ZOOLOGY

THE TEMPERATURE AND HUMIDITY PREFERENCES OF CERTAIN COLEOPTERA

BY

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1. *Introduction.*

Temperature and humidity are well known to be factors of major importance in the lives of terrestrial insects. In this field of research much work has been done on the temperature- and humidity preferences of insect pests, but thus far only a few free living species have been investigated. In the course of previous work by the author on *Forficula auricularia* L., the question arose to what extent the temperature- and humidity preferences might show a marked relation to the natural surroundings of insects.

To this end four species of Coleoptera, living in about the same habitat and being available in sufficient numbers, were chosen for these experiments, the points of investigation being: *a*) Do these insects have similar temperature- and humidity preferences? *b*) Do these preferences show any relations to the temperature and humidity of their habitat?

According to DEAL (1941) the term "preferendum" has been proposed by C. B. WILLIAMS in 1922, while more recently D. L. GUNN suggested "eccritic" temperature. HERTER (1923—'25) used "Thermotactisches optimum", BODENHEIMER c.s. (1928—'31) "Vorzugstemperatur" and NIESCHULZ (1935) "Wahltemperatur". WIGGLESWORTH (1941) called it: "preferred temperature". I will use in this paper the terms: thermo- and hygro-preferendum, (abbreviated: T.P. and H.P.)

2. *The thermopreferendum.*

a) Previous literature.

DEAL (1941) gave an extensive summary of previous publications, so only the more recent ones will be mentioned here: WIGGLESWORTH (1941) tested *Pediculus humanus corporis:* T.P. 25—30° C. According to GUNN and WALSHE (1942), *Ptinus tectus* showed a temperature preference of 3—8° and 22—26° C., the former value probably being that of immobilisation of the insects by low temperature.

HERTER (1943) determined the thermopreferendum of a large number of beetles and bugs. VAN HEERDT (1946) tested *Forficula auricularia:*

26—33° C., BUETTIKER (1948): *Culex pipiens* and finally BRO LARSEN (1949), working on certain Noctuids. It is a rather peculiar fact that the results of experiments with one species may show a notable variation. The thermopreferendum of *Ptinus tectus* stands at 8° C. according to DEAL (1941); it is recorded to be 3—8° C. and 22—26° C. by GUNN and WALSHE (1942) and lastly 30° C. by HERTER (1943). The explanation of this phenomenon may be found in differences of physiological condition of the insects or of the construction of the gradient apparatus used by the various authors. On the other hand, one may find a better agreement between the results, for instance in *Forficula auricularia*, which insect, owing to conditions of war in Western Europe, has been tested independently by three investigators: DEAL (1941): 25—30° C.; HERTER (1943): 31.79 ± 0.18° C. and VAN HEERDT (1946): 26—33° C.

b) Description of the temperature gradient apparatus.

The apparatus used is made of a bar of aluminium 120 cm long, 5 cm wide and 3 cm in thickness. On this bar a case of zinc has been built, leaving free a 10 cm piece at each end of the bar. This runway is covered by a strip of glass ½ cm in thickness. One free end is placed in a small insulated ice-box, the other is wound with resistance wire and heated by the mains electricity supply.

The thermometers in this type of apparatus are sunk in holes, drilled in the bar and no false floor is used. This is of great advantage in this special case, as these Coleoptera tend to press their bodies against the floor of the gradient apparatus and mainly percieve the temperature of the aluminium bar. Moreover, this construction leaves the floor free of obstacles, an important fact, as these beetles show strong thigmotactic tendencies.

The actual runway being 100 cm long, was divided by painted lines into twenty parts, of 5 cm each; these lines were numbered from 5 to 95. The thermometers were placed at:

5—15—25—35—45—55—65—75—85—95 cm, the average temperatures being: 3—8—12—16—20—24—29—35—42—50° centigrade.

This gradient could be kept constant for a long period, the cold end incidently showing deviations of 2 or 3° C., when the ice in the box was melting down.

It is impossible to have a temperature gradient, without also having an inverse gradient of relative humidity, i.e. the R.H. will be lowest at the warm end of the gradient and highest at the cool end. The only way of maintaining a constant R.H. in a temperature gradient would be either completely drying the air or keeping it saturated (cf. GUNN, 1934; DEAL, 1941). It seems then that the observed preferred temperature represents a kind of balance between a pure temperature reaction and a humidity reaction. However, it is the author's opinion that in fresh, well fed animals the humidity reaction in the temperature gradient apparatus is fairly obscured by the temperature reaction. No relative humidity has been recorded in this series of experiments.

c) Methods.

