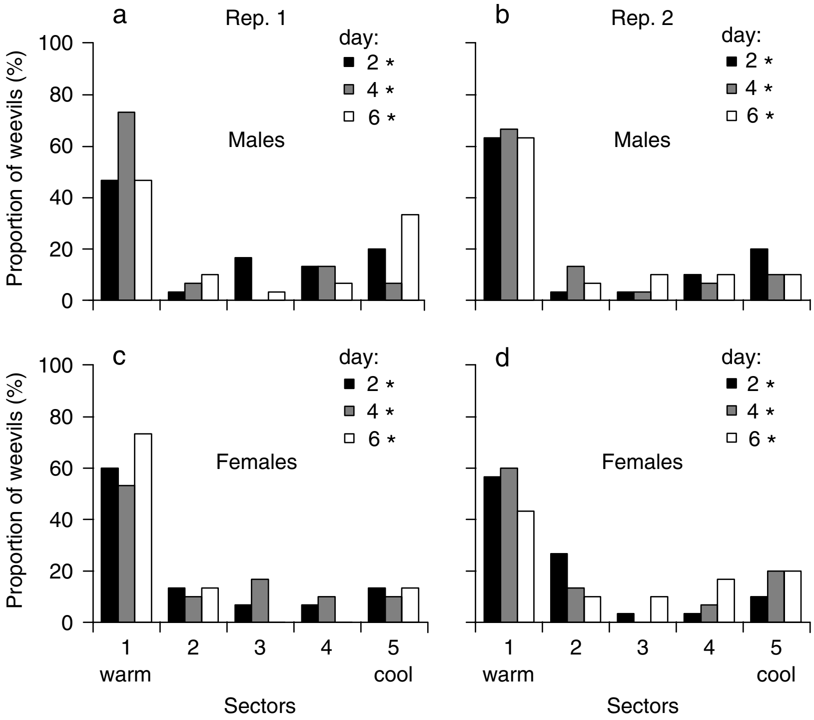

Fig. 1. Number of male (a, b) and female (c, d) *Anthonomus pomorum* after 60 min in the different sectors of the temperature gradient arena during photophase ($n = 30$ per treatment). Sector 1 represents the warmest, and sector 5 the coolest, sector. 'Day' refers to the number of days after termination of diapause. Asterisks indicate that the distribution of the weevils is significantly different from an equal distribution (χ^2, $P < 0.05$).

