

Thermoregulation behaviour in codling moth larvae

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Abstract. The thermoregulation behaviour of the codling moth, *Cydia pomonella*, is investigated in temperature gradient experiments with larvae feeding within apples, and with mature larvae searching for cocooning sites. Feeding larvae appear to prefer the apple hemisphere with a higher temperature (i.e. they build larger cavities in the radiated, warmer part of the fruit). The proportion of larval cavities in the warmer hemisphere is positively related to increasing apple temperature on that side, as well as to the temperature difference between the warm and the cool fruit hemisphere. The mechanism in feeding larvae can be termed as cryptic basking because, during microhabitat selection, the caterpillars exploit temperature differences that are caused explicitly by incident solar radiation. Fifth-instar larvae in search of cocooning sites show no temperature preference within the large gradient offered (9–29 °C), with no difference between males and females. During larval development, the insect changes its thermoregulation behaviour in response to a possible shift in benefits of an elevated body temperature with respect to environmental conditions. Both the thermoregulation behaviour and such a shift of behavioural response should be respected when simulating body temperatures of the species.

Key words. Behaviour, cryptic basking, *Cydia pomonella*, habitat selection, microhabitat, temperature, thermoregulation, thermotaxis.

Introduction

Thermoregulation enables insects to maintain a relatively stable body temperature or temperature range, either above or below ambient temperature, by behavioural or physiological means (Heinrich, 1981; Heinrich, 1993). Thereby, body temperature (T_b) is regulated independently of passive processes, such as radiation, convection, evaporation and metabolism during different activities (Heinrich, 1993). Probably the most common and most effective mechanism of behavioural control of T_b in insects is microhabitat selection (May, 1979; Casey, 1981), which is the short-term selection of thermally favoured microclimates, especially of sunny or shaded substrates (May, 1979). Such temperature selection behaviour has been reported for a number of species, including caterpillars (Casey, 1976; Kukal, 1993; Bryant *et al.*, 1997; Frears *et al.*, 1997), grasshoppers

(Uvarov, 1977; Lactin & Johnson, 1996; Samietz & Köhler, 1998), beetles (May, 1982; Ward & Seely, 1996; Kreuger & Potter, 2001; Hausmann *et al.*, 2004a) and termites (Steward, 1981; Cabrera & Rust, 1996).

The codling moth, *Cydia pomonella* L., is a key pest insect of apples worldwide (Dorn *et al.*, 1999). Predicting the appearance of susceptible stages is one important method to time interventions in integrated management. Commonly used prediction models are based on standardized measurements of air temperature and known developmental rates. The relationship between temperature and developmental rate of the codling moth has been evaluated in a number of studies. The developmental rate increases with increasing temperatures between the lower and upper developmental thresholds of 10 °C and around 32–35 °C, respectively, and reaches a maximum at approximately 30 °C (Glenn, 1922; Williams & McDonald, 1982; Rock & Shaffer, 1983; Pitcairn *et al.*, 1991; Howell & Neven, 2000). Although considerable research has been carried out on the influence of body temperature on development, little is known about the temperature-related behaviour of the different codling moth stages and possible thermoregulation mechanisms.

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Prediction models for the codling moth that are based on air temperature are effective in forecasting the adult flight of the overwintered generation and the egg stage of the first generation. However, there often is a time discrepancy between the simulation results and direct observations, particularly for later generations. This deviation is likely to be due to the difference between the temperatures from weather stations used to drive the models and the micro-environmental temperatures experienced by developing individuals (Shaffer & Gold, 1985; Blago & De Berardinis, 1991; Blago, 1992). Insect body temperature is a critical parameter in models for computing developmental rates. In most prediction models, T_b is taken to be equal to standardized air temperature, measured 2 m above the ground. However, ambient or habitat temperatures influencing the insects' T_b often differ substantially from standardized air temperatures, mainly due to solar radiation influx in orchards (Schroeder, 1965; Landsberg *et al.*, 1973; Thorpe, 1974; Blago & Dickler, 1990; Graf *et al.*, 2001; Howell & Schmidt, 2002).

