BEHAVIOURAL THERMOREGULATION IN THE FREEZE-TOLERANT ARCTIC CATERPILLAR, *GYNAEPHORA GROENLANDICA*

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Summary

Larvae of the high arctic caterpillar, *Gynaephora groenlandica* (Wöcke) (Lepidoptera: Lymantriidae) spent most (60 %) of their time orienting towards the sun (i.e. basking) and only 20 % feeding, primarily near midday. Larvae usually basked after feeding, then either fed again or moved to a new feeding site. Basking larvae reached their highest body temperatures (T_b) of $\approx$30°C ($\approx$20°C in excess of the ambient temperature) when surrounded by snow on a calm day in the midday sun. Setae significantly decreased larval cooling rates. Maximal metabolic rates were attained in basking larvae, but at body temperatures below 10°C oxygen uptake was greatly reduced. Our studies indicate that *G. groenlandica* larvae are behaviourally adapted to utilize available solar radiation for growth and development.

Introduction

Gynaephora groenlandica is found only in the Canadian high arctic archipelago and Greenland, where it survives the low annual heat budget, low temperatures, xeric conditions, seasonal photoperiod and short growing season (Downes, 1964; Danks, 1981; Svoboda & Freedman, 1988). The restricted seasonal growth period results in an extended individual life cycle (Downes, 1964; Ryan & Hergert, 1977) estimated to last at least 14 years at Alexandra Fiord, Ellesmere Island (Kukal & Kevan, 1987). All except one of these years are spent in the larval stage; the only overwintering phase. Pupation, emergence, mating, egg laying, eclosion and moulting to first and second instar larvae occur in 3–4 weeks in a single summer season (Kukal & Kevan, 1987). Despite the short time available for foraging, the larvae cease feeding prior to the peak of the summer season (Kukal & Kevan, 1987).

The larvae of *G. groenlandica* (Kukal, 1984) and *G. rossii* (Kevan *et al.* 1982), as well as some other high arctic insects (Bertram, 1935; Krog, 1955; Kevan & Shorthouse, 1970; Kevan, 1975), raise their body temperatures by basking.

Key words: behavioural thermoregulation, arctic, *Gynaephora groenlandica*.

Although elevation of body temperature can enhance development (May, 1979; Scriber & Slansky, 1981), *G. groenlandica* nevertheless requires 14 years to complete its life cycle. Basking may enhance the rate of larval development but probably also interferes with other activities, such as feeding.

Solar radiation is a scarce and limiting resource for organisms inhabiting the Alexandra Fiord lowland (Svoboda & Freedman, 1988). The heat budget is limited seasonally by the number of sunny days, and also daily by changes in the intensity of sunshine with the height of the sun above the horizon. We think that development of *G. groenlandica* larvae at Alexandra Fiord lowland is related to their behavioural utilization of sunshine. In this study we examine larval thermoregulatory behaviour in relation to their daily activity pattern and energy budget.

Materials and methods

Behaviour

Larvae of *Gynaephora groenlandica* were observed during June 1983 and 1985 at Alexandra Fiord, Ellesmere Island, NWT (78° 53′ N; 75° 55′ W). Observations of behaviour were made for larvae encountered on the open tundra and in a circular area of tundra (diameter ≈ 6 m), containing approximately 40 % *Dryas integrifolia*, 30 % *Salix arctica*, 10 % *Cassiope tetragona*, 10 % *Saxifraga oppositifolia* and 10 % *Luzula confusa* that was surrounded by snow. The snow enclosure was only about 10 cm high and had no effect on the weather conditions inside.

The temporal diel pattern of behaviour was determined by hourly recordings of the proportion of enclosed larvae ($N = 500$) engaged in particular types of behaviour (i.e. basking, feeding, moving) over 24 h. Sequential organization of behaviour was recorded for 10 larvae observed continuously from 13.00–17.00 h on a sunny, calm day (ambient temperature, $T_a = 8°C$). Duration of different behaviours was scored by minutes for each single larva, and frequencies of transitions between behaviours were analysed in a transition matrix of preceding *vs* following behaviours, with the diagonal held to logical zeros (assuming a behaviour cannot follow itself, Fagen & Young, 1978). A kinematic graph of behavioural states and sequences was constructed from the transition matrix by showing average durations of different behaviours and frequencies of transitions among different behavioural states (Sustare, 1978). Transitions from one behaviour to another were tested for significance with the χ^2-statistic for each 2×2 contingency table (Leonard & Ringo, 1978; Nelson & Fraser, 1984).

