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METABOLIC OPPORTUNISTS: FEEDING AND TEMPERATURE INFLUENCE THE RATE AND PATTERN OF RESPIRATION IN THE HIGH ARCTIC WOOLLYBEAR CATERPILLAR *GYNAEPHORA GROENLANDICA* (LYMANTRIIDAE)

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Summary

Arctic woollybear caterpillars, *Gynaephora groenlandica*, had the capacity to rapidly and dramatically increase respiration rates up to fourfold within 12–24 h of feeding and exhibited similar decreases in respiration of 60–85 % in as little as 12 h of starvation. At the peak of their feeding season, the respiration rates of caterpillars also increased significantly with temperature from 0.5 to 22 °C for both fed and starved caterpillars (Q_{10}=1–5). Indicative of diapause, late season caterpillars had depressed respiration rates which were less sensitive to temperature changes (Q_{10}≈1.5), while respiration rates for caterpillars that had spun hibernacula were even lower. *G. groenlandica* did not appear to demonstrate metabolic cold adaptation compared with other temperate lepidopteran larvae. The seasonal capacity to adjust metabolic rate rapidly in response to food consumption and temperature (which can be elevated by basking) may promote the efficient acquisition of energy during the brief (1 month) summer growing and feeding season, while conserving energy by entering diapause when conditions are less favorable. These adaptations, along with their long 15–20 year life cycle and the retention of freeze tolerance year-round, promote the survival of *G. groenlandica* in this harsh polar environment.

Key words: caterpillar, *Gynaephora groenlandica*, metabolic rate, feeding, temperature, respiration, specific dynamic action, arctic insects.

Introduction

Polar environments impose great challenges upon organisms, the most obvious being extremely low temperatures and short summer growing seasons. Polar organisms, therefore, must be masters at meeting these challenges: they endure long periods of darkness, cold, desiccation and starvation between short periods of relatively milder temperatures, limited moisture and patchy food sources. During these brief windows of opportunity, it is critical, particularly for ectotherms, that they maximize energy input for growth and reproduction, while minimizing energy expenditure during periods of less favorable conditions.

The arctic woollybear caterpillar [*Gynaephora groenlandica* (Wöcke), Lymantriidae] has one of the longest life cycles of all insects. It requires 14 years to complete its developmental life cycle at Alexandra Fiord, Ellesmere Island (Kukal and Kevan, 1987), and probably closer to 20 years further north at Lake Hazen (O. Kukal, unpublished data). With the exception of 1 month during a single summer, their entire life span is spent in the larval stage. When acclimated to winter conditions, the larvae are freeze-tolerant to at least −70 °C and, unlike most freeze-tolerant invertebrates, they retain the capacity to survive freezing to −15 °C even during the summer months (Kukal et al., 1988b).

During the feeding period in June, the larvae spend most of their time thermoregulating by basking in the sunshine, raising their body temperature by as much as 25 °C above the ambient temperature (Kukal et al., 1988a). Curiously, before the main peak of summer in July, the caterpillars cease feeding and spin hibernacula concealed within plant cushions and crevices (Kukal, 1995). This diapause may provide some protection from the parasitoids *Hyposoter pectinatus* and *Exorista* sp. by behavioral avoidance (Kukal, 1993); however, it also further restricts an already narrow window of opportunity to exploit another potential month of warm temperatures and abundant food used by many other arctic insects. Within these hibernacula, the larvae remain inactive, at temperatures close to 0 °C, until they freeze in late summer at approximately −8 to −10 °C. During this period of hypothermic conditioning before the onset of very low winter temperatures, the larvae undergo mitochondrial degradation and demonstrate a lowered oxidative metabolic rate (Kukal et al., 1989). This hypoxic state occurs concomitantly with a build-up of cryoprotective compounds, particularly glycerol, which may enhance their increased freeze tolerance during the winter. The mitochondria are resynthesized relatively rapidly when the caterpillars emerge from winter hibernacula the following spring.

Metabolic rate is an indirect indicator of the energy status of ectothermic animals, such as most insects (Heinrich, 1993; Mill, 1985). The overriding factor that dictates the diel and seasonal changes in behavior, and consequent changes in metabolic rate, of these larvae appears to be temperature (Kukal, 1991). However, our study indicated that the metabolic rate is not only dependent on temperature but is also under the influence of seasonal phenology and the feeding and physiological state of the caterpillars.

