Behavioural Thermoregulation by High Arctic Butterflies[1]

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ABSTRACT. Behavioural thermoregulation is an important adaptation of the five high arctic butterflies found at Lake Hazen (81°49'N., 71°18'W.), Ellesmere Island, Northwest Territories. Direct insolation is used by arctic butterflies to increase their body temperatures. They select basking substrates and precisely orientate their wings with respect to the sun. Some experiments illustrate the importance of this. Wing morphology, venation, colour, hairiness, and physiology are briefly discussed.

RÉSUMÉ. *Comportement thermo-régulatoire des papillons du haut Arctique.* Chez cinq espèces de papillons trouvés au lac Hazen (81°49' N, 71°18' W), île d'Ellesmere, Territoires du Nord-Ouest, le comportement thermo-régulatoire est une importante adaptation. Ces papillons arctiques se servent de l'insolation directe pour augmenter la température de leur corps: ils choisissent des sous-strates réchauffantes et orientent leurs ailes de façon précise par rapport au soleil. Quelques expériences ont confirmé l'importance de ce fait. On discute brièvement de la morphologie alaire, de la couleur, de la pilosité et de la physiologie de ces insectes.

РЕЗЮМЕ. *Механизм регулирования температуры тела бабочек на Крайнем Севере.* Регулирование температуры тела является важным методом адаптации бабочек, обнаруженных на оз. Хейзен (о. Элсмира, 81°49'N., 71°18'W.), к суровому климату Крайнего Севера. Выбирая соответствующие субстраты и тщательно ориентируя свои крылья, бабочки используют непосредственное облучение солнцем для повышения температуры тела. Дается краткое описание крыльев, иннервации, волосистости и физиологии исследованных бабочек.

INTRODUCTION

Basking in direct sunlight has long been known to have thermoregulatory significance for poikilotherms (Gunn 1942), particularly reptiles (Bogert 1959) and desert locusts (Fraenkel 1930; Stower and Griffiths 1966). Clench (1966) says that this was not known before in Lepidoptera but Couper (1874) wrote that the common sulphur butterfly, *Colias philodice* (Godart) when resting on a flower leans sideways "as if to receive the warmth of the sun". Later workers, noting the consistent settling postures and positions of many butterflies, did not attribute them to thermoregulation, but rather to display (Parker 1903) or concealment by shadow minimization (Longstaff 1905a, b, 1906, 1912; Tonge 1909). Longstaff (1906) mildly discredits Couper's (1874) observations, but later (Longstaff 1912) concedes that this point of view may be valid in conjunction with his own ideas. A clarification of this difference in opinions is found in Tulloch's (1913) observa-

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tions on the great sulphur, *Catopsilia pomona* (F.). These butterflies, he says, bask laterally (see below) during cool times, and are then visible from 50 yards; but normally they stand upright and are difficult to see. Most of Longstaff's data come from warm countries, where concealment would be more important than thermoregulation. Other contemporary observations on the thermoregulatory postures of butterflies are given in Radl (1903), Pictet (1915), and Winn (1916).

Winn (1916) discusses two resting postures of butterflies in relation to thermoregulation. The first, exemplified by *C. philodice* is termed "lateral basking" by Clench (1966) and corresponds to Couper's (1874) description. These butterflies hold their wings closed, and their bodies so that the wings are normal to the sun's rays. The second, called "dorsal basking" by Clench (1966) is exemplified by the mourning-cloak, *Vanessa antiopa* L. and described most lucidly by Parker (1903). These butterflies hold their wings wide open to insolation with various angles of orientation to the sun. Most commonly they settle facing directly away from the sun with the anterior part of the body held higher than the posterior. Clench (1966) adds two other behavioural devices used by butterflies to absorb radiant heat. In "body basking", which he saw only in the cabbage butterfly, *Pieris rapae* L., the wings are held open just enough to allow insolation of the body. In "ground contact", which is restricted to species living in places where bare ground is part of the natural environment (e.g. arctic and alpine tundra), the butterflies appress themselves to the substrate and absorb conducted, convected, and radiated heat.