Due to the body size, the body temperature of all codling moth stages is expected to be determined nearly exclusively by ectothermic influences. Thus, T_b should be approximately equal to the operative environmental temperature (T_e). T_e represents the air temperature of the immediate microhabitat plus or minus a temperature increment that includes radiative heat-up and evaporative cooling (Bakken & Gates, 1975; Campbell & Norman, 1998). First-instar codling moth larvae feed immediately beneath the surface of the fruit before boring radially to the centre of the apple to feed in the second and third instar (Geier, 1963). The fourth-instar larvae feed on pulp and form large cavities around the pericarp, which fifth-instar larvae extend back to the fruit surface (Geier, 1963). All instars appear to return to the surface occasionally. Mature fifth-instar larvae finally leave the apple in search of cocooning sites mainly under the bark of tree trunks. Therefore, with respect to the pre-imaginal stages of the codling moth, the T_b of feeding larvae depends on the temperature of apple fruits, whereas the T_b of mature larvae and pupae mainly depends on bark temperature of the apple trees.

Temperatures in the habitats of the codling moth show a high variability, mainly due to the varying solar radiation (Thorpe, 1974; Graf *et al.*, 2001; Kührt *et al.*, unpublished data). To regulate body temperature within an optimum range, the mobile codling moth stages should exploit this heterogeneity in their environment by selecting microhabitats with favourable temperatures. Indeed, such thermoregulation by habitat selection is clearly adaptive and virtually all animals exhibit some capacity to seek appropriate thermal regimes (Casey, 1981). However, behavioural mechanisms regulating body temperature in the larval instars of the codling moth have never been investigated systematically.

The purpose of the present study is to investigate the selection of thermally different microhabitats, focusing on the behaviour of the first- to fifth-instar larvae feeding in apples and of the mature larvae searching for cocooning

sites. The behavioural response of feeding and mature larvae to temperature is assessed inside apple fruits and in cocooning shelters, respectively. Understanding the temperature-related behaviour in the key stages of the life cycle, together with the impact of these mechanisms on the development rates, will help to improve forecasting of the population dynamics of this insect species.

Materials and methods

Experimental insects

Codling moth larvae were obtained from infested wind-fall apples collected in an apple orchard with untreated high-stem trees in northern Switzerland from June to August 2003. The infested apples were kept under a photoperiod of LD 16:8 h with cyclically changing temperatures (day: 24 °C, night: 18 °C) and 60% relative humidity (RH). Emerging fifth-instar larvae were removed daily from the cages. At this stage, the larvae were sexed by detecting the black testicles under the cuticle of the males. The insects were used directly for the temperature gradient experiments with mature larvae.

For the experiments with feeding larvae inside apples, the fifth-instar larvae were overwintered in a cooling chamber (SR Kältetechnik, Switzerland) at 4 ± 1 °C, in total darkness. Corrugated cardboard was offered for cocooning. After 3 months of hibernation, the codling moth larvae were held at cyclically changing temperatures (day: 24 °C, night: 18 °C), LD 16:8 h and 60% RH. Newly emerged adults were transferred to polystyrene cylinders (110 × 140 mm) covered with gauze and lined with transparent plastic as oviposition substrate. The adults were provided with water in 50-mL vials with a wet cotton-wool wick. Small apples fruits (from thinning fruit density) were offered to stimulate oviposition. Subsequently, the eggs laid were kept under the same conditions until the larvae hatched and were used for the experiment with first-instar larvae. To increase the number of test insects, first-instar larvae from a laboratory strain were also included in this experiment and analysed separately. This laboratory strain originated from diapausing larvae collected in cardboard strips around high stem apple trees in north-eastern Switzerland and had been maintained in the laboratory for approximately 60 generations. The larvae of the laboratory strain were reared singly on a semiartificial medium (Huber *et al.*, 1972). All codling moth stages were kept in a climate chamber at 24 ± 1 °C, LD 16:8 h and 60% RH.