This study examined how the respiration rate and pattern reflect the energy status of *Gynaephora groenlandica* larvae. More specifically, the interaction between nutritional status and temperature was examined in the following contexts: (1) by analyzing changes in larval respiration rate during alternating periods of feeding and starvation; (2) by investigating the influence of body temperature on the rate of respiration and how this relationship changes in feeding *versus* starved larvae; (3) by comparing the respiration rate of larvae at the peak of their feeding season with that once they have stopped feeding and have spun hibernacula; (4) by comparing the respiration rates of this polar species with those of other Lepidoptera.

Materials and methods

Study site, microhabitats and animals

The experiments were conducted during June 1995 at Hazen Camp, Ellesmere Island, North West Territories, Canada (81°49′N, 71°22′W). This site is one of the largest polar oases in the Canadian High Arctic Archipelago. It is characterized by higher temperatures and moisture levels compared with the surrounding polar desert (Parks Canada, 1994).

Two major microhabitats utilized by the larvae of *G. groenlandica* are found in the Lake Hazen area: patches of arctic willow *Salix arctica*, which are the primary site of feeding, and hummocks of *Dryas integrifolia*, where hibernacula are frequently found (Kukal, 1995). *S. arctica* microhabitat temperatures were recorded during the feeding season of the larvae in June using StowAway temperature loggers (Onset Computer Corp., Pocasset, MA, USA). The surface temperature probes were placed so that they were fully exposed to the rays of the sun. Ambient temperature at ground level was recorded using a shaded probe in the *S. arctica* habitat.

Most of the caterpillars were collected during the first 2 weeks of June near Hazen Camp and at nearby Ekblaw Lake (81°39′N, 75°47′W). The larvae were kept in ventilated outdoor enclosures (40 cm×25 cm×15 cm) and regularly supplied with their preferred host plant, *S. arctica* (Kukal and Dawson, 1989).

Respiration measurements

Rates of oxygen consumption were measured using a microrespirometer originally devised by Engelmann (1963), modified by Conradi-Larsen (1974) and then by Lee (1995). The animals were sealed by a weighted plunger in disposable 5 ml plastic syringes which were placed in a constant-temperature bath (2L-M Isotemp Water Bath, Fisher Scientific, Pittsburgh, PA, USA). A disposable 20 µl micropipette was attached using hot glue to the tip of each syringe prior to sealing the larva into the syringe. Once equilibrium had been reached in the temperature bath, approximately 2.5 µl of 10 % KOH (which was sufficient to absorb all the CO_2 produced) was introduced into the micropipette tip to function as a manometer and to absorb CO_2. An empty syringe with KOH in its micropipette tip provided a control. When the larvae had equilibrated for at least 15 min, the distance moved by the KOH column as the larvae consumed O_2 was read to the nearest millimeter every 0.5–10 min, depending on bath temperature. New syringes and micropipettes were used for each new set of measurements. Once a steady rate of oxygen consumption had been established, a mean value was calculated. Caterpillar live masses were the same before and after respiration measurements (V. A. Bennett, O. Kukal and R. E. Lee, unpublished data); therefore, there was no detectable water loss during the course of measurements. This method produces results that closely match those of other techniques (see Lee and Baust, 1982a,b).

Influence of larval body temperature and feeding status on metabolic rate

The relationship between body temperature and larval metabolic rate was determined for larvae early in their feeding season by measuring rates of oxygen consumption in 11 larvae of similar body mass (instars IV and V) collected during the first week of June. Respiration rates were assessed at 0.5, 15, 22 and 30 °C.

The influence of starvation on the metabolic rate in larvae collected during the second week of June (peak feeding season) was determined. Nine larvae were held individually in plastic 25 ml vials at 0 °C for 48 h in darkness, and then transferred directly to 15 °C for repeated oxygen uptake measurements over 12–24 h, during which time the larvae were starved. Subsequently, they were removed from respiration chambers and fed for 12 or 24 h with young leaves of *S. arctica* at 15 °C. Oxygen uptake was again determined repeatedly at 15 °C over the next 12–24 h post-feeding. These cycles of feeding and starving with corresponding oxygen uptake measurements were repeated three times over the course of 96 h.