Herter (1953) gives a brief discussion of the significance of solar warming in butterflies based on some early work. The subject seems to have remained dormant for nearly 40 years after Winn's (1916) research, until Vielmetter (1954, 1958) examined in detail the physiology of temperature regulation by *Argynnis paphia* L. (a fritillary). He found that these dorsal baskers may have body temperatures as great as 17°C. above the ambient air temperature, and that through changing the position of their wings they could maintain their body temperatures between 32°C. and 37°C. in direct sunlight. Clench (1966) discusses heat-conserving behaviour (e.g. wind avoidance) and "myothermic" body warming in the evening, as well as basking at different times of the day. Of particular interest are his remarks on the morphological devices used to effect more efficient absorption of radiation; these devices pertain mainly to the wings; in particular, their colour, tracheation, venation, circulation, cuticular thickness dorsally and ventrally and over the veins, and mobility.

At Hazen Camp (81°49′N., 71°18′W.) where most of the present work was done, there are 5 species of butterfly (Oliver 1963) which are all widespread arctic forms: a sulphur, *Colias hecla* Lef. (Pieridae); two fritillaries, *Boloria chariclea* Schnied. and *B. polaris* Bvd. (Nymphalidae); a copper, *Lycaena feildeni* McLach. and a blue, *Plebius aquilo* Bvd. (Lycaenidae). The two species of *Boloria* are superficially virtually identical in appearance. Thus the term *Boloria* in the first part of the present text includes both species; specimens used in experiments were subsequently identified to species.

Downes (1965) mentions basking by arctic insects and relates this to increased melanism and hairiness in these species. Hairiness may increase absorption of radiation, as well as decreasing heat loss (Krog 1955). Freeman (1958) mentions that these adaptations enable the adult butterflies to trap heat from solar radiation, which allows them to become active when the sun is shining, even though the temperature of the air is too low.

OBSERVATIONS: SUBSTRATE SELECTION, BODY POSITIONING, AND FLIGHT

The most important factor that influences the flight activity of arctic butterflies is their body temperature. Parry (1951) has considered the importance of the increased temperature of the air immediately above the ground in conjunction with poikilotherm activity. This is especially important in the high arctic where the flight of most insects is restricted to within the first metre above the ground. Out of 47 observations made on the flight height of *Boloria* spp. one was observed at 60 cm., all others at 45 cm. or below. Parry (1951) also mentioned the effect of the decrease in wind strength close to the ground.

Gunn (1942) stated that there must be some conduction of heat between an insect and any solid surface with which it may be in contact, but that little is known about the magnitude of any such exchange. The direct conduction of heat from the substrate to insects' bodies is used extensively by both species of *Boloria,* and by *Plebius aquilo*. By carefully selecting basking substrates, or orienting their wings with respect to the sun, or both, all species of butterflies at Hazen Camp can increase their body temperatures to allow frequent flights.

Notes on the characteristics of forty-five of the substrates used by *Boloria* spp. were made. A representative sample of these is presented in Table 1, from which it can be seen that the substrate temperature was always well above the air temperature at 24 cm., the difference ranging from 2.0°C. to 8.5°C. The most frequented settling substrate, apart from flowers (Kevan 1970), was the side of *Dryas integrifolia* Vahl. hummocks, on either the vegetation or bare soil, as in Fig. 1a. This accounted for 40 per cent of the observations. Grey soil, with 14 records, accounted for 31 per cent of the observations. Less frequently used were wet mud (5 records), small boulders in creek beds (4 observations), rock faces (2 records. See Fig. 1b), and other soils (2 records).

TABLE 1. Substrate Selection.