The compass orientations of larvae during basking (i.e. orientation perpendicular to the sun's rays) and while spinning cocoons prior to pupation were recorded in the enclosure and compared with the orientation of larvae and pupae in the field. A compass could not be used to determine orientation because of the proximity of the magnetic north pole, therefore landmarks were used in correlation with their compass position on a topographical map. Field records were made of the number of larvae on the sun-facing *vs* shaded side, and windward

vs leeward side of tundra hummocks ($\approx$20 cm high; $\approx$40 cm wide). Larval position on hummocks was recorded under sunny but windless conditions at T_a ranging from -7.5 to 9.0°C and also in the sun at a wind speed of $\approx$30 km h^{-1} from the northeast recorded by a microclimatic data station (Campbell Scientific CR-21, Logan, Utah). The observed distribution of larvae on the sun-facing or shaded and leeward or windward sides of hummocks was compared with expected numbers using a chi-square test. The expected frequency distribution of larvae over a hummock is 60 % on the sun-facing side *vs* 40 % on the shaded side and 50 % on the leeward *vs* 50 % on the windward side, assuming no preference for a certain portion of the hummock. The 60 % frequency can be calculated from the height of the sun above the horizon since only 40 % of a hummock will be shaded if the sun is 10–33° above the horizon (Kevan *et al.* 1982). We determined if the larvae responded to magnetic field or to solar radiation while spinning cocoons. Ten final instar larvae were placed into a clear plastic box (25 cm × 20 cm × 10 cm) for pupation. The bottom was covered with natural substrate. All but two (opposite) sides of the box were covered with black (opaque) plastic. The box was placed in a north-facing window so that direct sunlight penetrated one clear side while low-level diffuse light penetrated the other (south) side of the box. The orientation of the pupated larvae was checked after 9 days.

Mobility of larvae on the tundra was estimated from the average distance moved by 13 larvae (instars V and VI) over a period of 21 h during sunny, calm conditions ($T_a = 2$–18°C). The larvae were marked with a dot of paint on their dorsum and the distance and direction of their travel was recorded every 3–4 h. The mean distance moved was calculated for all the larvae and also for 'slow' *vs* 'fast' larvae, which were compared by *t*-test. The direction of movement with respect to the sun was tested for randomness using a chi-square test.

Physiological effects of behaviour

Effects of different types of behaviour on larval body temperatures (T_b) were recorded in the enclosure at constant ambient conditions. Larval T_b was obtained in 2–4 s by indenting the dorsal cuticle with the tip of a copper–constantan thermocouple (Bailey Bat-12; type MT-29/1, time constant $= 0.025$ s, diameter $= 0.33$ mm) read to the nearest 0.1°C. (The larvae did not alter their behaviour subsequent to measurements of their T_b.) Air and substrate temperatures (T_a recorded $\approx$1 m above larvae; T_s within 1 cm of larvae by touching the ground with the thermocouple) were always measured with the same thermocouple as T_b. The changes in T_b of eight larvae were followed in the field; records of T_b, T_a and T_s were made every 0.5–2 h over a 38-h period beginning at 10.00 h. The mean T_b values for larvae basking, moving, feeding, moulting or spinning or for parasitized larvae were compared by *t*-tests. Coefficients of variation were computed as indicators of variance within each behavioural state. Effects of different ambient conditions on T_b were compared for larvae basking and spinning cocoons. The effects of sun, cloud cover, wind and time of day on larval T_b were tested by

measuring T_b of basking and spinning larvae while only one of the ambient conditions varied. The degree of cloud cover was estimated from a measurement of the relative light intensity with a 'super-sensitive darkroom meter' (S & M model A-3, Science and Mechanics, New York), and wind velocity was recorded by the microclimatic data station at 0, 10 and 25 cm above ground. T_b values of larvae basking at noon without cloud cover were compared with those of larvae basking at midnight, at noon with cloud cover, and in sun with wind from the direction of insolation.