To determine whether this experimental protocol of alternate feeding and starving had compromised larval cold tolerance, the nine larvae were frozen for 24 h at −6 °C in darkness immediately after the final respiration rate measurements. Viability after freezing was verified on the basis of normal movement and reflexive curling in response to handling.

Seasonal changes in larval metabolic rate

To test for possible seasonal changes in the influence of body temperature on the metabolic rate, three groups of larvae (N=8–11 per group) were collected at different times during June on the surface of the tundra. Rates of oxygen uptake were analyzed from 0.5 to 30 °C in larvae at the peak of their feeding

season during the second week of June and at the end of their feeding period during the final week of June (see Kukal and Dawson, 1989). At the end of their feeding period, a comparison was made between larvae that had spun hibernacula and those that had not; both groups were provided with fresh *S. arctica* leaves in outdoor enclosures (see above).

Results

Comparison of metabolic rate in fed and starved larvae

Larvae of *G. groenlandica* showed dramatic increases in respiration rate after feeding and rapid decreases in respiration rate within 12 h of starvation (Fig. 1). The larvae used for this experiment had a mean dry mass of 51.7±5.4 mg (mean ± S.E.M., N=9). Prior to respiration measurements, feeding larvae were held in the dark at 0 °C for 48 h, during which time digestion and assimilation could not take place even though their gut was full of food. Upon warming to 15 °C and exposure to light, respiration rates increased rapidly to peak levels within 3 h, as digestion proceeded. Larval metabolic rate decreased by 70 % after 24 h of starvation (Fig. 1, time 24 h), at which time digestion was probably complete (as indicated by the lack of further excretion of frass). Although respiration rates were extremely low at this time, approximately two-thirds of the larvae appeared to be healthy and active; the other third appeared limp or moribund. After feeding for 24 h on fresh *S. arctica* leaves, all the larvae appeared active and healthy, and excreted frass. Their rate of oxygen consumption showed a fourfold increase compared with levels measured prior to feeding (Fig. 1, time 48–54 h). Once again, respiration rates decreased by 58 % after only 12 h of starvation (time 60 h), even though all the larvae appeared healthy and active. Feeding for 12 h (time 60–72 h) increased respiration rates by the same magnitude. During the final 24 h of starvation, larval respiration rates dropped by 84 % from levels measured immediately after feeding. The mean rate of oxygen uptake measured sequentially after feeding or starvation showed a significant difference between the two treatments, with the maximal respiration rate after feeding (Fig. 1, time 48, 51, 54, 72, 75 h) being three- to fourfold higher than the minimal respiration during starvation (time 12, 24, 60, 96 h). These cycles appeared to be independent of any diurnal cycles, consistent with the fact that *G. groenlandica* experience continuous 24 h of light at this time of year.

The mean rate of oxygen uptake at the end of these feed/starve cycle experiments (time 96 h, 24 h of starvation) was only 11.0±4.5 $\mu l\, O_2\, h^{-1}$ (mean ± S.E.M., N=9) at 15 °C. These starved larvae still exhibited a temperature-dependent increase in respiration rate to 95.5±18.8 $\mu l\, O_2\, h^{-1}$ at 22 °C and 150.3±9.4 $\mu l\, O_2\, h^{-1}$ at 30 °C, which was statistically significant (P<0.05, repeated-measures ANOVA). Since all larvae subsequently survived 24 h of freezing at −6 °C, these repeated feed/starve cycles did not appear to compromise larval freeze tolerance and were consistent with previous reports of summer freeze tolerance in this species (Kukal et al., 1988b).