Date	*Substrate*	*Substrate Temp. °C*	*Temp. 24 cm. °C*	*Temp. 1 m. °C*
Boloria spp.				
14-VI-67	*Dryas* hummock	11.5	10.3	10.0
20-VI-67	" "	9.5	7.0	4.5
26-VI-67	" "	20.5	13.3	11.0
27-VI-67	" "	26.0	22.0	17.8
19-VI-67	Grass on side of *Dryas* hummock	10.0	8.3	6.0
20-VI-67	Grey soil	17.8	10.0	4.0
26-VI-67	" "	16.0	12.8	7.8
15-VII-67	" "	16.0	12.8	7.8
27-VI-67	Grey soil at base of a rock	26.8	18.3	17.0
15-VI-67	Mud in creek	15.5	11.7	6.0
26-VI-67	Large rock face	22.0	17.8	15.0
Plebius aquilo				
16-VII-67	Rocky hollow	24.0	18.5	12.8
19-VII-67	Grey soil	24.0	16.0	15.0

The only thermoregulatory position observed for *Boloria* spp. was with the wings spread and pressed against the substrate. The butterflies always attempted to adopt a position with their wings at approximately 90 degrees to the sun's rays,

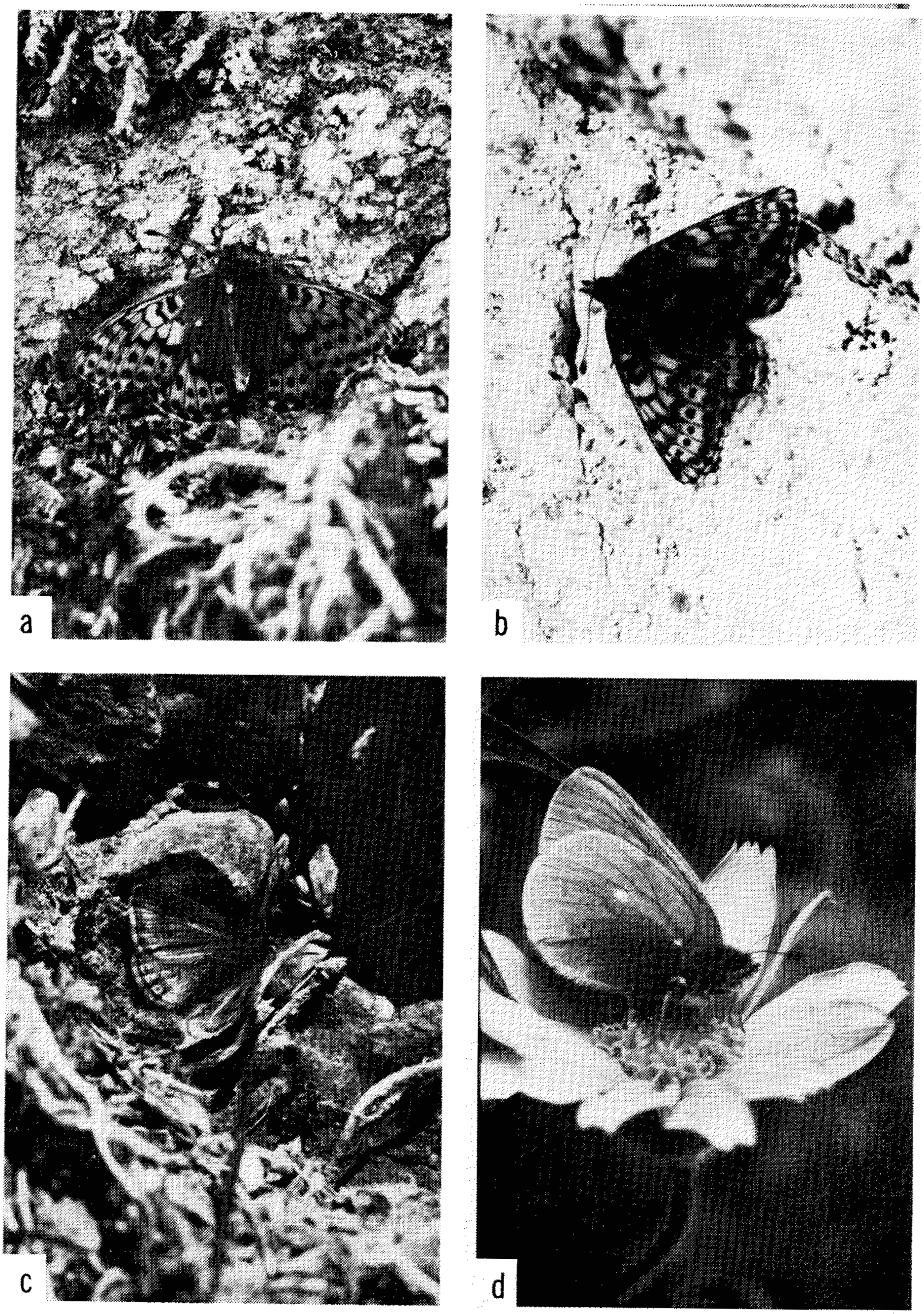

FIG. 1. Thermoregulating butterflies: a) *Boloria* sp. on *Dryas* hummock, b) *Boloria* sp. on rock face, c) *Plebius aquilo* in hollow of rocky creek bed, d) *Colias hecla* on *Arnica alpina*.

and with their heads away from the sun. When landing on flat ground, *Boloria* spp. raised the anterior part of the body to bring the wings closer to normal to the sun's rays. However, one individual which landed as a cloud was covering the sun did not orient itself until the sun reappeared. On four other occasions *Boloria* spp. already in the basking position were seen to close their wings as the sun was obscured by passing clouds.

Fifty-seven individuals of *Boloria* spp. were observed feeding on the inflorescences of such plants as *Arnica alpina* (L.) Olin., *Dryas integrifolia,* and *Salix arctica* Pall. (Kevan 1970). While feeding they always held their wings spread, although the precise orientation of the head away from the sun was displaced as the butterflies probed around the flowers for nectar. Even in copulation they maintained the dorsal basking posture, although orientation was not precise (from a photograph by K. W. Richards at Hazen Camp, 22 June 1968). *Boloria* spp. are "dorsal baskers" and combine this with "ground contact" as is shown in Figs. 1a and b.