The experiments were conducted in a room with 3 north windows. The temperature gradient apparatus was placed at a distance of 7 m (about 20 ft.) parallel to the windows and was kept completely dark by covering it with board, cut to fit exactly over the glass plate. This cover was lifted for the purpose of making observations. A dim uniform light was then cast over the gradient, which was an advantage, as a few moments after the cover had been lifted, the insects became restless, so no stirring device was needed.

Each experiment was carried on for one day only, the tested insects being fed and replaced in their terrarium after this period. If the amount of data thus obtained were considered too low, the experiment was continued a few days later with the same individuals.

This is of major importance as many insects, when even so slightly desiccated, tend to lower their preferendum. (Without doubt this is the explanation of the phenomenon stated by DEAL (1941, p. 349) in *Apanteles congestus*).

Every half-hour the positions of the insects were recorded, the first record usually being taken no sooner than one hour after the animals had been introduced into the temperature gradient. Controls showed all of the 4 species of beetles concerned to have definite end preferences, owing to their strong thigmotactic reactions.

Not more than 10 individuals were used in each series of experiments, these species being too large to allow more of them at the time in the apparatus. The number of readings and the temperature were originally plotted against position in centimeters. Each time, when the experiments had been terminated, the apparatus was thoroughly sponged out with cottonwool, soaked in 76 % alcohol and the runway was left open till next morning.

HERTER, BODENHEIMER c.s. and other German workers used to express the T.P. as an average obtained by mathematical operation of the total number of readings along the gradient, e.g. *Liogryllus domesticus:* 35.98 $\pm$ 0.62° C. The statement of the T.P. as a single point, correct to two places of decimals, is of little ecological significance, as it is a range rather than a point (DEAL, 1941, p. 352; BUETTIKER, 1948, p. 64), and knowledge of the range may give us information on the habitat of the insect.

The positions of the beetles in the temperature gradient are expressed in a block graph, every unit in the abscissae corresponding with one division in the temperature gradient. In this way the number of animals staying in each division is shown directly in the graph.

In addition the preferred temperature has been estimated by a mathematical method:

Mean value of the T. P., $M = \frac{\Sigma n T}{N} \pm \frac{S}{\sqrt{N}}$, where N = total number of readings, n = number of readings in each division of the gradient apparatus, T = temperature in each division and $S = \sqrt{\frac{\Sigma n (T - M)^2}{N - 1}}$ (standard deviation).

The preferred range, which comprises 67 % of the readings, is limited in this case between $M \pm S°$ C.

It should be understood that the average value of the T.P. has been noted in this case only as a means of comparison with the results of other workers.

3. *The hygropreferendum.*

a) Previous literature.

In the field of humidity preference, there is little work compared with that on preferred temperature, probably owing to hygrometric difficulties. LECLERCQ (1947) gives an extensive review of the existing publications.

Many papers on humidity preference concern insect pests e.g. MARTINI and TEUBNER (1933), DE MEILLON (1937), HUNDERTMARK (1938), THOMSON (1938), BUETTIKER (1948), working on various kinds of mosquitoes and GUNN and COSWAY (1938), PIELOU and GUNN (1940), BENTLEY (1944) on insects in stored products. It has been observed that many insects in normal condition are fairly indifferent to humidity, but show a positive reaction when desiccated (e.g. *Blatta orientalis*, GUNN and COSWAY, 1938; *Forficula auricularia*, VAN HEERDT, 1946).

The same fact may be noted in species, which are normally hygronegative (e.g. *Tenebrio molitor*, PIELOU and GUNN, 1940; *Ptinus tectus*, BENTLEY, 1944).

Anopheline mosquitoes (according to BUETTIKER, 1948) preferred in summer 100 % R.H., for hibernation, however, they went to drier places (60—80 % R.H.).

The results of a number of experiments on preferred humidity at different temperatures (THOMSON, 1938: *Culex fatigans;* PIELOU and GUNN, 1940: *Tenebrio molitor*) suggest that the animals react to the relative humidity rather than to the saturation deficiency. This is an interesting fact, as the water loss caused by evaporation is usually proportional to the S.D.

b) Methods.

