SELECTION OF OVERWINTERING MICROHABITATS USED BY THE ARCTIC WOOLLYBEAR CATERPILLAR, *Gynaephora groenlandica*

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Abstract

In extreme environments such as the High Arctic, climatic conditions challenge physiological tolerance of insects resulting in prolonged dormancy and extended life cycles. Therefore, the selection of suitable microhabitats for overwintering is crucial. At two field sites on Ellesmere Island, we located hibernacula (silk overwintering structures) used by the Arctic woollybear caterpillar, *Gynaephora groenlandica* (Wöcke) (Lepidoptera: Lymantriidae) during their 11 month dormancy. All hibernacula found were anchored to the base of rocks and were not associated with vegetation. Rocks may function to absorb solar radiation and re-radiate heat, accelerating localized snowmelt, thus allowing caterpillars to emerge as early as possible in spring to begin foraging. Temperatures experienced by *G. groenlandica* in hibernacula throughout the winter were well within their physiological tolerance range. During late summer aestivation, hibernaculum temperatures were similar to, but more stable than, nearby soil surface temperatures. Lower maximum daily hibernaculum temperatures during the warmest month (July) may reduce metabolic rates and provide some energy savings. Since hibernacula were not randomly distributed around rocks, this suggests that *G. groenlandica* key in on some feature of the hibernaculum site. The northeast orientation of hibernaculum at Eastwind Lake corresponds to the leeward side of rocks. Therefore wind patterns may be important in hibernaculum site selection. Other potential cues that may guide selection of hibernacula sites remain unclear: no seasonal changes in preference for light or soil moisture were observed between active and dormant caterpillars, and thigmotaxis could not be distinguished from thigmotaxis.

Keywords: hibernaculum, Lepidoptera, microhabitat, temperature, behavior

INTRODUCTION

Most insects survive winter by entering a dormant stage, that involves a combination of behavioral, physiological, and biochemical adaptations allowing insects to either avoid or tolerate seasonally unfavorable environmental conditions such as low temperature, low humidity, and lack of food (12, 49). Physiological and biochemical mechanisms for cold-tolerance include seasonal synthesis of cryoprotectants, depression of supercooling points,
and synthesis of antifreeze proteins (36, 46). Seasonal changes in cuticular lipids and reduction of water loss rates contribute to desiccation resistance in winter (15, 18, 19). By accumulating lipid and/or carbohydrate stores in the autumn and reducing metabolic rates for the winter, insects are able to tolerate long periods of starvation (12, 51).

Winter survival also depends on selection of appropriate microhabitats where conditions are within an insect’s physiological tolerance range. However, there is much spatial and temporal variability in microhabitat conditions as compared to the macroclimate. Consequently, understanding how insects choose overwintering sites and what microclimate conditions insects actually experience is central to comprehending fully the role of physiological and biochemical adaptations for winter survival. Some insects become dormant in the same place where they are active in summer, while others may move to specific overwintering sites (13, 35). Selection of appropriate overwintering sites is critical. Once insects become inactive and immobile, they are susceptible to predation, parasitism, and are unable to escape unfavorable conditions. Although exposed sites may capture more solar radiation and benefit insects by allowing them to become active earlier in the spring, insects at these sites may experience the harshest winter conditions and may be easy targets for predators or parasites. Sheltered sites offer protection from cold, wind, desiccation, predators and parasites, but they also may delay spring emergence due to attenuation of environmental cues (13).

The Arctic woollybear caterpillar Gynaephora groenlandica (Wöcke) (Lepidoptera: Lymantriidae) experiences one of the coldest and longest winters on the planet. These caterpillars are active for only one month of the year (June), when they are found feeding, basking, and moving about the tundra. They enter dormancy by late June or early July. In captivity, dormant caterpillars spin silken hibernacula and anchor themselves to the sides of holding containers (42, personal observations), or within leaf litter of arctic willow (Salix arctica) in field enclosures (29, 39). However, for free-ranging caterpillars the location and microhabitat conditions of hibernaculum sites are unknown.

The timing of entry into dormancy in G. groenlandica is rather unusual: the highest summer temperatures and peak period of activity for most other arctic arthropods occur in July, not June (11). Although there are benefits to curtailing activity early in the summer [e.g. temporal avoidance of parasitoids (29); decrease in food quality (30)], there are also obvious costs, most importantly a reduction in stored energy reserves that must last through winter. High temperatures during dormancy can be costly in terms of accelerated use of limited energy reserves (20).