Temperature selection of feeding larvae

Fructified dwarf apple trees were transferred from outdoor-conditions to a climate chamber with natural light conditions complemented with artificial light and 20 ± 1 °C, LD 16:8 h and 60% RH. To establish a temperature gradient within the apple fruits, infrared lamps

(PAR38, 100 W, Philips, The Netherlands) permanently heated the apples from one side. The infrared lamps were installed in front of the apple trees and fixed at different heights according to the position of the apples. The distance between an apple and its corresponding infrared lamp was adjusted to approximately 35 cm.

For infestation, one newly hatched larva per fruit was placed with a small brush on top of the apples on the boundary between the irradiated and the shaded apple hemispheres. The apples were initially infested in the evening (3–2 h before dark) with the infrared lamps switched off to avoid an influence of radiation influence and surface temperature of the apples. The infrared lamps were switched on the morning after initial infestation, 3 h after light. This procedure also prevented dehydration of the larvae before they entered the apples. After the first week, the apples were checked for frass as an indication of a successful infestation. If no frass was found, the infestation of the apple was repeated. After 25 days, the apples were harvested regardless of the developmental stage of the feeding larvae. Before harvest, the boundary between the irradiated and the shaded part of the apples was marked to facilitate allocation of these two hemispheres.

The diameter of each apple was measured from the point of the apple closest to the infrared lamp (0° to source) to the point farthest away (180° from infrared lamp). Three times during the experiment (i.e. before noon, after noon and at night), the surface temperature of each apple fruit was measured with a thermocouple (Type BT-1, Physitemp Instruments, Clifton, New Jersey). The temperature was measured on the side exposed to infrared illumination (0° to infrared lamp: T_{0°) as well as on the opposite side (180° from infrared lamp: T_{180°). The temperature gradient generated across the apple fruits ranged for T_{0° from 23.7 – 33.1°C and for T_{180° from 20.7 – 26.4°C . The temperature difference between both sides ($\Delta T = T_{0^\circ} - T_{180^\circ}$) ranged between 2.2 and 8.6°C .

The thermal response of feeding larvae within apples was quantified by the distribution of the feeding tunnels over the two hemispheres. To examine these cavities, the apples were cut perpendicularly to the boundary between the two hemispheres into 5-mm thin slices. The upper side of each apple slice was photographed with a digital camera. Larval cavities on the slice were then highlighted in the digital images using Adobe Photoshop 7.0 (Adobe Systems, Inc., San Jose, California). For each of the slices, the area covered by the larval cavity on the slice surface was calculated with Scion Image software program (Version 1.6, Scion Corporation, Frederick, Maryland). For each individual larva, the corresponding areas of all slices were summed up separately for the irradiated (A_{0°) and shaded (A_{180°) hemisphere, and referred to as 'cavity areas'.

For the experiment, dwarf apple trees were categorized according to cultivar. Larval cavities and frass were found in 66 of the 93 infested apples ($28 \times$ Gala, $12 \times$ Rubinette, $11 \times$ Braeburn, $6 \times$ Gloster, $6 \times$ Boskoop, $3 \times$ Golden Delicious). Of those apples analysed for temperature selection of the larvae, 36 were infested with larvae originating from the

field strain and 30 with larvae from the laboratory strain. Apple cultivar and codling moth strain were considered as possible factors influencing analysis.

Temperature selection of mature larvae

For the temperature gradient experiments, a transparent cylinder (length 300 mm, diameter 60 mm) of 0.13-mm thick polystyrene was used, covered at both ends with gauze. Within the cylinder, a 300×30 -mm strip of corrugated cardboard with 35 short corrugations perpendicular to the length axis was offered as shelter for cocooning. The temperature gradient was generated by illuminating one end of the cylinder with an infrared lamp (PAR38, 100 W, Philips). The infrared lamp was positioned at a distance of 100 mm from the cylinder resulting in a nearly linear temperature gradient along the length of the lying cylinder from approximately 29 – 9°C . Four of these cylinders were set up in a climate chamber with 5°C ambient temperature, no light and $90 \pm 10\%$ RH. Temperatures were measured with a thermocouple probe (type T, Physitemp Instruments, Clifton, New Jersey) on top of every second of the 35 corrugations. The relative humidity within the cylinders was approximately 60%. A control trial was concurrently carried out at constant temperature in the climate chamber where the infested apples were stored (day: 24°C , night: 18°C , LD 16:8 h, 60% RH).

