

The Heat Rigor Temperature of Swedish Mountain Lepidoptera.

By

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One of the most characteristic traits in the ecology of Lepidoptera is the striking difference in phototropism occurring within the group. Heliophilous and scotophilous species and many intermediate stages exhibit this phenomenon. It seems in advance most probable that heliophilous species shall have a higher temperature resistance than the others, and facts known hitherto point in this direction (cf. e. g. Krogérus 1932 p. 146). This paper deals with this question and also with the relation between habitat and resistance.

I have investigated heat rigor temperature not heat resistance. As only two of the specimens awakened from the experiments the former will be somewhat higher, but there will surely be a very high correlation between these two points. We must also keep in mind that the temperatures obtained are not absolute, but change with the experimental technic.

For my experiments the following arrangement was used: A beaker with water was placed on a stand over a spirit-lamp. The specimens were kept in 4 test-tubes (one in each), all of which were placed in the beaker and maintained upright by a wooden support similar to one of the cross pieces in a test tube rack. In the test-tubes lead shot was used to keep the lower part under the water level. The animals are prevented from escaping by cotton pellets placed at the water level in each of the tubes. The pellets and the lead shot were moistened to avoid death by water loss.

The beaker was heated from 20° to 50° C. in about 50 min. The temperature was measured in the water outside the test tubes, since a control had shown that no differences could be measured between the temperatures inside and outside the test tubes.

When heat rigor sets in, the first effect is that the wings become paralyzed, so that the animals are unable to fly. They are still able to move, especially their legs, even at a higher temperature. The heat rigor temperature was measured at the point when the animals made no movement upon a shake of the test tubes.

It is of course impossible to calculate the error of estimation, e. g. by means of double determinations, but a simple estimate gives a standard error for a single determination of less than half a degree, a rather unimportant value in comparison with the differences measured. The standard error of the group most thoroughly investigated (*Cnephasia osseana* from Enafors, cfr. table 1) is 0.13. As systematic errors of this magnitude can occur very easily, a calculation of the standard errors of the means could be misleading.¹

The investigation was carried out during the summer 1946 from the 17th of July to the 11th of August mainly in Enafors and Abisko in the Swedish mountains. So, an eventual adaptation to different seasons (Walkden 1940, Agrell 1941) cannot alter the results.

The results of the investigation are shown in table 1. Here are tabulated the number of specimens of the species from different localities investigated together with the mean of the heat rigor temperature. Some remarks on the ecology of the species are given as well. Heliophilous species are marked with an »H». All butterflies, *Anarta melaleuca* and *Pyrausta funebris* have been placed in this group. The mean heat rigor temperature of the heliophilous species is 48.3 ± 0.2 ($N = 14$). In calculating this value (as in all other cases, when nothing else is said) all specimens from *regio alpina* have been omitted. This value is thus representative for heliophilous Lepidoptera from the lower parts of the Swedish mountains. In the more heterogenous non-heliophilous group the heat rigor point lies much lower, 43.3 ± 0.7 ($N = 11$) (values from Gästrikland are not included). The difference 5.0 ± 0.7 is significant.

It must be assumed that this difference is rather small in this northern part of the world where solar radiation is weak. Solar radiation brings the body temperature a good deal above the temperature of the air (cfr. Bodenheimer 1929 p. 456). In countries with strong solar radiation selection pressure must be more powerful to adapt heliophilous species to high temperatures than elsewhere.

In the non-heliophilous group such species which live in open habitats have a higher heat rigor temperature than the others. On the one side we have *Carsia sororiata* (mires, 46.3), *Pygmaena fusca* (moors, 44.2), *Crambus culmellus* (grassy moors and meadows, 43.8), *Pleurota bicostella* (heaths, 45.7) and *Gelchia galbanella* (1 specimen from a mire 47.5). On habitats covered with trees and shrubs the following species were found: *Scopula ternata* (44.0), *Cidaria montanata* (41.1), *C. caesiata* (41.1), *C.*

¹ I will in this connection criticize the statistical treatment of the values obtained in preference experiments by some authors (cfr. e. g. Krumbiegel 1932 p. 196, Herter 1943). If three specimens of a species are investigated a hundred times each, the standard error of the species should be calculated for $N = 3$ and not for $N = 300$, as is often done. The latter procedure can be compared to the measurement of a morphological detail, e. g. the length of the antenna of three specimens a hundred times each and the estimation of the standard deviation for $N = 300$.