The effects of insolation and wind velocity on larval T_b were analysed in the laboratory by measuring cooling rates of normal, shaved and 'basking' larvae in a wind tunnel. Recently killed larvae were attached to a stage with beeswax, heated to 50 °C with a heat lamp and placed into a wind tunnel, facing into a laminar air flow at velocities of 417, 367, 87, 62 and 0 m min^{-1}. Since cooling is a passive, physical process it was more convenient to record T_b from dead animals. Larval T_b was monitored with a Honeywell potentiometric recorder, using two 0·03 mm diameter copper–constantan thermocouples, one within the abdomen and one as a reference in the wind tunnel. Basking conditions were simulated with a heat lamp which raised the larval T_b by ≈ 20 °C above T_a, a temperature difference recorded on the tundra. Cooling constants at different wind velocities were computed for unshaved *vs* shaved and 'basking' larvae from the linear regression of $\log(T_b - T_a)$ on time, as described by Bartholomew & Heinrich (1978). Because of the short time required for recording each cooling rate, we assumed no significant mass loss due to dehydration. Cooling and warming rates of larvae were also recorded on the tundra by shading and/or unshading a larva and recording T_b at 0·5-min intervals. Rates of warming were obtained by exposing cooled larvae to the sun and recording changes in T_b until it stabilized. The same procedure for measuring cooling and warming rates was repeated for different ambient conditions: noon, sunny; noon, cloudy; and midnight, sunny. Albedo effect was measured at noon under sun by recording cooling and warming rates of larvae surrounded by a 10-cm diameter circle of snow.

Oxygen consumption at different body temperatures

Oxygen consumption rates were measured with a S-3A Applied Electro-chemistry oxygen analyser capable of measuring to 0·001 % O_2 concentration using a flow-through system. The excurrent air was desiccated and passed through a CO_2 absorbent before being pumped to a Model N-37M sensor. Readings were taken every 30 min over 3 h for three groups of larvae kept in a 25-ml flask: (1) actively feeding prior to measurements, (2) active but starved, and (3) 'inactive' (i.e. immobile and spinning hibernacula, therefore presumably aestivating; see Kukal & Kevan, 1987). Ten larvae from each of the three groups were enclosed in a chamber with a thermocouple and their rate of oxygen consumption was recorded over a range of temperatures from 0 to 50 °C. The larvae were allowed to equilibrate for 30 min at each temperature recorded.

Results

Behaviour

Larvae spent 95 % of their time basking, moving or feeding and 5 % immobile in shaded crevices (hiding) or grooming. More than half the total time was spent basking, followed by feeding (20 %) and moving (15 %) (Fig. 1). In behavioural sequences, basking most often followed feeding ($\chi^2 = 50.22$, $P < 0.005$). The most frequent behavioural transition was from feeding to basking ($\chi^2 = 14.93$) and progressively less frequent were the transitions from moving to basking ($\chi^2 = 13.11$), feeding to moving ($\chi^2 = 8.53$), hiding to moving ($\chi^2 = 6.74$) and, finally, moving to hiding ($\chi^2 = 5.18$). All other behavioural transitions were insignificant. The transitions between basking and feeding and between moving and hiding were reversible; however, the transitions from basking to moving to feeding were rare and consequently not statistically significant.

The larvae showed a daily pattern of activity; at midday larvae were either basking, moving or feeding but around midnight most were basking (Fig. 2). While basking, during the course of a day, larvae followed the most direct angle of the sun's rays by orienting perpendicularly to its angle of insolation. Seventy-six percent of the larvae ($N = 139$) were located on the sun-facing side of hummocks ($\chi^2 = 5.59$; $P = 0.025$). Sixty-five percent of the larvae ($N = 82$) were located on the leeward side ($\chi^2 = 3.51$; $P = 0.025$). In both cases there was a significant difference between the observed and expected distribution of larvae over the hummocks, showing preferential orientation towards the sun and away from the wind.