Plebius aquilo may also land on the sides of Dryas hummocks to warm themselves, but when doing so it seems to select more protected parts of the microtopography (see Table 1). These butterflies are most frequently seen flying along the eroded courses of creeks. Here they may land and orientate in hollows (Fig. 1c) of the rocky bed, or they may land a short distance from such a hollow and then crawl into it. They rest with their wings open and sometimes pressed against the substrate, facing the sun, and with their heads directed away, much as in *Boloria* spp. Nine observations were made on the settling substrates used by this species; 5 were on grey soil, 3 in hollows as described above, and 1 on a rock face. On one occasion the temperature of the resting site was 11 deg. C. warmer than the air temperature at 1 metre above it.

When individuals of *P. aquilo* were engaged in other activities the basking posture was somewhat different. In 2 observations of their drinking water from wet moss and some 20 observations of nectar-feeding from flowers (Kevan 1970), they rested with their wings half open, but not appressed to the substrate. As previously, the head was directed away from the sun. This position corresponds closely to "body basking". On 13 occasions when these butterflies were observed feeding on the spikes of *Polygonum viviparum* L. for nectar they assumed an inverted position with their heads vertically downwards (this was noted by Parker (1903) for *Vanessa antiopa*), and with their wings still held open to allow irradiation of the body.

Lycaena feildeni is the least common butterfly around Lake Hazen. Adults were not observed 'thermoregulating' on the ground. While they were feeding on nectar [2 observations on *Taraxacum* sp., 1 on *Arnica alpina,* and 1 on *Polygonum viviparum* (Kevan 1970)] their posture was identical with that of *P. aquilo* as noted above.