The goal of this study was to locate and thermally characterize G. groenlandica hibernaculum sites in the field. Thermal characteristics of these microhabitats are discussed with respect to the insect’s overwintering physiology. Because they enter dormancy so early, G. groenlandica should have behavioral and/or physiological mechanisms to conserve energy during the remainder of the arctic summer as well as through the winter. To maximize energy acquisition during the brief active season, we hypothesize that G. groenlandica will select hibernaculum sites where snow melts relatively early allowing caterpillars to start feeding as soon as possible in spring. Additionally, we hypothesize that hibernacula will be cooler than exposed tundra surfaces in late summer, promoting metabolic depression and, consequently, energy conservation.

**MATERIALS AND METHODS**

*Hibernaculum sites*

Field studies were conducted at Eastwind Lake (80°07.34’N, 85°35.45’W) and Ekblaw Lake (81°39.16’N, 75°44.79’W) study sites on Ellesmere Island, Nunavut, Canada, during
June of 1999 and 2000. During the early stages of spring snow melt at the beginning of June 1999, hibernacula were located by searching snow-free patches of tundra in the vicinity of caterpillars which had just emerged. These sites were characterized by recording substrate type, aspect (compass direction was estimated based on landmarks), vertical distance between hibernacula and tundra surface, and distance to nearest vegetation and its type. In some cases more than one hibernaculum were found clustered together. Therefore we also noted the number of caterpillars using each site. Mean vectors were calculated to describe the distribution of hibernacula around rocks and were analyzed by Rayleigh’s test for Randomness (1).

Temperatures were monitored using HOBO® Pro HR dual channel temperature data loggers (Onset Computer Corp., Pocasset, MA) at one hour intervals over the course of a full year (June 1999 - June 2000). The external thermistor probe was inserted into an abandoned hibernaculum to measure “hibernaculum temperature”. The base of the unit (containing the internal thermistor sensor just below the top of the casing) was buried flush with the soil surface approximately 20cm away from its paired hibernaculum to record exposed soil surface temperature nearby (herein referred to as “surface temperature”). Three complete sets of hibernaculum and surface temperatures were obtained from Eastwind Lake, and two complete sets of surface temperatures and four complete sets of hibernaculum temperatures were obtained from Ekblaw Lake. When data loggers were retrieved the following season (June 2000), we checked to see if caterpillars had returned to the marked hibernacula.

RESULTS

Description of hibernaculum sites

In June 1999, 11 hibernaculum sites were located and marked at Eastwind Lake, and 13 sites at Ekblaw Lake. All 11 sites at Eastwind Lake were found within < 150 m², 2-10 m apart, on a slightly raised plateau which was approximately 30% covered with snow on June 12, 1999, although the entire lakeshore was still snow-covered (> 75%). The Ekblaw Lake study site was at least 80% snow-covered on June 14, 1999, when hibernacula were located in small snow-free patches (< 1 m diameter) which were widely scattered (1-100 m apart) across a large area (> 1000 m²). All hibernacula were anchored to the bases of rocks on gravel or bare soil substrates and typically were not associated with any vegetation. The size of the rocks varied widely from small rocks (4 x 5 x 1 cm) to large boulders (50 x 65 x 20 cm). No hibernaculum were found on bare substrate or within mats of vegetation, even after all snowcover had melted. Most sites contained an individual hibernaculum, although four sites contained two hibernacula, and one site at Ekblaw Lake contained a large cluster of at least six hibernacula.

We are confident that the hibernacula found in June 1999 were in fact used during winter 1998-1999 for two reasons: (1) G. groenlandica caterpillars were frequently found within 1 m of hibernacula, within small snow-free patches of tundra. Since snow appears to act as a barrier to caterpillar dispersal (Kukal, personal observations) and because the snow was just beginning to melt, we assumed that these caterpillars had just emerged from the corresponding hibernacula; (2) there were no signs of the same marked hibernaculum remaining when we returned in June 2000, suggesting that these delicate structures are destroyed (e.g., by blowing sand or wind) and do not persist for more than a year. The absence of caterpillars also suggests that G. groenlandica do not exhibit fidelity to hibernaculum site from year to year, as there were no new hibernacula at these same sites a year later.