While spinning cocoons on the tundra, larvae oriented over the 24-h period with their heads facing into the sun. When they had finished spinning, the majority of larvae pupated in the north–south orientation with the head facing south
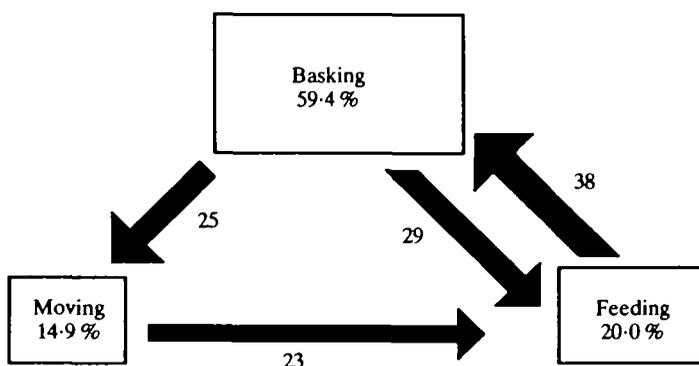

Fig. 1. Frequency and sequential organization of major behaviours in eight *Gynaephora groenlandica* larvae. Relative sizes of rectangles and arrows indicate the frequency of occurrence by the percentage of time spent in particular behaviours (within rectangles) and also the number of times one behaviour followed another (arrows) (see text for details of analysis). Infrequent behaviours, such as grooming and hiding among vegetation clumps, are excluded from the kinematic graph.
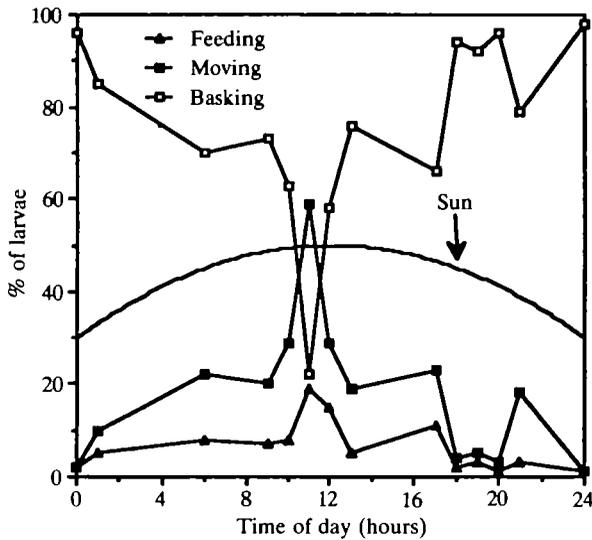
Fig. 2. Diel changes in the pattern of major behaviours (basking, feeding and moving) in *Gynaephora groenlandica* larvae ($N = \approx 500$) in a natural enclosure of the tundra under sunny and calm conditions (T_a at $1 m = 2\cdot0$–$6\cdot3$°C). Change in the height of the sun above the horizon is indicated; minimum at 10° and maximum at 33° above the horizon.

(Table 1). In a laboratory, where the sun was allowed to penetrate a box (see Materials and methods) only from the north and light from the south, all 10 larvae pupated in the east–west direction. However, all of them were lined up along the edge of the warmer, sun-facing side of the box. These results indicate that spinning larvae do not orient to the earth's magnetic field but to solar radiation.

The mean distance moved by the larvae ($N = 13$) in open tundra during a 21-h period was 3 m. Mobility of the larvae was bimodally distributed; six larvae moved a mean distance of 5·81 m, whereas seven larvae moved only 0·60 m. Movement was towards the sun; the larvae followed the solar trajectory in a circular path.