The Lycaenidae combine dorsal basking with ground contact (*P. aquilo* at least) and exhibit body basking while they are feeding.

Colias hecla was also rather uncommon in the Lake Hazen area. It, too, was never seen in any thermoregulatory position on the ground. On 13 occasions it was noted on flowers (10 of these on *A. alpina* at Gilman Camp; Kevan 1970) where it assumed the "lateral basking" position while at rest as in Fig. 1d. During feeding the lateral positioning was displaced, and the wings were still held closed over the body.

The great significance of solar basking is shown by the increased butterfly activity on sunny days. In 1968, 8 July and 4 August were the first and last days on which *Boloria, P. aquilo,* and *C. hecla* were all seen. During this period of 28 days, 11 were totally cloudy. On 7 of these 11 days no butterfly was seen, while only 2 of the 17 sunny days were without butterfly sightings; this, despite the temperatures in a Stevenson screen on some cloudy days being as much as 3.4 deg. C. higher than on sunny days when butterflies were seen.

Most of the flight activity of the butterflies in the High Arctic occurs in gullies and creeks, and in small cuts and depressions in the sides of hills. In both situations temperatures of the air and of the substrate are higher, and wind is considerably reduced compared with exposed places. On one occasion in 1967 as many as 15 of both *Boloria* and *P. aquilo* were seen flying and basking in a small depression about 2 m. long and 0.5 m. deep into the base of Mount McGill. These observations were made on a windy day, but the air within the depression was almost calm. Many butterflies flying outside this area were blown along by the wind and steered themselves into the depression for protection. The temperature of the substrate in the protected area was 24.5°C. compared with 12.7°C. outside; the temperature of the air 24 cm. above the ground was 12.7°C. within the protected area and 11.0°C. outside; and at 1 m. above the ground the air temperature was 11.1°C. in the depression, against 9.5°C. outside. During the next year 11 *Boloria* and 9 *C. hecla* were seen flying up and down the gully of an unnamed creek 55 km. east of Hazen Camp. The gully was windless and hot, while at the top of the steep banks there was a chill breeze and no butterfly was seen.

EXPERIMENTAL

The body temperatures of some specimens of *Boloria chariclea* in various postures and sites in sunshine and shade were measured. Copper-constantan thermocouples 0.2 mm. diameter and about 1 mm. long were used. One couple was introduced into the thorax from behind through the membrane between the abdomen and thorax and pushed through the foramen until it was judged to lie between the flight muscles. The reference couple was hung in the air close by to give a direct relationship between potential difference and the butterfly's thoracic temperature excess above ambient. The ambient air temperature was taken throughout the experiments with a bimetal strip dial thermometer in the shade next to the apparatus.

At Gilman Camp, 32 km. east of Hazen Camp, on 17 July 1967, during periods of no wind or cloud, a specimen of *B. chariclea* was mounted on three different substrates. Its wings were held wide open by two thin strips of paper pinned to the substrate and the butterfly was normally oriented to the sun's rays, with its head uppermost, as in the thermoregulatory posture, and allowed to equilibrate for 10 minutes. The 3 substrates used were black flock paper, assumed to absorb all the solar radiation; aluminum foil, the most reflective material available

TABLE 2. The Influence of Substrate on the Body Temperature of *Boloria chariclea*.

Substrate	*Mean body temperature °C*	*Range °C*	*No. of readings*	*Mean ambient temperature °C*
Black flock paper	30.8	28.3-32.0	6	16.0
Aluminum foil	27.8	27.8	2	16.0
Clay clod	27.2	—	1	16.0
Brown cardboard (dorsum up)	28.6	28.5-28.8	2	17.5
Brown cardboard (venter up)	26.3	—	1	17.5

(although known to absorb infra-red radiation quite strongly); and a clod of light brown clay, taken as a natural basking surface.