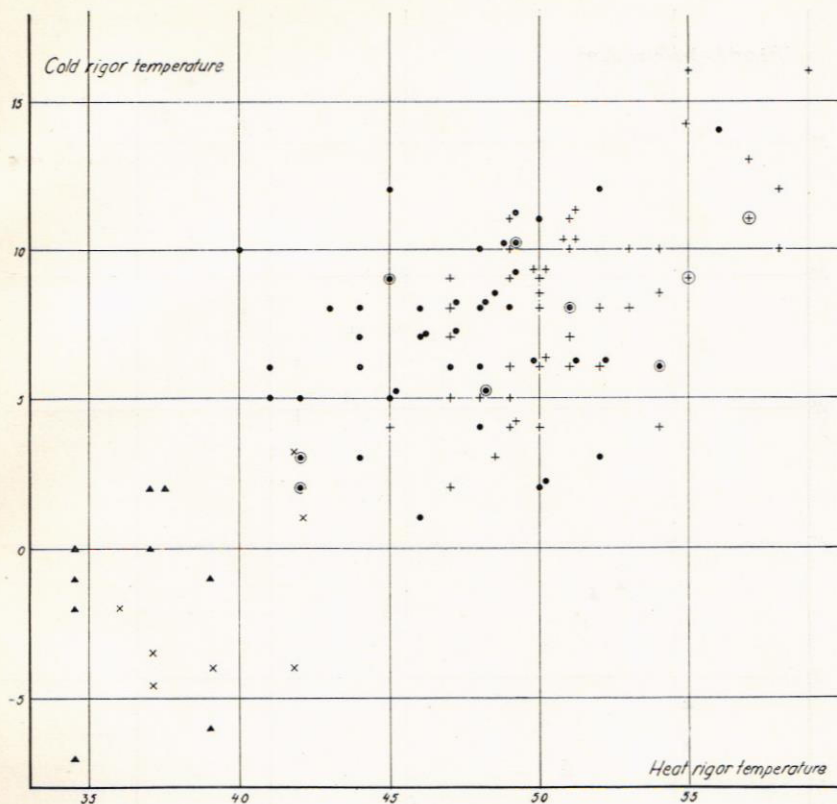


Fig. 1. Covariation between heat rigor and cold rigor temperature in some swedish and finnish arthropods, according to Krogérus 1932 (sand dune fauna, marked with ●), Nordberg 1936 (birds' nests' fauna, +), Agrell 1941 (collemboles, ▲) and Backlund 1945 (wrack fauna, ×). Lepidoptera encircled. The values are taken from tables and diagrams in the papers mentioned.

albulata (40.3), *C. munitata* (41.9), *Pelurga comitata* (43.2), *Pionea in-quinatalis* (42.0) and *Cnephasia osseana* (44.1).

The heat rigor temperature is in the latter group significantly lower than in the former. An analysis of variance gives $v^2 = 15.72^{**}$ ($f_1 = 1$; $f_2 = 11$). Systematic errors are in this case impossible, as the experiments of the groups treated were made indiscriminately. This result is in agreement with what can be expected. In open places the maximum temperature of the ground vegetation is naturally higher than where it is shaded by trees and shrubs. The maximum temperature is especially high in mires with *Sphagnum* (Krogérus 1939 p. 1221), which is in agreement with the high heat rigor temperature of *C. sororiata* and *G. galbanella*.