Physiological effects of behaviour

Behavioural changes significantly affected larval body temperatures (Table 2). Larvae attained a maximal T_b of 30·5°C by basking. Moving caused the mean T_b to drop by approximately 4°C and a further significant drop occurred when feeding

Table 1. *Orientation of* Gynaephora groenlandica *cocoons (N = 384) and pupal heads (N = 98) on the tundra surface*

	% Oriented			
	N–S	NE–SW	NW–SE	E–W
Cocoon	69·8	19·0	7·0	4·2
Head (direction)	90 (S)		10 (N/NE/NW)	

Table 2. *Mean body temperatures of* Gynaephora groenlandica *larvae in different behaviours observed between 12.00 and 13.00 h, 25 June, on the tundra (sunny, calm, $T_a = 7°C$, $T_s = 16·5°C$)*

Behaviour	N	Mean	Standard deviation	Coefficient of variation (%)
Basking	20	30·5*	2·2	7·2
Feeding	14	23·9†	2·2	9·2
Moving	15	26·7†	2·6	9·7
Spinning	22	24·1†	4·3	17·8
Moulting	5	25·5†	4·0	15·7
Parasitized	18	24·3†	3·1	12·8

Sample means followed by different symbols are significantly different (t-test, $P < 0·001$) from the mean T_b of basking larvae.

Mean T_b values of feeding *vs* moving larvae are also significantly different (t-test, $P < 0·01$).

commenced. The body temperatures of moulting and spinning larvae were similar to those observed in feeding and parasitized larvae. All the mean T_b values of different behaviours were significantly different (t-test, $P < 0·001$) from basking T_b, and the T_b values of moving larvae were statistically different from those of the feeding larvae ($P < 0·01$). Body temperatures of basking and spinning larvae were lowered by 16–17°C in cloud cover, wind and midnight sun (Table 3). All the mean T_b values at different ambient conditions showed significant differences (t-test, $P < 0·001$) from T_b under noon/sunny/calm conditions. Fig. 3 shows the mean T_b of eight larvae followed in the field over 38 h. Maximum T_b was reached at midday and minimum T_b at midnight; a trend also shown by T_a and T_s. Lower T_b was attained at midday on the first day under partial cloud cover than on the second day which was sunny. Variations among body temperatures of individuals are reflected in the large standard deviation ($\pm \approx 5°C$) from the mean T_b.

Under controlled conditions in the wind tunnel, cooling rates were lowest in basking larvae and highest in shaved larvae (Fig. 4). Cooling rates of unshaved larvae were intermediate in magnitude, but at the highest wind velocity an abrupt

Table 3. *Changes in mean body temperature of basking larvae of* Gynaephora groenlandica *(N = 20–30) under different weather conditions and at different times of day (T_a at 1 m = 2–6·5°C; windy = 30–40 km h^{-1})*

Conditions	Mean body temperature
Noon/sunny/calm	30·5 ± 2·2*
Noon/sunny/windy	14·2 ± 1·8†
Noon/cloudy/calm	12·4 ± 1·9†
Midnight/sunny/calm	13·2 ± 2·8†

Values are means ± s.d.

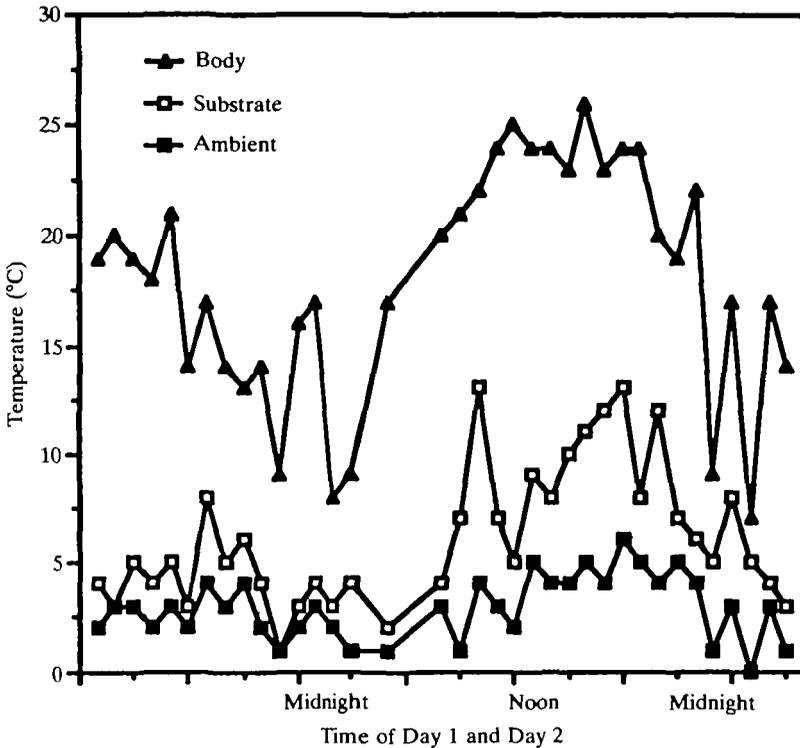Sample means followed by different symbols are significantly different (t-test, $P < 0·001$).