The results of this experiment (Table 2) show that basking in sunshine has a profound effect on the insect's temperature excess (9 to 13°C.). The nature of the substrate is also important, black flock paper contributing an extra 3.0°C. and 3.6°C. to the butterfly's body temperature when compared with the excess on aluminum foil and clay.

On the same day, and sometimes at the same time, warming and cooling rates were studied with specimens on the three substrates. At time zero the butterfly was shielded from the sun or exposed to it for cooling or warming respectively. Temperature readings were made every 15 seconds for the first 90 seconds, and subsequently as often as needed, until the butterfly's body temperature had reached equilibrium. The results of this experiment are presented in Fig. 2.

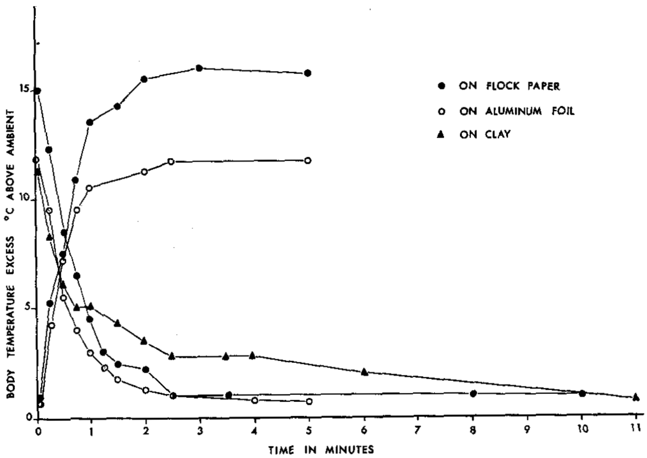

FIG. 2. Warming and cooling times of *Boloria chariclea* on different substrates: on black flock paper; on aluminum foil; on clay clod.

The warming and cooling rates on both the flock paper and aluminum were almost identical, although the temperatures attained were different as expected from Table 2. Equilibrium was reached after about 2.5 minutes, for both warming and cooling on these two substrates. Irregularities in the curves can be accounted for by small changes in the ambient air temperature, light gusts of breeze, and struggling on the part of the insect. The fact that both warming and cooling took the same time indicates that no effort was made by the butterfly to maintain its elevated body temperature by muscular activity. Similar results were obtained for various Diptera (Kevan 1970).

On the clay clod the cooling rate began similarly to that on the other two substrates, but after the butterfly's body temperature had dropped to 5°C. above ambient the cooling rate was greatly attenuated as the butterfly absorbed the re-radiated heat from the lump of clay. In this case cooling took 11 minutes or more. After this experiment the butterfly no longer responded to prodding and was assumed to be dead. The body temperature of a live butterfly never dropped quite to ambient, but remained between 0.7°C. and 1.0°C. higher.

On 19 July 1967 under similar weather conditions, an experiment was set up to compare the effects of the dorsal and ventral sides of the wings on the body temperature excess. A specimen was mounted as before, but on a sheet of brown cardboard, first venter and then dorsum to the sun. While "basking" on its back the temperature excess attained was 8.8°C., while in its natural position the excess was 11.1°C. (similar to the results obtained on clay, Table 2). This clearly indicates that the two sides of the wing are substantially different in their abilities to absorb solar radiation. Although they appear much the same colour, the underside is lighter with more white patches. In addition the dorsal cuticle overlying the veins may be thinner than that on the ventral side (*cf.* Dixey 1931; Clench 1966).

At the same time an experiment was made to investigate the effect of the angle of repose of basking butterflies. The insect was tilted about its transverse axis at various angles with respect to the sun, the plane of the insect passing from normal to the sun's rays, with its head uppermost, through to parallel to the sun's rays, with its head lowermost. Temperatures were taken after allowing time for equilibration at each angle.