The thermal response of mature codling moth larvae was assessed in 24-h trials starting within 1 day after emergence from the fruit. In a temperature gradient, the larvae were tested individually for their thermal preference in searching for a cocooning site. The larvae were introduced randomly onto the flat side of the corrugated cardboard strip, whereby the total number of tested larvae was aimed at being equally distributed. Therefore, the top of the cardboard strip was divided into 35 zones corresponding to the 35 corrugations. The larvae were able to move freely within the cylinder. The location of each larva was recorded at the beginning of the experiment and after 24 h. The zones were grouped into five equal-sized sectors and the total larvae therein considered for analysis. Only larvae actually cocooning inside the corrugations were considered in the analysis (gradient: 83 males, 79 females; control: 79 males, 80 females). To prevent influences of previously tested larvae, the cardboard strip was exchanged after each trial for every individual.

Statistical analysis

To analyse the thermal response of feeding larvae, the area index was calculated as the proportion of cavity area in the radiated hemisphere relative to the total cavity area: $A_{0^\circ}/(A_{0^\circ} + A_{180^\circ})$. A significant choice of one side (i.e. a deviation of the area index from equal distribution over both apple hemispheres; index area = 0.5) was analysed using a one-sample *t*-test. The influence of the temperature

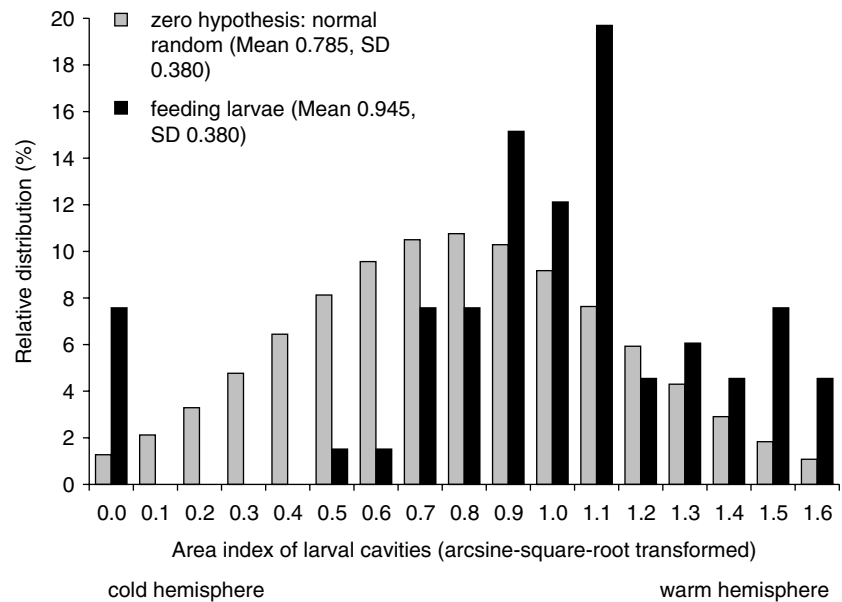


Fig. 1. Distribution of the arcsine-square-root transformed area index of larval cavities in apples [$A_{0^\circ}/(A_{0^\circ} + A_{180^\circ})$] and the hypothetical normal distribution around the value of 0.785 with no preference for an apple hemisphere. Larval choice of the warmer, radiated apple hemisphere is significant (one-sample *t*-test: $t = 4.15$, $P < 0.001$).

and of the temperature difference between the apple hemispheres on the thermal response of the larvae was analysed by Pearson's correlation. For this purpose, the relationships between the arcsine-square-root transformed area index and T_{0° and ΔT were tested. Pearson's correlation was also applied to test for significant relationship between the arcsine-square-root transformed area and the apple diameter. The influence of the temperature and of the temperature difference between the apple hemispheres on the area index (arcsine-square-root transformed) was analysed each with an analysis of covariance including the possible effects of the factors larval strain (field, laboratory) and apple cultivar. All analyses were run with SPSS 11.0.2 (SPSS Inc., Chicago, Illinois).