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Figure 1: Mean vectors indicating distribution of Gynaephora groenlandica hibernaculum sites at Eastwind Lake ($\varphi = 34^\circ$; $r = 0.87$; $n = 11$) and Ekblaw Lake ($\varphi = 176^\circ$; $r = 0.54$; $n = 13$) (Ellesmere Island, NT, Canada) in June, 1999.

Figure 2: Mean (± SEM) monthly Gynaephora groenlandica hibernaculum (solid lines) and soil surface (broken lines) temperatures at Eastwind Lake (triangles) and Ekblaw Lake (squares) (Ellesmere Island, NT, Canada) from June, 1999 to June, 2000. Asterisks indicate months during which mean monthly temperatures at Eastwind Lake and Ekblaw Lake were significantly different from each other (Bonferroni post-test, $P < 0.004$).
There was a distinctly non-random pattern to the placement of hibernacula at each study site. Hibernacula at Eastwind Lake were directed towards the northeast aspects of the rocks (mean vector \( \varphi = 34^\circ, r = 0.87 \)), whereas at Ekblaw Lake hibernacula were directed towards the south aspect of the rocks (mean vector \( \varphi = 176^\circ, r = 0.54 \); Fig. 1). For both sites, Rayleigh’s test for Randomness indicated a statistically significant directedness (\( P < 0.001 \) and \( P = 0.019 \) for Eastwind and Ekblaw Lakes, respectively).

**Seasonal hibernaculum and soil surface temperatures**

The temperatures recorded by the multiple sets of data loggers within each study site were similar, and therefore considered as replicates of each study site (\( F_{1,134} = 1.55, P = 0.33 \)). Over the course of the entire year, mean monthly hibernaculum temperatures were significantly higher than mean monthly surface temperatures, but by only 0.3-1.2°C (95% confidence interval; Two-factor factorial repeated measures ANOVA: \( F_{1,134} = 12.38, P < 0.01 \)) (Fig. 2). Although Eastwind and Ekblaw Lakes are separated by 245 km and 450 m elevation (Ekblaw Lake ~600m, Eastwind Lake ~150m), microhabitat temperatures at these study sites were remarkably similar during the warmer parts of the year: June–October 1999 and April 2000. Mean monthly temperatures at Eastwind Lake were significantly lower throughout the winter (November 1999–March 2000), but higher in May and June 2000 (effect of lake site: \( F_{1,134} = 25.50, P < 0.01 \); lake x month interaction: \( F_{12,134} = 42.23, P < 0.01 \)) (Fig. 2).

Maximum yearly hibernaculum and surface temperatures were similar at both Eastwind and Ekblaw Lakes (21-25°C; Table 1). In late August, the first frost occurred approximately 1 week later in hibernacula than on exposed soil surface. Minimum yearly hibernaculum temperatures occurred in late January and were much colder at Eastwind Lake (-41.4 ± 1.2°C) than at Ekblaw Lake (-33.1 ± 0.6°C) (Table 1). Spring thaw occurred later at Ekblaw Lake as reflected in May and June 2000 mean temperatures. Data loggers were exposed by June 12, 2000 at Eastwind Lake, while some data loggers were still buried under as much as 30 cm of snow on June 15, 2000 at Ekblaw Lake. Thermal buffering due to deeper snow cover may account for the higher winter temperatures recorded at Ekblaw Lake despite its higher elevation.

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<th>Table 1. <em>Gynaephora groenlandica</em> hibernaculum temperatures (°C; mean ± S.E.M., n=4) recorded at two study sites on Ellesmere Island, Nunavut, Canada, June 1999-June 2000 at 1h intervals.</th>
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<tr>
<td><strong>Ekblaw Lake</strong></td>
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<td><strong>Hibernaculum</strong></td>
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<td>Maximum yearly temperature (date)</td>
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<td>Date of first frost (minimum daily temperature &lt;0°C)</td>
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<td>Minimum yearly temperature (date)</td>
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<td>(January 27)</td>
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In July (the warmest month), under the influence of 24 h of sunlight, both hibernaculum and surface temperatures reflected distinct diel periodicities. Although the difference between hibernaculum and surface mean monthly temperatures was small (Fig. 2), daily temperatures fluctuated over a wider range at the surface (10.2 ± 0.4°C per day at Eklaw; 9.7 ± 0.5°C at Eastwind) than within hibernacula (7.8 ± 0.4°C per day at Eklaw; 5.1 ± 0.4°C at Eastwind) (Fig. 3). Mean monthly hibernaculum temperatures were less than 1°C higher than surface temperatures, but recorded temperatures were anywhere from 10°C higher during the coldest part of the day to 7°C lower during the warmest part of the day. In January, under snowcover, and without the influence of sunlight or wind, hibernaculum and surface temperatures fluctuated very little on a daily basis (1-2°C).