The results of this experiment are given in Fig. 3 and show that the body temperature falls off with the cosine of the angle of solar incidence, as expected. The cosine curve is drawn on Fig. 3 taking 11.1°C. at 90 degrees (normal to the sun) as the reference point. The minor differences obtained can be explained by experimental error, or may be due to the fact that the veins stand up slightly from the wing surface and are so exposed to more insolation than the cosine relationship would suggest. The experiment clearly demonstrated that these butterflies could regulate their body temperatures by altering the angle of incidence of their wings to the sun.

All the above experiments were conducted in the open air where conditions could not be controlled or measured. The results obtained, therefore, do not, nor were they intended to, give *absolute* values, but they do indicate the degree of body temperature excesses which *B. chariclea* can achieve by behavioural positioning and substrate selection. Although we did not duplicate individual experiments, the results complement one another and lend validity to the series. Our findings compare well with those of Vielmetter (1958).

It is not understood why the butterflies' body temperatures fell to ambient in the shade in some experiments, but failed to do so in others. In no experiment did the insect die before complete results were obtained, but there was no way to assess the extent of internal injuries caused by the insertion of the thermocouples.

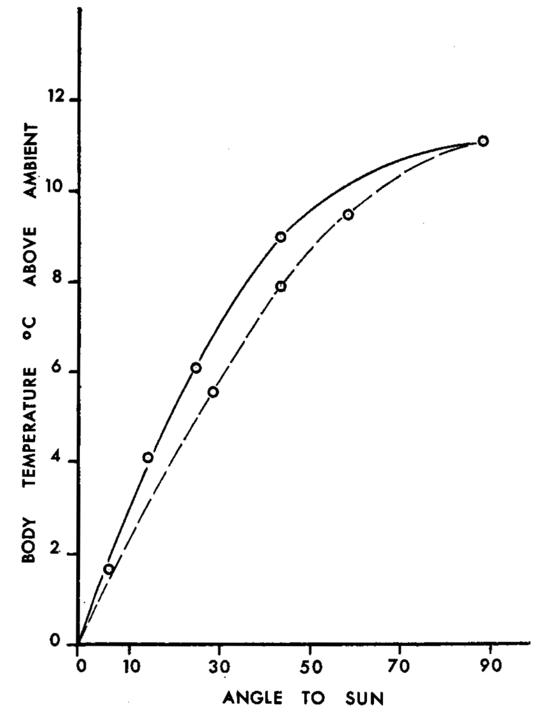

FIG. 3. Body temperature excess of *Boloria chariclea* according to the solar angle of incidence. Solid line, body temperature excess above ambient air (17.5 °C.); broken line, theoretical cosine relation using maximum body temperature excess as the reference point.

DISCUSSION AND CONCLUSIONS

Arctic animals have evolved mechanisms through which they maintain sufficient activity for survival in their harsh environment of low heat budget. In butterflies one such mechanism is behavioural thermoregulation by which they absorb solar heat directly and indirectly from the earth. The use of direct solar energy (i.e. basking) is more important and found in all species of butterflies studied. *Boloria* spp. are dorsal baskers, the Lycaenidae are body baskers, and *C. hecla* is a lateral basker. Experiments on *B. chariclea* show that body temperature excesses generated are great, and that the angle of the exposure of their wings to the sun is of paramount importance (Fig. 3). Thus dorsal baskers and body baskers settle on sunny slopes or elevate the anterior parts of their body, or both, to position themselves closer to the sun's rays; while the lateral baskers lean away from the sun to achieve the same end.

Basking butterflies, particularly dorsal and lateral baskers, regulate their heat gain by varying the area of wing surface exposed to the sun by controlling the overlap of the fore and hind wings. Vielmetter (1958) concluded that *Argynnis paphia* did this for fine control of its body temperature. We did not examine this aspect of behavioural thermoregulation although a comparison of Figs. 1a and 1b suggests that it may occur in *Boloria*.