The thermal response of mature larvae was analysed using a chi-square test (Zar, 1998). For this purpose, the homogeneity of the distribution of the larvae was tested after 24 h in relation to that at the start of the experiment, and in relation to that in a control after 24 h. The distribution of female and male fifth-instar larvae was also compared using a chi-square test. Diapause and nondiapause larvae were not discriminated because the number of nondiapause larvae was too low for a separate analysis and comparison.

Results

Feeding larvae within apples

Feeding larvae built larger cavities in the irradiated, warmer apple hemispheres than in the cooler apple hemispheres (Fig. 1, one-sample *t*-test: $t_{65} = 4.15$, $P < 0.001$). The average area index was 0.64 ± 0.03 (mean $\pm$ SE). A total of 74% of the larvae built larger cavities in the warmer than in the

cooler apple hemisphere, and 4% of these larvae fed exclusively in the radiated hemisphere. A larger cavity area in the cooler than in the warmer apple hemisphere was found for 24% of the larvae, and 8% of these larvae fed exclusively in the cooler hemisphere. Feeding cavities of equal size in both apple hemispheres were observed for only 2% of the larvae.

The proportion of cavities in the warmer apple hemisphere (i.e. arcsine-square-root transformed area index) increased with increasing temperature at the radiated apple surface T_{0° (Pearson's $r = 0.376$, $P = 0.002$) (Fig. 2a). The proportion of cavities in the warmer apple hemisphere also increased with increasing temperature difference between both apple sides ΔT (Pearson's $r = 0.276$, $P = 0.025$) (Fig. 2b).

When analysed together with the factors apple cultivar and larval strain, apple surface temperatures (T_{0° , T_{180°) influenced the behavioural response of the feeding larvae to temperature (Table 1). Apple cultivar and larval strain did not affect the influence of T_{0° , T_{180° and ΔT on the arcsine-square-root transformed area index and hence on the positive thermotaxis. Both field-collected and laboratory strain larvae showed consistently positive thermotaxis in all apple cultivars. Furthermore, the apple diameter had no significant influence on the larval response (i.e. the arcsine-square-root transformed area index) (Pearson's $r = 0.095$, $P = 0.44$).

Mature larvae searching for a cocooning site

Cocoon-forming, fifth-instar larvae of both sexes were most frequently found at either end of the cardboard arena in the temperature gradient (males: $\chi^2 = 34.5$, d.f. = 4, $P < 0.001$; females: $\chi^2 = 38.2$, d.f. = 4, $P < 0.001$) (Table 2). Male and female larvae showed no behavioural