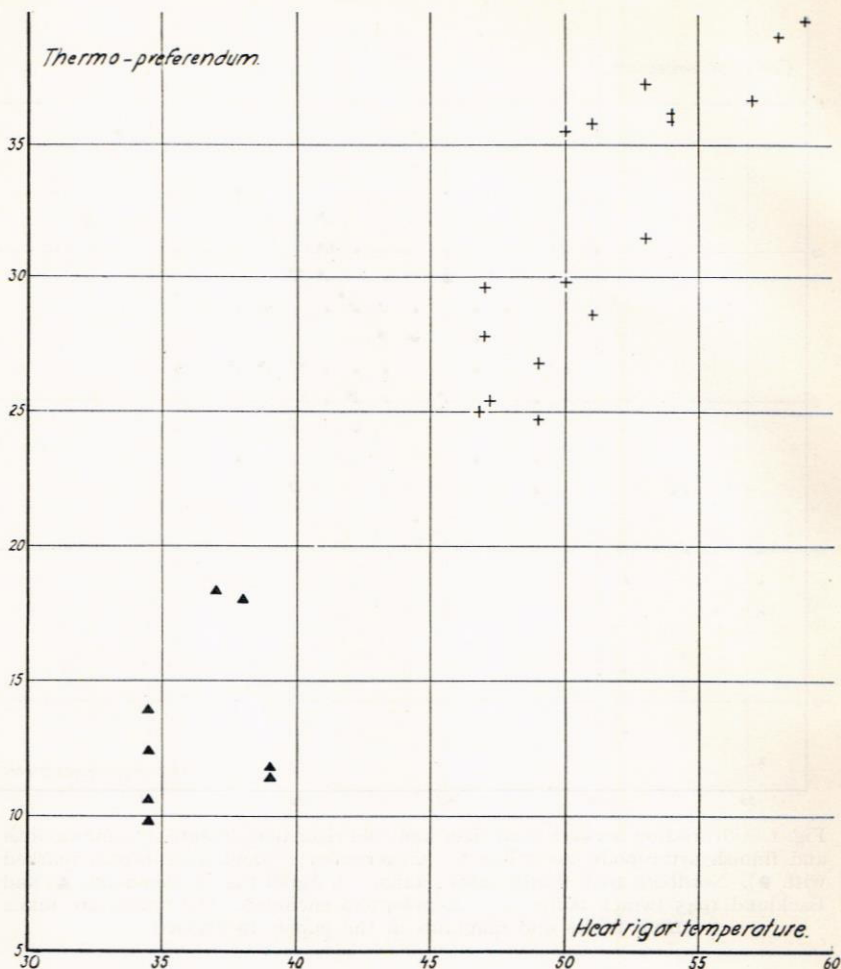


Fig. 2. Covariation between heat rigor temperature and thermo-preferendum in some swedish and finnish arthropods according to Nordberg 1936 (birds' nests' fauna, +) and Agrell 1941 (collemboles, ▲). The later values are calculated from the diagrams. Specimens in the coldest parts have been omitted, as it must be assumed that their position depends on cold rigor and not on thermotaxis.

The few experiments made on specimens from *regio alpina* show, that these have a somewhat lower heat rigor point than specimens of the same species from lower parts of the mountains. The difference for *Plebejus idas* is 0.5° , for *Chrysophanus hippothoë* 0.7° , and for *Cnephasia osseana* 0.6° . Here however a source of error must be considered, which perhaps can produce this difference. Specimens taken in *regio alpina* have on an

average been brought from longer excursions, during which they are kept under rather unfavourable conditions. So a greater material without these objections is needed to corroborate this result. This source of error must of course be considered for other alpine species too.

Any significant difference in heat rigor point between specimens from Enafors and Abisko was not obtained. Material of 8 species was investigated from both localities. Three have a higher value in Enafors, five in Abisko, and the differences are rather small. The ecological interspecific variation is in this case much greater than the geographical intraspecific.

During the study of the ecology of poikilothermous animals three points were especially interesting; heat and cold resistance, and thermo-preferendum. For other points see, e. g., Chapman 1926, Bodenheimer 1929 p. 478, Krogérus 1932 p. 145 and Kozhantschikov 1933.

An investigation of heat resistance will naturally gain in interest if this point is correlated to the other two just mentioned. There are, of course, in this case different sources of error, which demand a certain caution. Adaptation to different seasons pointed out by Agrell (1941 p. 91) are not of primary importance in my opinion. Adaptation to fall by specimens from Abisko starts at the end of August. I think experiments of this kind never have been made later than this date without special reference to that fact.

More important in this connection are differences in method of investigation. In preferenda experiments, e. g. either the air temperature or that of the bedplate is measured. Moreover, for a purpose like this the species investigated must be chosen at random. If only a few experiments have been made, there is a great probability, that some species have been chosen on the basis of special ecological traits.

An introductory investigation showed that species from other parts of the world did not fit well into the scheme of species from Sweden and Finland, a matter which I hope to study in the future. Thus, material from only these, two countries was assembled. The four authors (Krogérus 1932, Nordberg 1936, Agrell 1941 and Backlund 1945) have used nearly the same methods. Yet Backlund has changed the temperature 1° per minute contrary to $1/2^{\circ}$ per minute for the other authors, which of course can alter the comparison a little.

Fig. 1 shows the correlation between heat rigor and cold rigor temperature. The values lie along the same regression line in spite of so different faunas as those of sand dunes, birds' nests, wrack, and collemboles from the swedish mountains. Fig. 2 indicates a correlation between heat rigor and thermo-preferendum. As species from only a few habitats have been investigated it is impossible to say how far this agreement extends, and to what extent the faunas of other habitats lie along quite other regression lines.