Relationship between body temperature and respiration rate

There was a significant increase in the respiration rate as the body temperature of larvae increased from 0.5 to 30 °C (Fig. 2; P<0.0001, $F_{3,83}$=32.85, two-factor ANOVA). The larvae used for this experiment had a dry mass of 104.5±14.9 mg (mean ± S.E.M., N=11) and therefore exhibited higher respiration rates than those used in the previous experiment because of the greater dry mass (compare Figs 1 and 2). The variation in respiration rates was greater at higher temperatures (Fig. 2). This temperature-dependent increase in respiration rate was present in larvae regardless of their energy status with regard to feeding, starvation or seasonal phenology (Figs 2, 3). Fed larvae tended to consume more oxygen than starved larvae; however, the differences in the rate of oxygen uptake between fed and starved larvae at any given temperature were not significant (P>0.05, Fig. 2). Q_{10} values decreased with

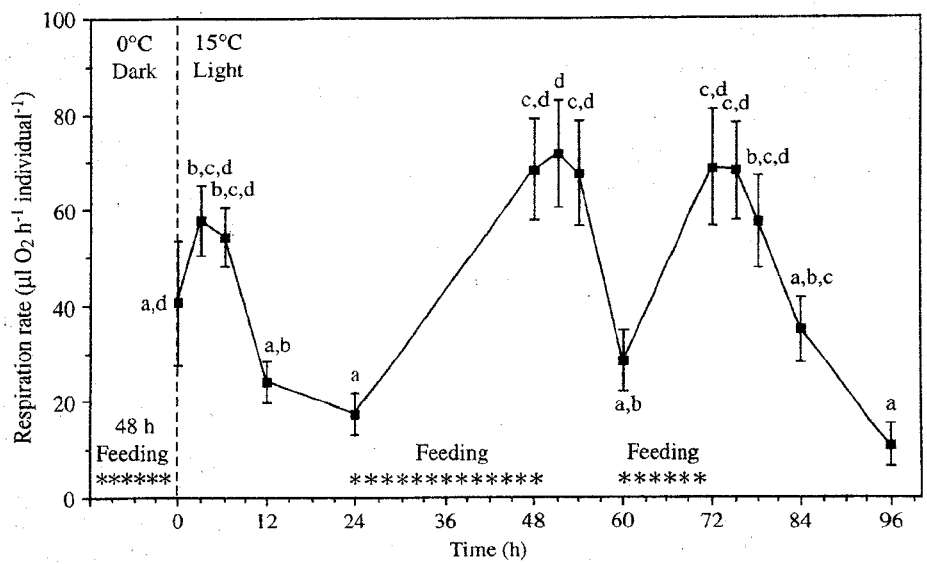

Fig. 1. Respiration rates for larvae (mean dry mass 51.7 mg) of *Gynaephora groenlandica* during feeding and starving cycles at 15 °C. Larvae were tested at the peak of the feeding season (the second week of June). Mean values that do not share any common letters are significantly different (P<0.05, repeated-measures ANOVA and Tukey–Kramer multiple comparisons test). Values are means ± S.E.M., N=9.

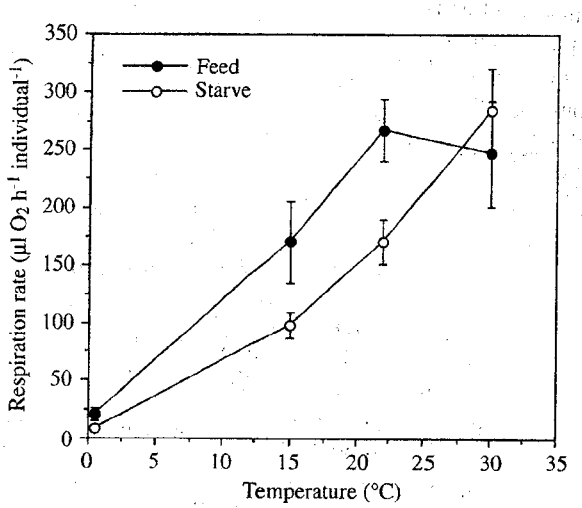

Fig. 2. Temperature profile of respiration rates (means ± S.E.M., N=11) for fed and starved larvae (mean dry mass 104.5 mg) of *Gynaephora groenlandica* collected during the peak feeding season. Two-factor ANOVA showed a significant effect of temperature (P<0.0001, $F_{3,83}$=32.85), but neither the effects of feeding/starving (P>0.05, $F_{1,81}$=3.59) nor the interaction with temperature (P>0.05, F=2.45) was significant.