Fig. 3. Diel changes in mean body temperature ($\pm$s.d. $\leqslant 5$) of eight *Gynaephora groenlandica* larvae relative to ambient and substrate temperatures recorded approximately bihourly over 2 days (an overcast day followed by a sunny one) on the open tundra.

increase in cooling rate was caused by disruption of the boundary air layer trapped by the setae (Fig. 4). In nature, the cooling rates induced by shading were not changed by different environmental conditions (Fig. 5A). However, the initial excess T_b differed, being highest under midday sun and snow and lowest at midnight. This initial T_b influenced the rate of warming which was much lower in midnight larvae (Fig. 5B).

Oxygen consumption at different body temperatures

The relationship between body temperature and oxygen consumption was exponential to sigmoidal in the three groups of larvae (Fig. 6). Q_{10} was lowest between 0 and 10°C for all groups of larvae. The highest Q_{10} for active larvae was between 10 and 20°C, whereas for starved larvae it was between 20 and 30°C. However, no significant difference was found between the mean oxygen uptake of starved *vs* active or inactive larvae (*t*-test, $P > 0.05$), or between active *vs* inactive larvae. Hence the inactive larvae were unlikely to be in aestivation since their metabolic rate was the same as that of the active larvae. Similarly, starvation did not alter the larval metabolic rate.
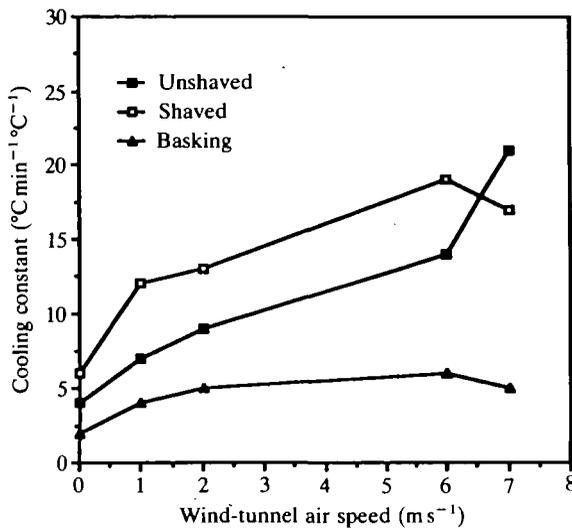
Fig. 4. Influence of increasing wind velocity on the cooling constants (see text for explanation) of unshaved, shaved and basking larvae of *Gynaephora groenlandica* ($N = 3$, $\pm$s.d. $\leqslant 1 \cdot 5$).