In fig. 1 the values of Lepidoptera are encircled. It shows that they

Species	Locality	Date	N	Temp.	Rem.	Species	Locality	Date	N	Temp.	Rem.
<i>Pieris napi</i> L.	Abisko	27/7	5	47.2	H	<i>Anarta melaleuca</i> Thnbg.	Abisko	27/7-3/8	4	48.1	H
<i>Colias palaeno</i> L.	Enafors	24/7	1	49.7	H	<i>Scopula ternata</i> Schranck	Enafors	22/7	1	43.5	
»	Abisko	27/7-11/8	4	48.1	H	»	Abisko	3/8	1	44.5	M
<i>Argynnis aglaja</i> L.	Enafors	22-23/7	6	48.4	H	<i>Carsia sororiata</i> Hb. . .	Enafors	23-24/7	6	46.3	
<i>Arg. selene</i> Schiff.	Abisko, alp.	11/8	2	49.3	H	<i>Lygris populata</i> L.	Abisko, alp.	3-11/8	4	43.0	
<i>Arg. euphrosyne</i> L.	Abisko	3/8	4	49.1	H	<i>Cidaria montana</i> Schiff. .	Abisko	27/7-3/8	2	41.1	A
<i>Arg. pales</i> Schiff.	Enafors	22/7	1	48.5	H	<i>Cid. polata</i> Dup.	Abisko, alp.	30/7	1	42.2	
»	Abisko	3/8	1	49.3	H	<i>Cid. caesiata</i> Schiff. . .	Abisko	27/7	2	41.1	
<i>Arg. arsilache</i> Esp.	Enafors	23/7	2	48.7	H	<i>Cid. abulata</i> Schiff. . .	Abisko	27/7	1	40.3	
<i>Chrysoyhanus hippothoe</i>						<i>Cid. munitata</i> Hb.	Enafors	22/7	2	42.0	
L.	Enafors	22/7	3	48.5	H	»	Abisko	27/7	2	41.8	
»	Abisko	27/7	1	49.2	H	<i>Pelurga comitata</i> L. . .	Storvik	21/7	2	43.2	
<i>Chr. phlaeas</i> L.	Abisko, alp.	11/8	1	48.5	H	<i>Pygmaena fusca</i> Thnbg.	Abisko	3/8	1	44.2	(A)
<i>Plebejus idas</i> L.	Abisko	27/7	1	49.2	H	<i>Crambus culmellus</i> L. . .	Enafors	22-23/7	5	43.8	
»	Enafors	22/7	5	48.5	H	<i>Cr. furcatus</i> Zett. . .	Enafors, alp.	24/7	1	44.0	A
»	Abisko	27/7	13	49.5	H	<i>Pyrausta funebris</i> Ström	Abisko	3/8	2	45.8	H
<i>Polyommatus semitargus</i>	Abisko, alp.	29/7-8/8	2	49.0	H	<i>Pionea inquamata</i> Z. .	Abisko	3/8	1	42.0	
Rott.	Enafors	22/7	1	48.3	H	<i>Cnephasia osscana</i> Sc. .	Enafors	22-23/7	14	44.1	
<i>Pol. icarus</i> L.	Abisko	27/7	3	48.4	H	»	Abisko	28/7	5	44.2	
<i>Erebia ligea</i> L.	Enafors	22/7	7	47.9	(H)	<i>Pleurota bicostella</i> Cl. .	Abisko, alp.	29/7-8/8	10	43.6	h
»	Abisko	27/7	2	47.8	(H)	<i>Gelechia galbanella</i> Z. . .	Sandviken	17/7	1	45.7	M
							Enafors	24/7	1	47.5	

Table 1. Heat rigor temperature of some Lepidoptera from Sandviken and Storvik i Gästrikland, Enafors in Jämtland and Abisko in Torne lappmark. A = occurs only in regio alpina; H = heliophilous; h = occurs on moors; M = occurs on mires; N = number of investigated animals. When the latter is put in brackets the character is not so pronounced. If the specimens are captured in regio alpina this is marked with «alp.» after the locality.

behave as most other animals investigated, showing the same correlation and regression. It can often be observed, and was studied by Radl (1903), that heliophilous butterflies expose their wings against the sun in the morning and afternoon, but keep them parallel to sun rays only during the very warmest part of the day. This behaviour indicates a rather high preferendum, surely higher than that of the non-heliophilous group. So a correlation seems to be present here too.

Summary.

The heat rigor temperature of some swedish mountain Lepidoptera has been determined by warming from 20° to 50° in 50 min. at high humidity. The mean heat rigor temperature of heliophilous species was determined to be 48.3 ± 0.2 , that of non-heliophilous to be 43.3 ± 0.7 .

Non-heliophilous species from open habitats have a significantly higher heat rigor point than those from habitats covered with trees and shrubs. The point lies especially high for two species from mires, a habitat, which is known to have an extremely high maximum temperature.

The heat rigor point is positively correlated with the cold rigor point and thermo-preferendum (fig. 1 and 2) since four (resp. two) very different faunas from Sweden and Finland show a fair agreement with one and the same regression line.

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