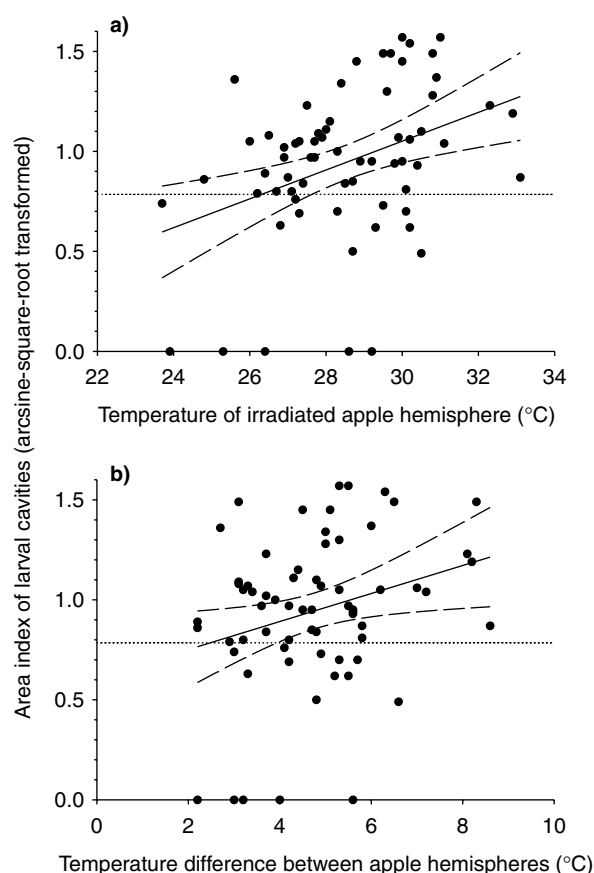


Fig. 2. Area index of larval cavities (arcsine-square-root transformed) in apple fruits as a function of (a) the temperature of the irradiated apple hemisphere and (b) the temperature difference between the irradiated and shaded apple hemispheres. Linear regression $\pm$ confidence interval for the relationships: (a) $y = -0.758 + 0.049x$ (ANOVA: $F_1 = 9.1$, $P = 0.004$) and (b) $y = 0.417 + 0.047x$ (ANOVA: $F_1 = 4.5$, $P = 0.038$).

difference in the temperature gradient ($\chi^2 = 5.84$, d.f. = 4, $P > 0.25$). There was no difference in the distribution of the mature larvae between the temperature gradient and the control (males: $\chi^2 = 5.44$, d.f. = 4, $P > 0.1$; females: $\chi^2 = 0.65$, d.f. = 4, $P > 0.95$). In the control, most fifth-instar larvae were found at both ends of the cardboard strip avoiding the centre (males: $\chi^2 = 21.3$, d.f. = 4, $P < 0.001$; females: $\chi^2 = 31.9$, d.f. = 4, $P < 0.001$) (Table 2). There was no difference in behaviour of the two sexes ($\chi^2 = 2.34$, d.f. = 4, $P > 0.5$).

Discussion

Codling moth larvae developing in apple fruits appear to exhibit thermoregulation behaviour by microhabitat selection, whereas mature larvae searching for a cocooning site exhibit no comparable distribution. Larvae feeding inside apple fruits select the irradiated, warmer apple hemisphere

Table 1. Influence of apple-surface temperature on the arcsine-square-root transformed area index of radiated and shaded apple hemispheres [$A_{0^\circ}/(A_{0^\circ} + A_{180^\circ})$] analysed by analyses of covariance (ANCOVA) including the factors apple cultivar and larval strain.

Covariate	d.f.	F	P	Factor	d.f.	F	P
T_{0°	1	7.354	0.009	Apple cultivar	5	0.274	0.925
T_{180°	1	7.099	0.010	Apple cultivar	5	0.978	0.439
ΔT	1	2.352	0.130	Apple cultivar	5	0.206	0.959
T_{0°	1	9.102	0.004	Larval strain	1	0.234	0.630
T_{180°	1	4.919	0.030	Larval strain	1	0.279	0.599
ΔT	1	4.782	0.032	Larval strain	1	0.930	0.339

for building feeding tunnels. Mature larvae, before cocooning, do not select for any of the temperatures tested in the present study. The results reveal a possible shift in benefit of an elevated body temperature in relation to the environmental conditions along the life cycle of the codling moth. Both the thermoregulation behaviour of one stage and the possible shift in behavioural response should be taken into consideration when simulating body temperatures of this species.

In general, the major benefit of behavioural thermoregulation in caterpillars is thought to be a reduction in the duration of the larval stage by enhancing growth rates (Casey, 1981; Heinrich, 1981). Consequently, the time period that the caterpillars are exposed to predators, parasites and pathogens, as well as to intraspecific competitors, is reduced (Heinrich, 1981).

Thermoregulation behaviour has been previously observed in a number of lepidopteran species. For example, behavioural thermoregulators are the white-lined sphinx caterpillar, *Hyles lineata* (Casey, 1976), the small tortoiseshell, *Aglais urticae*, and the peacock, *Inachis io* (Bryant *et al.*, 2000), the eastern tent caterpillar, *Malacosoma americanum* (Knapp & Casey, 1986) and some *Colias* butterfly larvae (Sherman & Watt, 1973). Behavioural thermoregulation is also used to prevent overheating, such as in the mopane worm *Imbrasia belina* (Frears *et al.*, 1997). In other species, such as the tobacco hornworm, *Manduca*

Table 2. Distribution of fifth-instar codling moth larvae in a temperature gradient and in the control experiment.