Linked with the patterns of basking behaviour are some special features of the wings, notably their colour. The experimental evidence on the comparative absorption of solar radiation by dorsal and ventral surfaces of the wings of *B. chariclea* confirms that their colour is important. The dorsal surface has veins strongly picked out in black (Figs. 1a and b) and is darker and hairier than the ventral surface, which has patches of whitish-silver and less prominent venation. The lighter-coloured venter may reduce radiative heat loss. In *C. hecla* the ventral surfaces of the wings, particularly the hind wings, are darker than the bright yellow dorsal surfaces. It is significant that this lateral basker makes most use of the ventral surface of one hind wing at a time (Fig. 1d). The veins in *C. hecla* wings are not notably darker than the general wing surface on either side.

Increased melanism at higher latitudes is notable in both *Boloria* spp. and *Colias* spp., but the reverse appears to be true in the Lycaenidae where both *L. feildeni* and *P. aquilo* show loss of colour when compared with their more southerly counterparts (Downes 1964). Presumably increased melanism would be of minor importance for body basking. In *P. aquilo* the undersides of the wings are lighter, with patches of white or off-white (*cf. Boloria,* above), than the dorsal surfaces. On both wing surfaces the veins are picked out in darker shades.

Although our data agree in part with Clench's (1966) remarks on the colours of butterflies, melanism and colour patterns in insects generally seem to have minor effects on body temperature excesses due to non-differential absorption in the infra-red (*cf.* Digby 1955; Gunn 1942).

One other matter for consideration is the possibility of a thinner cuticle being present over the veins on the insolated side of the wings; dorsally in dorsal baskers and ventrally in lateral baskers. This aspect of morphology needs further study before a conclusion can be drawn.

Butterfly resting sites so far described in the literature are usually attributed to feeding, or cryptic protection, or both, rather than to thermoregulation; nevertheless ground contact is important for thermoregulating butterflies receiving heat re-radiated from the earth. Clench (1966) says "I have not seen ground contact heating used except where bare ground was a part of the natural environment." Hummocks with very low vegetation, and bare ground are characteristic of the high arctic environment, and are used for ground contact warming (combined with basking) by *Boloria* spp. and at least *P. aquilo* of the Lycaenidae. Table 1 gives some examples of temperature elevations of insolated natural surfaces used by butterflies combining basking and ground contact. The diversity of substrates used suggests that substrate selection has less significance than body positioning, although experiments (Table 2 and Fig. 2) indicate that it could be important. More work is needed to elucidate this problem. Certainly butterflies using ground contact have more heat available to them than those resting on plants above ground level. The slow cooling of the soil during cloudy spells attenuates the cooling rates of the butterflies in contact with it (Fig. 2). This would enable them to become active sooner after the sun reappeared than those resting on the plants above.

Observations on the activity of high arctic butterflies show that they are most often found in warm, relatively windless, sheltered places where, on sunny days, they fly in the warmest air close to the ground.

It seems, therefore, that the butterflies of the High Arctic around Lake Hazen are dependent on sunshine for heat to maintain sufficient activity for survival. At present it is only possible to hint at the extent of the influence of extensive cloud cover on the zoogeographical range of high arctic butterflies, or other butterflies using solar radiation for increasing their body temperature. One might expect fewer of these species in areas with little sunshine, as compared with northern Ellesmere Island, Peary-land (Greenland), and Axel Heiberg Island which are all in a belt of lesser cloud cover (Gavrilova 1963). McAlpine (1964) reports only 1 lepidopteran, a moth (*Psychophora sabini* (Kirby) (Geometridae)), on the northwestern Queen Elizabeth Islands, which are far more cloudy. Needless to say, insolation is not the only answer to problems of the zoogeography of high arctic butterflies (*cf.* Downes 1966; McAlpine 1964; Freeman 1956), but lack of it may play some role in limiting their distribution.

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