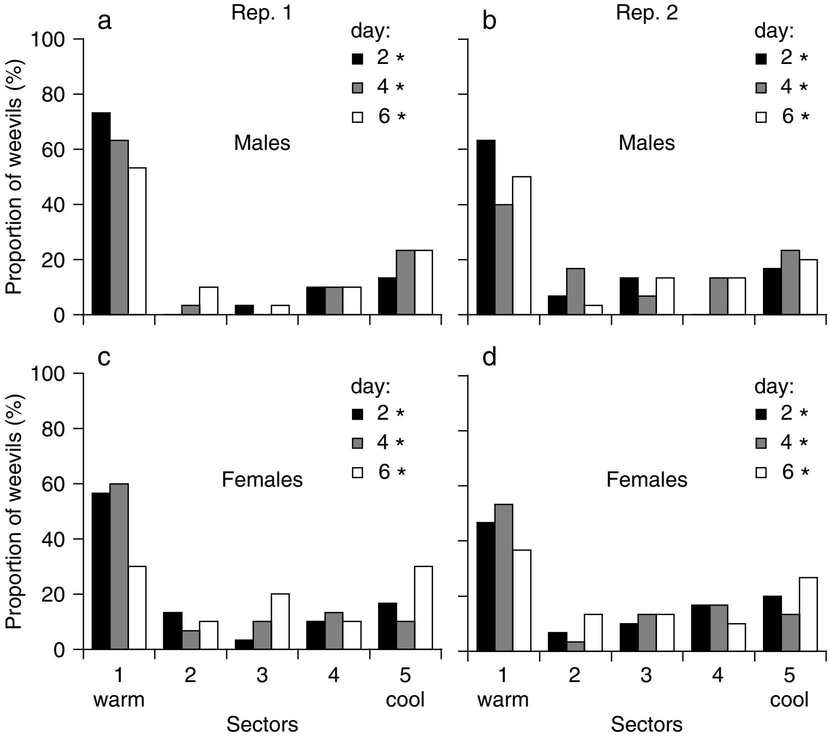

Fig. 2. Number of male (a, b) and female (c, d) *Anthonomus pomorum* after 60 min in the different sectors of the temperature gradient arena during scotophase ($n = 30$ per treatment). Sector 1 represents the warmest, and sector 5 the coldest, sector. 'Day' refers to the number of days after termination of diapause. Asterisks indicate that the distribution of the weevils is significantly different from an equal distribution (χ^2, $P < 0.05$).

Discussion

The study demonstrates that overwintered apple blossom weevils perform active behavioural thermoregulation by selection of warm microhabitats. In early spring, when weevils terminate their diapause, they are active at relatively low temperatures because they use apple blossom buds in an early stage for ovarian maturation and for oviposition

(Ctvrtecka & Zdarek, 1992; Brown *et al.*, 1993). Thermal orientation is crucial for an insect that becomes active so early in the spring. Higher body temperature allows for a higher activity level and thus the weevils can benefit in colonizing trees, finding mating partners, oviposition and feeding. Disappearance of a thermal preference in females 6 days after termination of diapause could indicate a change in behavioural priority related to the status of gonad development, as discussed below.

The supercooling point of the apple blossom weevil is low (−11 °C) in fed individuals (Kostal & Simek, 1996), and the weevils have been observed to crawl and feed at temperatures of approximately 0 °C (Duan *et al.*, 1996). Even if weevils show physiological attributes necessary for the exploitation of early stages of apple bud development, their total activity (i.e. crawling, feeding and mating) was significantly suppressed at temperatures below 5 °C (Duan *et al.*, 1996; Toepfer *et al.*, 2002). Twenty-five to 30% of the weevils are active at temperatures between 0 and 12 °C; 85% of the weevils were active at temperatures above 12 °C (Toepfer *et al.*, 2002).

During photophase, female and male apple blossom weevils may benefit from higher temperatures with a higher activity level. Tree colonization occurs mainly during photophase and landing in particular was recorded solely during photophase and not during the night (Hausmann *et al.*, 2004). Flight initiation in the laboratory rarely occurred at temperatures of 12 °C or below (Duan *et al.*, 1996). This dependency of relatively high temperatures in spring was demonstrated in the present study by the preference of weevils for the warmer sectors of the arena during photophase. Thermoregulation during photophase is also related to the weevils under study showing a strong ectothermic behaviour due to their body size: radiative heat up takes only few minutes but the weevils also cool down again in such a time frame (Samietz *et al.*, unpublished data). Therefore, in early spring, heating up the weevils body for flight activity is predominantly possible during the day using solar radiation. Adults of the Colorado potato beetle, *Leptinotarsa decemlineata*, show a similar thermoregulation behaviour during photophase. They apparently modify body temperature by seeking sunlit substrates at low ambient temperatures and by moving into the shade at high ambient temperatures during daylight hours (May, 1982). Other coleopteran species also showed thermal orientation in a temperature gradient; for example adults of *Tribolium castaneum* (Hagstrum *et al.*, 1998), *Cryptolestes ferrugineus* (Jian *et al.*, 2003) and *Dermestes maculates* (Osuji, 1975).