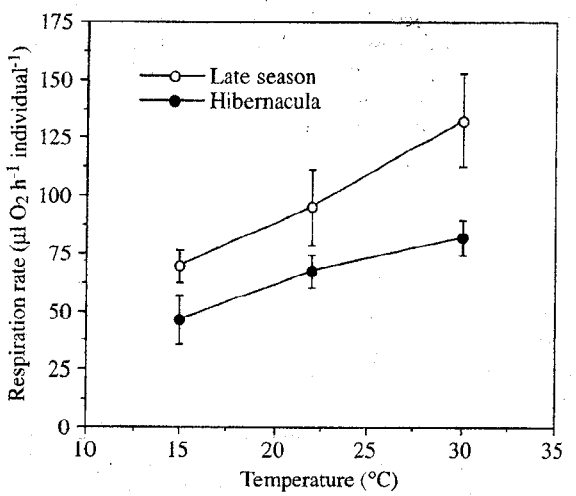

Fig. 3. Temperature profile of respiration rates (mean ± S.E.M., N=8) for larvae of *Gynaephora groenlandica* collected at the end of their feeding season (late June), which were either still active (mean dry mass 68.1 mg) or had already spun hibernacula (mean dry mass 93.7 mg). Two-factor ANOVA showed a significant effect of both temperature (P<0.01, $F_{2,44}$=7.89) and activity status (P<0.01, $F_{1,43}$=11.14), but no significant interaction between the two factors (P>0.05, $F_{2,44}$=0.70).

increasing temperature for both fed and starved larvae (Table 1). Over any given temperature range, Q_{10} was greater for starved larvae than for fed larvae.

During the June 1995 field season, temperatures at the surface of the *S. arctica* microhabitat (where *G. groenlandica* larvae fed) ranged from 0 to 32 °C, with a mean value of 10.6 °C. The experimental temperatures used in this study were therefore consistent with the thermal environment normally experienced by these larvae in the field.

Seasonal changes in larval respiration rate

When compared with mid-season larvae described above, larvae collected late in June (at the end of their feeding season) that had not yet spun hibernacula, but were still active and feeding, exhibited a similar temperature-dependent increase in respiration rate (Fig. 3), although actual respiration rates were much lower than those for fed or starved mid-season larvae (Fig. 2). Those larvae that had already spun hibernacula showed even lower rates of oxygen consumption (Fig. 3). For all temperature ranges, Q_{10} values for respiration rates were approximately 1.5 for both active late season larvae and those that had spun hibernacula (Table 1).

Table 1. *Q_{10} values for* Gynaephora groenlandica *larval respiration rates*

	Temperature range (°C)		
	0.5–15	15–22	22–30
Mid-season			
Fed	4.20	1.90	0.91
Starved	5.33	2.23	1.89
Late season			
Active	–	1.57	1.52
In hibernacula	–	1.73	1.27

Discussion

Larvae of *Gynaephora groenlandica* live 'on the edge' metabolically. Therefore, the ability to rapidly speed up or shut down metabolically with changing temperatures or food availability is important for efficient energy acquisition and utilization. We have demonstrated that larvae of *G. groenlandica* can rapidly and dramatically increase respiration rates after periods of feeding as brief as 12 h. This ability would allow larvae to take full energetic advantage of a feeding opportunity when food is available and conditions are favorable. Their feeding phase in June coincides with the highest nutritional quality of their primary host plant, the arctic willow *S. arctica* L. (Kukal and Dawson, 1989). Unlike most Lepidoptera, which can feed and assimilate food simultaneously, these arctic caterpillars go through alternating periods of feeding and basking, during which time they digest and assimilate food (Kukal, 1993).