Zone	Temperature gradient			Control (constant temperature)	
	Mean T (°C)	Males	Females	Males	Females
1	26.8	20	26	26	23
2	20.7	7	9	9	10
3	17.3	6	8	8	7
4	15.5	13	8	9	7
5	12.8	33	32	27	33
Sum		83	79	79	80

Mean T refers to the average zone temperature in the temperature gradient. Temperature in the control (constant T) was 24 °C during the day and 18 °C at night.

sexta, behavioural thermoregulation is not apparent (Casey, 1976).

An often reported mechanism of behavioural thermoregulation in caterpillars is basking (i.e. the absorption of direct solar radiation to elevate body temperature; Casey, 1976; Porter, 1982; Knapp & Casey, 1986; Stamp & Bowers, 1990). Concealed-living caterpillars, such as the larvae of the codling moth, cannot bask in the sun. Nevertheless, they are able to exploit temperature differences within their environment by microhabitat selection. This study demonstrates that feeding codling moth larvae prefer to build their cavities in warmer rather than in cooler apple hemispheres. Thus, the larvae spend a higher time fraction in apple regions with higher temperature. In ectotherms, such as the caterpillars studied here, this consequently leads to higher body temperatures (T_b). Feeding rate, foraging yield and growth rate are positively correlated with T_b (Casey, 1976; Heinrich, 1981). It is postulated that the feeding larvae actively increase their development rate by selecting favourable temperatures within the apple fruits. Because caterpillars exploit temperature differences during microhabitat selection inside the apple that, under field conditions, are caused explicitly by incident solar radiation, the mechanism observed here can be termed as 'cryptic basking'.

In the field, the effect of solar radiation on the increase of larval body temperature within the apple might even be more pronounced than indicated by the present laboratory results. Newly hatched larvae prefer to enter the fruit from the side directly exposed to solar radiation (Hall, 1934; Plourde *et al.*, 1985). They feed beneath the apple surface for the duration of their first larval instar, before they bore radially to the centre of the fruit (Geier, 1963).

Late fifth-instar codling moth larvae did not orientate towards a certain temperature when searching for a suitable cocooning shelter within the extended temperature range tested here. Theoretically, both mature larvae and pupae could benefit from higher body temperatures due to increased development rates. Indeed, larvae that hibernated in the southern sector of an apple tree trunk emerged earlier in spring than larvae in the northern sector due to higher habitat temperatures (Graf *et al.*, 2001). On the other hand, larvae that cocoon at sites exposed to high temperatures likely bear a higher risk of desiccation because high temperatures are coupled with low relative humidity. Furthermore, respiration rate of codling moth fifth-instar larvae, and thus mortality, increases with increasing temperatures (Neven, 1998). Obviously, late fifth-instar larvae are faced with a trade-off between fast development and the risk of desiccation in warmer shelters. Facing this trade-off, the advantage of individuals exposed to higher temperatures by speeding up their development apparently did not result in an adaptation with respect to temperature selection behaviour. In good accordance with the present laboratory results, Graf *et al.* (2001) report no preference of codling moth larvae for the sun-exposed southern sector of tree trunks in the field.

Bimodal distributions as reported here for mature codling moth larvae in the temperature gradient, as well as in

the control set-ups, have been mentioned before in other insects (Deal, 1941; Toye, 1970; Cabrera & Rust, 1996). All larval instars of the codling moth appear to be thigmopositive, and this preference for a tight and dark place is most pronounced in the fully developed larvae at cocooning time (McIndoo, 1929). The preference of either end of the gradient and the control set-up could be explained either by such a thigmopositive behaviour towards the cylinder limits (gauze) or by giving up searching at the end of the cardboard strips. In either case, the larvae do not show a temperature preference.