Figure 3: Soil surface (solid lines) and Gynaephora groenlandica hibernaculum (broken lines) maximum (closed symbols) and minimum (open symbols) daily temperatures (°C) during July 1999 at a representative site at Eastwind Lake (Ellesmere Island, NT, Canada).

DISCUSSION

For insects that spend the winter season in dormancy, survival depends on a combination of behavioral, physiological, and biochemical adaptations. In extreme environments such as the High Arctic, where climatic conditions challenge physiological tolerance resulting in prolonged dormancy and extended life cycles, the selection of suitable microhabitats for overwintering is crucial. The microhabitat (in contrast to macroclimatic) conditions experienced by arctic insects were characterized in the 1950’s and 1960’s when extensive meteorological and climatic work was done at Lake Hazen, Ellesmere Island (Nunavut, Canada) (7-9, 11, 23, 42, 43). Additional studies have focused on explaining the presence and distribution of insect fauna in the Arctic based on climatic conditions (17, 18) and the influence of extreme environmental conditions on life-history characteristics of polar insects (4-6, 10, 15). Later studies focused on the importance of microhabitat temperatures for behavioral thermoregulation and physiological performance during the brief arctic summer (24-27, 31, 33). The present study focuses specifically on how microhabitat conditions during prolonged dormancy contribute to winter survival of an arctic insect (G. groenlandica) for
which physiological mechanisms associated with cold-hardiness and winter survival have already been documented (3, 29, 32, 35).

Hibernacula used by *G. groenlandica* caterpillars were consistently found anchored to the base of rocks in the present study, although previous studies reported that *G. groenlandica* spin hibernacula within vegetation and leaf litter (30, 41). However, in those previous studies caterpillars were confined to field enclosures from which large rocks were excluded to maximize vegetation coverage, thus restricting their microhabitat choices. One potential advantage to overwintering away from vegetation may be the avoidance of parasitoids (30, 34), since most insect activity is associated with vegetation (12). In addition, caterpillars may also reduce the risk of being trampled or accidentally ingested by large herbivores, such as muskoxen (*Ovibos moschatus*) and arctic hares (*Lepus arcticus*) (39, 47), which also feed on the same vegetation.

**Seasonal hibernaculum and soil surface temperatures**

Although hibernaculum temperatures were not significantly higher than soil temperatures, the hibernaculum sites selected by *G. groenlandica* were the first areas to become snow-free in spring, which would facilitate early emergence. On a featureless tundra, where even vegetation is prostrate (43, 45, 46), darker rocks which protrude to the surface of the snow pack can function to absorb solar radiation and re-radiate heat, accelerating localized snowmelt. Selection of such overwintering microhabitats allows caterpillars to maximize the length of their summer active season by emerging as early as possible in spring.

During winter (September through April), hibernaculum temperatures were well below the supercooling point of *G. groenlandica* (-7 to -8°C) (35). The lowest recorded winter temperatures (-33 to -43°C; Table 1) were still well within the physiological tolerance range of *G. groenlandica* which readily survive to -70°C (35). Because of snowcover and the onset of continuous polar night (sun below the horizon), there were no signs of diel fluctuations.