During scotophase, male apple blossom weevils favour the warmer sectors of the temperature gradient on all days tested after termination of diapause. Females also prefer the warmer sectors 2 and 4 days after diapause. However, 6 days after diapause they show no thermal preference during scotophase. This pattern of thermal orientation corresponds with data gathered in a field study whereby weevils were found in shelter traps that mimic relatively warm resting sites only on the first days after arrival (Hausmann *et al.*, 2004). Upon termination of diapause, females have only slightly developed gonads (Ctvrtecka & Zdarek, 1992). It is possible that the feeding status and degree of egg maturation determines the behavioural priority between thermal orientation and oviposition-site selection. Indeed, oviposition-orientated behaviour is affected by endogenous factors, and often correlates with conditions of the ovaries (Browne, 1993). Further investigations are required to evaluate whether the time when thermal orientation in female weevils ceases coincides with a distinct nutritional status and/or egg development stage. The timing of this behavioural change, approximately 1 week after the termination of diapause, both under laboratory (this study) and field conditions (Hausmann *et al.*, 2004), is compatible with the hypothesis that the endogenous factor regulating female behaviour is of hormonal nature. On the other hand, males have sperm in their spermatic ducts already on the first day after termination of diapause (Ctvrtecka & Zdarek, 1992). They may benefit from higher temperatures in general by having a higher level of activity (e.g. for searching females and for mating).

The present study highlights the importance of behavioural thermoregulation in an insect species that is active early in the year when temperatures are still relatively low. The apple blossom weevil is shown to perform active thermoregulation by choosing warm microhabitats in a temperature gradient. In the field, weevils might choose sunny spots during photophase and warm shelters during scotophase. The data indicate that the thermal choice of female *A. pomorum* in the scotophase changes with time after the termination of diapause.

Acknowledgements

Thanks are due to Sibylle Stöckli and Slavica Katulic for assistance with experiments. We are grateful to Anja Rott, Kathrin Tschudi-Rein, Jim Hardie and an anonymous referee for valuable comments on previous versions of the paper.

References

Brown, M., Szentkiralyi, F. & Kozar, F. (1993) Spatial and temporal variation of apple blossom weevil populations (Col., Curculionidae) with recommendations for sampling. *Journal of Applied Entomology*, **115**, 8–13.

Browne, L.B. (1993) Physiologically induced changes in resource-oriented behavior. *Annual Review of Entomology*, **38**, 1–25.

Bursell, E. (1974) Environmental aspects – temperature. *The Physiology of Insecta* (ed. by M. Rockstein), pp. 1–41. Academic Press, New York, New York.

Casey, T.M. (1981) Behavioral mechanisms of thermoregulation. *Insect Thermoregulation* (ed. by B. Heinrich). Wiley & Sons, New York, New York.

Casey, T.M. & Hegel, J.R. (1981) Caterpillar setae: insulation for an ectotherm. *Science*, **214**, 1131–1133.

Clench, H.K. (1966) Behavioral thermoregulation in butterflies. *Ecology*, **47**, 1021–1034.

Cloudsley-Thompson, J.L. (1962) Microclimates and the distribution of terrestrial arthropods. *Annual Review of Entomology*, **7**, 199–222.

Cokendolpher, J.C. & Francke, O.F. (1985) Temperature preferences of four species of fire ants (Hymenoptera: Formicidae: Solenopsis). *Psyche*, **92**, 91–101.

Ctvrtecka, R. & Zdarek, J. (1992) Reproductive diapause and its termination in the apple blossom weevil (*Anthonomus pomorum*) (Coleoptera, Curculionidae). *Acta Entomologica Bohemoslovaca*, **89**, 281–286.

Deal, J. (1941) The temperature preferendum of certain insects. *Journal of Animal Ecology*, **10**, 323–356.

Digby, P.S.B. (1955) Factors affecting the temperature excess of insects in sunshine. *Journal of Experimental Biology*, **32**, 279–298.

Duan, J.J., Weber, D.C., Hirs, B. & Dorn, S. (1996) Spring behavioral patterns of the apple blossom weevil. *Entomologia Experimentalis et Applicata*, **79**, 9–17.

Duan, J.J, Weber, D.C, Hirs, B.A & Dorn, S. (1999) A new character for sex differentiation of adults of *Anthonomus pomorum* L. (Col., Curculionidae). *Journal of Applied Entomology*, **123**, 319–320.