Predator pressure represents one of the dominant selective factor determining activity pattern of many caterpillars. Therefore, caterpillars should thermoregulate only if the risk of predation is reduced, eliminated or outweighed by other, stronger environmental pressures (Knapp & Casey, 1986). With respect to the two stages investigated here, the feeding codling moth larvae reduce the predator pressure by developing inside apple fruits. Larvae within apples suffer an approximate 35–52% mortality, mainly caused by competition, disease and nutritional effects (Ferro *et al.*, 1975; Jackson, 1982). On the other hand, cocooning larvae, although under tree bark, are exposed to much higher predation and parasitism rates. The total mortality of the overwintering population ranges between 50 and 78% (MacLellan, 1962; Ferro *et al.*, 1975; Subinprasert, 1987). The principal source of mortality is bird predation, but also parasitism, pathogens and climatic factors are of importance (Garlick, 1948; MacLellan, 1958; Hagley, 1969; Solomon & Glen, 1979; Glen *et al.*, 1981; Stairs, 1985; Subinprasert, 1987). Because the larvae are exposed to predation particularly during their search for cocooning sites, a time- and risk-intensive search for thermally advanced shelters might not be adaptive.

Additionally, the risk of moving to higher temperatures is lower in feeding larvae compared with mature ones because the humidity level within apples is constantly high. Consequently, the low desiccation risk in concealed larvae allows them to exploit their small, but thermally heterogeneous, microhabitat freely with relatively low environmental hazards. Hence, thermoregulation in these larval stages by cryptic basking does not compromise their need for protection from predation or for avoidance of desiccation.

In conclusion, codling moth larvae appear to change their thermoregulation behaviour during development, according to the changing benefits, needs and constraints. Such a shift has also been reported in other insect species. Gypsy moth caterpillars and tent caterpillars change their thermoregulation behaviour during development (Knapp & Casey, 1986). Early-instar gypsy moth caterpillars (*Lymantria dispar*) are observed to bask on the dorsal surface of the leaf whereas late instar caterpillars remain shielded from direct solar radiation. Early-instar tent caterpillars (*M. americanum*) maximize their T_b whereas late instars show a smaller temperature excess over ambient temperature throughout the day. The change in the late instars of both caterpillar species has been postulated to have evolved in response to predator pressure (Campbell, 1981; Knapp &

Casey, 1986). Female apple blossom weevils, *Anthonomus pomorum*, seek for warmer shelters, especially during the coldest periods of the day shortly after terminating diapause (Hausmann *et al.*, 2004). However, 6 days after diapause termination, the females lose this temperature preference, indicating a change in behavioural priority that is possibly related to the status of gonad development (Hausmann *et al.*, 2005).

The study shows that presence of thermoregulation behaviour in one stage is no reliable evidence of such behaviour in other stages. Depending on the benefits and constraints, thermoregulation behaviour can change or disappear during the insect life cycle. With respect to the simulation of insect phenology, it is suggested that the demonstrated thermal response should be implemented in models dealing with codling moth development over the season. Because the larvae change their temperature related behaviour during their life cycle, each stage investigated in the present study should be regarded separately with its particular habitat temperature and radiation regimes. Consequently, for feeding larvae, an estimate of body temperature can be approached by modelling apple temperature with respect to irradiation, ambient temperature and wind speed (cf. Thorpe, 1974). Due to their thermoregulation behaviour by cryptic basking, T_b of feeding larvae corresponds to the average apple temperature in the irradiated apple hemisphere. On the other hand, fifth-instar codling moth larvae appear to be thermoconformers because thermoconformity is the norm in caterpillars that do not or cannot thermoregulate using behavioural means (Casey, 1993). Consequently, T_b of cocooning codling moth larvae will correspond to the temperature of their shelter (i.e. mostly bark). Because the integrated management of pest insects relies on precise forecasts of susceptible stages, consideration of the impact of thermoregulation behaviour on T_b , and consequently on the development rate, can improve the understanding of insect phenology and, finally, the precision of prediction models.

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