Discussion

Sunshine-dependent behavioural thermoregulation is crucial for the survival of *G. groenlandica* at Alexandra Fiord, where low ambient ($<5°C$) and ground temperatures (usually $<10°C$) prevail during their brief activity in June (Kukal, 1984; O. Kukal & T. E. Dawson, in preparation). Although ambient and substrate temperatures gradually increase and peak in July, the intensity of incoming solar radiation declines after the summer solstice (Svoboda & Freedman, 1988). The
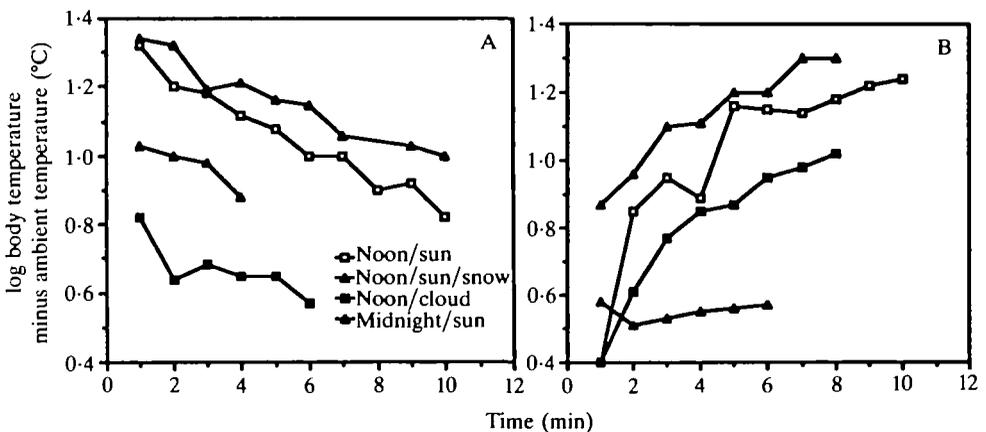

Fig. 5. Cooling rates (A) and warming rates (B) of individual *Gynaephora groenlandica* larvae ($N = 10$–15) on the tundra under different weather conditions and at different times of day (mean values $\pm$ s.d. $\leqslant 0 \cdot 2$).
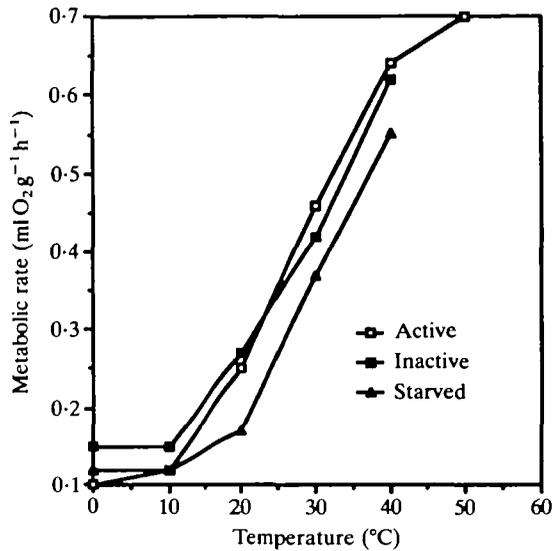
Fig. 6. Metabolic rate as a function of body temperature (range from 0 to 50°C) recorded for 10 actively feeding, active but starved and inactive larvae of *Gynaephora groenlandica* ($\pm$ s.d. $\leqslant 0\cdot03$).

activity (i.e. feeding and basking on the tundra surface) of *G. groenlandica* larvae coincides with the period of most intense solar radiation during June.

The energy cost of different types of activities is best seen from the effect of different behaviours on the body temperature, which can in turn be related to metabolic rate. Maximal T_b in excess of the ambient temperature, which is attained by basking at midday, decreases by 4–6°C when the larvae start moving, feeding, moulting or spinning. Body temperature is decreased by 16–17°C in basking larvae at midnight, under cloud cover at midday, or in a strong wind. However, if the larvae stop basking under these conditions and start moving they would suffer an additional drop in T_b. Evidently, energy balance of larvae is influenced by the different behaviours which are in turn affected by the larval food status and habitat temperature. Raising body temperature in fed larvae enhances digestion rate by stimulating activity of gut enzymes since no bacterial flora is present to aid digestion (Kukal, 1988). Thus body temperature and energy status of larvae is probably pivotal in controlling the type of behaviour. At higher T_b more energy can be obtained in a limited time from the food ingested. However, when energy from food is depleted, feeding commences at the expense of energy lost as heat. However, at higher T_b the 'maintenance metabolism' is increased, hastening the utilization of energy reserves obtained from food (O. Kukal & T. E. Dawson, in preparation), as also noted in other thermoregulating ectotherms (Brett, 1971). The energy content of *Salix arctica*, the primary food plant of *G. groenlandica* larvae, shows a sharp decline towards the end of June (O. Kukal & T. E. Dawson, in preparation). Larval behaviour is consequently further

modified by the energy balance between maintenance metabolism and changes in food quality.