Ferguson, D.E. & Land, J.D. (1961) Some temperature studies on the beetle, *Popilius disjunctus*. *Ecology*, **42**, 195–197.

Flinn, P.W. & Hagstrum, D.W. (1998) Distribution of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) in response to temperature gradients in stored wheat. *Journal of Stored Product Research*, **34**, 117–112.

Hagstrum, D.W., Flinn, P.W. & Gaffney, J.J. (1998) Temperature gradient on *Tribolium castaneum* (Coleoptera: Tenebrionidae) adult dispersal in stored wheat. *Environmental Entomology*, **27**, 123–129.

Hamilton, W.J. (1975) Coloration and its thermal consequences for diurnal desert insects. *Environmental Physiology of Desert Organisms* (ed. by N. F. Hadley), pp. 67–89. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

Hausmann, C., Samietz, J. & Dorn, S. (2004) Monitoring the dynamics of orchard colonisation by *Anthonomus pomorum* in spring. *Entomologia Experimentalis et Applicata*, **110**, 207–216.

Heinrich, B. (1993) *The Hot-Blooded Insects – Strategies and Mechanisms of Thermoregulation*. Springer-Verlag, Germany.

Heinrich, B. (1995) Insect thermoregulation. *Endeavour*, **19**, 28–33.

Jian, F., Jayas, D.S. & White, N.D.G. (2003) Movement of adult rusty grain beetles, *Cryptoestes ferrugineus* (Coleoptera: Cucujidae), in wheat in response to 5 °C/m temperature gradients at cool temperatures. *Journal of Stored Product Research*, **39**, 87–101.

Kostal, V. & Simek, P. (1996) Biochemistry and physiology of aestivo-hibernation in the adult apple blossom weevil, *Anthonomus pomorum* (Coleoptera: Curculionidae). *Journal of Insect Physiology*, **42**, 727–733.

Kreuger, B. & Potter, D.A. (2001) Diel feeding activity and thermoregulation by Japanese beetles (Coleoptera: Scarabaeidae) within host plant canopies. *Environmental Entomology*, **30**, 172–180.

Lapointe, S.L. (2000) Thermal requirements for development of *Diaprepes abbreviatus* (Coleoptera: Curculionidae). *Environmental Entomology*, **29**, 150–156.

May, M.L. (1979) Insect thermoregulation. *Annual Review of Entomology*, **24**, 313–349.

May, M.L. (1982) Body temperature and thermoregulation of the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata*, **31**, 413–420.

Osuji, F.N.C. (1975) Distribution of larvae of *Dermestes-maculatus* (Coleoptera-Dermestidae) in a radial temperature-gradient. *Entomologia Experimentalis et Applicata*, **18**, 313–320.

Roy, M., Brodeur, J. & Cloutier, C. (2002) Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). *Environmental Entomology*, **311**, 177–187.

Schmitz, H. (1994) Thermal characterization of butterfly wings – 1. Absorption in relation to different color, surface structure and basking type. *Journal of Thermal Biology*, **19**, 403–412.

Stathas, G.J. (2000) The effect of temperature on the development of the predator *Rhyzobius lophanthae* and its phenology in Greece. *Biocontrol*, **45**, 439–451.

Toepfer, S., Gu, H. & Dorn, S. (1999) Spring colonisation of orchards by *Anthonomus pomorum* from adjacent forest borders. *Entomologia Experimentalis et Applicata*, **93**, 131–139.

Toepfer, S., Gu, H. & Dorn, S. (2002) Phenological analysis of spring colonisation of apple trees by *Anthonomus pomorum*. *Entomologia Experimentalis et Applicata*, **103**, 151–159.

Willmer, P.G. (1982) Microclimate and the environmental physiology of insects. *Advances in Insect Physiology*, **16**, 1–57.

Zar, H.J. (1998) *Biostatistical Analysis*. Prentice Hall International Limited, U.K.

Accepted 1 October 2004