Even though *G. groenlandica* metabolic rates and Q_{10} values are significantly reduced upon entry into dormancy (3), the thermal characteristics of hibernaculum sites chosen by *G. groenlandica* can influence their overwintering energetics. During late summer aestivation, hibernaculum temperatures were not significantly lower than nearby soil surface temperatures (based on mean monthly temperatures), as we had hypothesized (Fig. 2). However, on a daily basis, hibernacula provided a more thermally stable microhabitat (Fig. 3) in which hibernacula were warmer than exposed soil surfaces during the coldest part of the day but colder during the warmest part of the day. The energetic benefit of lower maximum daily temperatures may outweigh the cost of higher average and minimum daily temperatures. Irwin & Lee (21) clearly demonstrated that microhabitats with slightly depressed temperatures, especially under warmer conditions, provide a significant energetic savings for overwintering *Eurosta solidaginis* larvae by keeping metabolic rates lower, and consequently result in higher survival and fecundity. In addition, lower oxygen consumption and slower growth rates have been reported for aquatic insects in more stable, but fluctuating thermal environments (49, 50). Further analysis and modeling of *G. groenlandica* metabolism during dormancy is warranted.

**Selection of hibernaculum sites**

Since hibernacula were not randomly distributed around rocks (Fig. 1), it appears that *G. groenlandica* key in on some feature of the hibernaculum site. Therefore, to determine seasonal changes in preferred microhabitats, active and dormant caterpillars were compared in terms of their behavioral preferences for light, surface temperature, and soil moisture. However, potential cues that may serve to guide *G. groenlandica*’s selection of hibernacula sites remain unclear. Both active and dormant *G. groenlandica* showed a moderate
preference for light. No preference for soil of a particular moisture content was observed for either active or dormant caterpillars. In our attempt to test for seasonal changes in temperature preference (thermotaxis), we encountered a confounding effect of thigmotaxis (i.e., a tendency for caterpillars to maximize body contact with their surroundings), which was manifest as a significant preference for the ends of the test chamber even in the absence of a thermal gradient. The observed thigmotaxis is consistent with the fact that hibernacula were always found against rocks in "nooks and crannies", suggesting that thigmotaxis is an important cue in selection of hibernaculums and is worthy of further investigation. Positive thigmotaxis promotes the formation of overwintering aggregations in some species of caterpillars (28, 36, 50), and has been associated with "hiding behavior" and entry into hibernating sites in diapausing Cletus punctiger (22).

Another possible cue for further investigation is rheotaxis, or movement in response to the direction of prevailing winds. The orientation of hibernacula differed between Eklblaw and Eastwind Lakes: hibernacula were directed towards the northeast aspects of the rocks at Eastwind Lake, but towards the south aspect of the rocks at Eklblaw Lake (Fig. 1). This suggests that some environmental component to which the caterpillars respond, perhaps wind, differed between these two field sites. At Eastwind Lake during the summer months (June – August) prevailing winds were from the southwest/west (1995 and 1996; G.H.R. Henry, unpublished data). Therefore it appears that G. groenlandica place their hibernacula on the leeward sides of rocks, perhaps to minimize the desiccating effects of the wind. Although leeward locations accumulate the deepest snow in winter (38), which would delay snow melt and resumption of caterpillar activity in spring, during most of the year prevailing winds at Eastwind Lake are from the southeast (1995 and 1996; G.H.R. Henry, unpublished data). Hibernacula were found on the sides of rocks that were perpendicular to accumulated drifts where snow cover would be shallower and caterpillars would be able to emerge during the earliest stages of spring snowmelt (14, 36). Although no data on prevailing winds are available for Eklblaw Lake, we observed obvious snowdrifts extending east and west from large rocks at Eklblaw Lake, where hibernacula were generally found on the south faces of rocks.

Physiologically, G. groenlandica are well suited to the thermal challenges of the High Arctic. Furthermore, success in this extreme environment can be attributed in part to selection of overwintering microhabitats which (1) allow G. groenlandica to maximize their active season by emerging as early as possible each spring, and (2) are thermally stable in late summer, possibly providing some energetic savings. In addition, the correlation between hibernaculum orientation and prevailing wind direction suggests that G. groenlandica may select overwintering microhabitats which minimize desiccating effects of wind. Future studies should explore and model the relationship between hibernaculum temperatures and G. groenlandica energetics, as well as behavioral cues, such as thigmotaxis and rheotaxis, which may guide hibernaculum site selection and explain hibernaculum distribution.

Acknowledgements: This work was supported by the Polar Continental Shelf Project, NSERC, Atlantic Low Temperature Systems, Ltd. (to O. Kukal), and by NSF grant IBN 0090204 to R.E. Lee. Thanks to M. Hughes and E. Szepesi for assistance with data analysis.

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Accepted for publication 9/6/03