This phenomenon of a post-feeding increase in respiration rate above basal levels is termed 'specific dynamic action' (SDA) or 'digestive pause' (McEvoy, 1984). The magnitude of this increase in the rate of oxygen consumption with feeding among insects typically ranges from 40 % in the cockroach (Wigglesworth, 1972), to 55 % in cinnabar moth larvae (*Tyria jacobaeae*) (McEvoy, 1984), to 105 % for larvae of the

armyworm *Spodoptera exempta* (Aidley, 1976) or even to as much as 200 % in larvae of *Manduca sexta* (Gies et al., 1988). The 300 % increase observed in the present study for *G. groenlandica* is therefore remarkable. SDA can also be expressed in terms of the observed decrease in respiration rate after feeding, digestion and absorption are complete. Insects demonstrate variable responses to starvation or cessation of feeding, reducing their metabolic rate by 10–90 % (Slansky and Scriber, 1985; Danks, 1987). For example, larvae of the tobacco hornworm *Manduca sexta* exhibit a 60 % decrease in the rate of CO_2 production when they cease feeding (Alleyne et al., 1997). Some predatory spiders (*Loxosceles* sp.) even suppress their metabolic rate below basal levels during extended periods of starvation (Greenstone and Bennett, 1980). *G. groenlandica* were at the high end of this spectrum in terms of the magnitude of metabolic depression, decreasing respiration rates by 60–85 % in response to starvation. This response appears to be adaptive since it promotes energy conservation and limits nutrient demands during unfavorable conditions when food is spatially or temporally patchy (Kukal, 1993; Slansky and Scriber, 1985).

The duration of SDA varies widely among ectotherms, and *G. groenlandica* appeared to fall among those with the shortest period of elevated metabolic rate; larval respiration rate returned to basal levels in as little as 12 h post-feeding. Hervant et al. (1997) observed changes of similar magnitude in the rates of oxygen consumption of the aquatic micro-crustaceans *Niphargus virei*, *N. rhenorhodanensis* and *Stenasellus virei* in response to feeding and starving. In contrast, the time course of this response was of the order of days or weeks for these crustaceans, rather than within hours as observed in our present study. SDA also lasted 8–14 days in the crustaceans *Carcinus maenas* and *Cragnon vulgaris* studied by Marsden (1973). The 64 % increase in respiration rate for the Antarctic brachiopod *Liothyrella uva* peaked 5 days after feeding, but respiration rate did not return to basal levels until 18 days post-feeding (Peck, 1996). Respiration rate in the Antarctic mite *Alaskozetes antarcticus* at 10 °C decreased by only 30 % after 2 weeks of starvation (Young and Block, 1980). Clarke (1957) reported that the respiration rate of the desert locust *Locusta migratoria* fell gradually over a 50 h starvation period, even though the gut was empty after only 9 h. Gies et al. (1988) reported a two-thirds decrease in respiration rate in *Manduca sexta* within 10–15 h of starvation, although they did not indicate whether this represented a full return to basal levels. The shorter duration of SDA in *G. groenlandica* could potentially increase assimilation efficiency by decreasing the metabolic cost component of the energy budget, allowing them to store more energy instead (Kalarani and Davies, 1994; Wightman and Rogers, 1978).

The capacity to increase respiration rates rapidly with temperature in the low- to mid-temperature ranges (0–22 °C) (Table 1) allows these larvae to take advantage of thermal opportunities for metabolism and food assimilation as daily temperatures increase (Kukal and Dawson, 1989). Basking is also crucial in elevating larval body temperatures, thereby increasing their metabolic rate to levels required for assimilation of their food (Kukal et al., 1988a). This occurs at body temperatures of approximately 15 °C that would not ordinarily be achieved by the larvae in early to mid June without basking, since the mean ambient temperature is only approximately 10 °C (Kukal and Dawson, 1989). At sustained high temperatures of approximately 30 °C, the larval respiration rate appeared to level off or even to decrease for some individuals (Fig. 2; Table 1), indicating that 30 °C may be a physiologically stressful temperature. Furthermore, at these high temperatures, Kukal and Dawson (1989) found that *G. groenlandica* are unable to assimilate energy efficiently from their food.