The precarious energy balance is reflected in the daily behavioural pattern of larval *G. groenlandica* and also in the sequential organization of different behaviours. Larvae spend most (60 %) of their time basking (even during pupation the basking position is assumed) which increases their body temperature and metabolic rate, and may lead to an increased rate of digestion. Feeding activity provides the source of energy and ranks in its frequency second to basking, whereas movement, in search of food or new basking sites, ranks last. These three most prominent behaviours follow a definite sequence; most often from feeding to basking, less often from basking to feeding or from basking to moving and then feeding. Interestingly, the reverse sequence of behaviours, from feeding to moving and then basking, very rarely occurs. This suggests an intimate reciprocity between basking and feeding with movement restricted to finding new food sites or changing basking position. During the course of a day the relative importance of the three bahaviours changes; more larvae feed and move at midday and relatively more larvae bask at night. This temporal partitioning of activity may be caused by lower ambient temperatures at night which lower larval T_b. During the day, greater incoming solar radiation raises larval T_b, enhancing feeding and mobility. In contrast to *G. groenlandica*, 'thermally independent' gypsy moth (*Lymantria dispar*) larvae feed mostly in the early morning and evening and are immobile at midday (Knapp & Casey, 1986), an adaptation attributed to the avoidance of predation and parasitism (Campbell, 1981). Although more than two-thirds of *Gynaephora* are killed by parasitoids (Kukal & Kevan, 1987), these thermally dependent larvae probably cannot sacrifice their basking time to hiding from parasitoids. The larvae probably compromise by maximizing development during the period of lowest parasitoid activity in June (Kukal & Kevan, 1987).

The larval metabolic rate increases exponentially with body temperature, even during starvation or apparent inactivity, and approaches $0.1 \, ml \, O_2 \, g^{-1} \, h^{-1}$ below 10°C as in a majority of insects which also lack metabolic compensation to cold (Scholander *et al.* 1953). Consequently, without the aid of 24-h sunlight to raise their T_b by as much as 20°C, the larvae would probably remain below their developmental threshold temperature most of the time. Similar excess body temperatures have been recorded in basking larvae of the nearctic–alpine congener of *G. groenlandica*, *G. rossii* (Kevan *et al.* 1982). In contrast to the strict dependence of the arctic larvae on solar radiation, gypsy moth larvae are 'thermoconformers'. Thermoregulation is apparently unnecessary for gypsy moth larvae since the ambient temperature is well above their developmental threshold (Knapp & Casey, 1986).

Conservation of heat by the larvae is best viewed from an anatomical perspective. As the wind-tunnel experiments showed, the cooling rate is minimized by the dense, dark setae combined with radiant energy input. Larval setae create a boundary layer of undisturbed air which, nevertheless, can be disrupted by high-velocity air currents (see Fig. 4). The insulative quality of larval setae has

also been demonstrated in the gypsy moth (Casey & Hegel, 1981). Similarly, in the field, heat was best conserved as excess T_b at midday under sunny conditions and further enhanced by the albedo effect of surrounding snow. Noteworthy is the decreased ability of larvae to warm up in the midnight sun.

The albedo effect may be involved in the disappearance of larvae from the tundra surface early in the arctic summer. Melting of snow from the larval habitat and surrounding ice fields is the main cause of the sharp decrease in incoming radiation (Svoboda & Freedman, 1988). Because of the strict dependence of these larvae on the sun's heat, it may be energetically more viable for them to cease feeding than to maintain activity at a lower body temperature. This brief period available for feeding extends the developmental time of *G. groenlandica* to 14 years. The evolutionary strategy of *G. groenlandica* appears to involve a brief period of 'maxithermy' (see Hamilton, 1973) followed by a 'voluntary hypothermia' (see Regal, 1967) in mid-summer.

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