On the basis of behavioural and metabolic indicators, as

Table 2. *Comparative standard respiration rates for several temperate species of lepidopteran larvae*

Species	Temperature (°C)	Respiration rate ($\mu l\ mg^{-1}$ dry mass h^{-1})	Reference
Arctic			
Gynaephora groenlandica	22	1.64	This study
Temperate			
Bombyx mori	23	0.15–0.2*	Keister and Buck (1973)
Platysamia cecropia	25	0.3*	Keister and Buck (1973)
Galleria mellonella	25	5.5*	Keister and Buck (1973)
Euproctis chrysorrhoea	20	3.06	Migula (1974)
	25	5.06	
Malacosoma neustria	20	3.09	Migula (1974)
	25	4.76	
Spodoptera exempta	25	0.14*	Aidley (1976)
Tyria jacobaeae	25	0.75–0.96*	McEvoy (1984)
Heliothis zea	30	0.5*	Edwards (1970)

*Converted from $\mu l\ mg^{-1}$ live mass h^{-1} assuming 75 % water content.

defined by Danks (1987), the larvae of *G. groenlandica* appear to enter a summer diapause or 'estivo-hibernation' at the end of June. Although caterpillars tend to hide in crevices and vegetation to spin their hibernacula, they are still exposed to abundant sunshine and warm ambient temperatures in July and August before they freeze. Being relatively insensitive to temperature would help to keep metabolic rate low while thermoconforming, thereby conserving energy for the long winter of starvation and subfreezing temperatures.

Previous behavioural observations (i.e. cessation of feeding and spinning of hibernacula) and slowed growth suggest entry into diapause (Kukal and Kevan, 1987; Kukal and Dawson, 1989), and our findings of a distinct metabolic depression in late June confirm this. For larvae collected at the end of June (the end of their feeding season), respiration rates were much lower than they were in mid-June (compare Figs 2 and 3). This effect was even more dramatic in larvae that had already stopped feeding and spun hibernacula (Fig. 3). At this time, the respiration rate was relatively insensitive to changes in temperature (Q_{10}≈1.5; Table 1, Fig. 3), despite the fact that environmental conditions are seemingly favorable, with metabolically permissive warm temperatures persisting through July and into August (Parks Canada, 1994). This seasonal shift to low Q_{10} values of approximately 1.5 was comparable with that observed for the temperate-zone freeze-tolerant larvae of the goldenrod gall fly *Eurosta solidaginis* (Layne and Eyck, 1996). The metabolic suppression and thermal insensitivity accompanying entry into this summer dormancy in *G. groenlandica* may, at least in part, reflect the mitochondrial degradation observed by Kukal et al. (1989).

We compared standard respiration rates (non-feeding) for *G. groenlandica* with those of several temperate species of Lepidoptera over the range of 20–25 °C (Table 2). The arctic species appears to fall well within the range of respiration rates observed for temperate species (Table 2), suggesting that metabolic cold adaptation is not present. Evidence for metabolic cold adaptation would have been provided by a higher standard metabolic rate for the polar species (as reflected by the rate of oxygen consumption) than for corresponding temperate or tropical species at a given temperature (Scholander et al., 1953; Block and Young, 1978; Block, 1981). Many factors contribute to variations in standard respiration rates, including differences in experimental protocols, in methods of measuring oxygen consumption and particularly in species mass. It is well known that the metabolic rates of animals scale allometrically as a power function of body mass. This scaling can be applied either across species of different sizes or to individuals of different mass within a species (Ultsch, 1995). Until the recent development of techniques for precise microrespirometry, it has been difficult to determine this allometric relationship accurately for small arthropods (Lighton and Fielden, 1995). Allometry can account for the wide range of respiration rates reported for lepidopteran species.

The environmental constraints of living in the high arctic imposed on *G. groenlandica* larvae are reflected in their relatively slow growth and long life-cycle compared with those of their temperate counterparts. In combination with the capacity to rapidly and dramatically increase their metabolic rate in response to increasing temperatures and food availability, *G. groenlandica* have addressed the challenges and extremes of a polar environment and thrived. They are metabolic opportunists, using behavioral (basking) and physiological mechanisms to acquire energy efficiently when food is abundant and of high quality and when temperatures are warm. They are also able to conserve energy by rapidly decreasing their metabolic rate when conditions are less favorable. Diapause characterized by suppressed respiration, cessation of activity and retreat to a sheltered, cold microhabitat by larvae after the end of June may also be an important mechanism for conserving energy. The constraints of temperature and a short growing/feeding season imposed by the polar environment on *G. groenlandica* larvae obviously not only have an impact on its metabolism but also shape the evolution of its life history.

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