Description of the linear humidity gradient apparatus: In the first experiments which were made, the Coleoptera were offered a wide range of humidities. A trough, made of zinc, 60 cm long and 10 cm wide was provided with a perforated false floor, also made of zinc. There was a distance of about 2½ cm from the false floor to the glass plate covering the trough. This is an important factor, as owing to convection a greater distance counteracts the establishment of a stable gradient. A small door was made in one of the short sides of the apparatus, making possible the introduction of animals without disturbing the humidity gradient.

Under the false floor 6 petri-dishes were placed, containing a series of saturated solutions of various kinds of salts. The gradient, thus obtained, however proved to be not quite satisfactory, so another arrangement was used. The three petri-dishes at one side of the gradient apparatus were filled with $CaCl_2$, those at the opposite side with distilled water, giving a gradient as shown below [1]):

$$CaCl_2 - CaCl_2 - CaCl_2 - H_2O - H_2O - H_2O$$
$$45-45-45-50-62-70-80-88-95-100-100\ \%\ \text{R.H.}$$

This gradient is fairly steep and gives satisfactory results. The R.H. has been recorded by means of a hair hygrometer, which was usually kept at 75 % R.H. This hygrometer was moved up and down the humidity gradient by means of a couple of strings passing through small holes, drilled in the short sides of the apparatus. The hygrometer records a different value (ca. 4 % R.H.) at a certain point, when moved either up or down the gradient. The humidities noted are the average of these deviations. A drawback in this apparatus is found in the "end preference" of the Coleoptera, which tend to gather in the corners.

The "alternative chamber": This apparatus has been described by many workers (GUNN and KENNEDY, 1936; GUNN and COSWAY, 1938; PIELOU and GUNN, 1940; WIGGLESWORTH, 1941) and has been used in the course of these experiments with minor adjustments only, so no description is needed in this paper.

The experiments were conducted in the same room and in the same situation as described for the temperature gradient apparatus, the linear humidity gradient apparatus and the alternative chamber being covered with black paper. Half way through each experiment each apparatus was rotated through 180° in case there were any differences.

These experiments, unlike the temperature preference tests, were carried on for two days. The Coleoptera, if well fed, showed only a weak reaction to humidity. After one day in the gradient, a slight desiccating effect became evident and clear results could be obtained. Every half-hour the positions of the objects were recorded, the first record usually being taken after the animals had been in the gradient for about 24 hours. Controls showed a 50—50 distribution in both sides of the apparatus, end preference being strong, as may be seen in the results. The same number of individuals was used as in the previous experiments.

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[1]) I am much indebted to Dr D. L. GUNN, who gave me useful advice on this subject.

The runway of the linear humidity gradient apparatus was divided into 6 parts of 10 cm each. The numbers of insects were plotted according to their position, in divisions 1—6.

The intensity of reaction can be expressed in two ways: (1) as the ratio of position records on the wetter side to those on the drier side (W/D ratio: GUNN, 1937) and (2) as the excess percentage of records on the wetter side ($\frac{100(W-D)}{W+D}$: GUNN and COSWAY, 1938). (see table 1, 2, 3 and 4). If one half of the trough or chamber is not preferred to the other, the animals should give about 50 % readings in each half. Divergence from this ratio may be tested by the following formula for the normal deviate: $t = \frac{W - W_{th}}{\sigma}$, where W = number of individuals on the wetter side, if this side is preferred; W_{th} = number of individuals, if one half of the apparatus is not preferred to the other (about 50 % readings in each half) $= \frac{1}{2} n$; $\sigma = \sqrt{\frac{1}{4} n}$ (n = total number of readings).

If $t \geqq 3.29$, the probability (P) of this result by random occurrence is $\leqq 1 : 1000$, hence the divergence may be considered significant.

4. *Insects used:*

Four species of Coleoptera living in the layer of fallen leaves of a Querceto-betuletum (Baarn, Holland) were used in these experiments: *Carabus nemoralis* Mull., *C. catenulatus* Scop., *Abax ater* Vill. (Carabidae) and *Geotrupes sylvaticus* Panz. (Scarabaeidae). Only newly caught and well-fed individuals were tested in order to eliminate the influence of humidity in the temperature gradient apparatus. During their stay in the laboratory the beetles were kept in a vivarium, where the floor had been covered with a 10 cm layer of damp soil and on top of this, a layer of half-decayed leaves, thus imitating their natural surroundings. The *Carabids* were fed on dead cockroaches or meat, *Geotrupes* on fresh sheep manure. Mortality was low during their stay in the vivarium, the insects apparently being in good health.

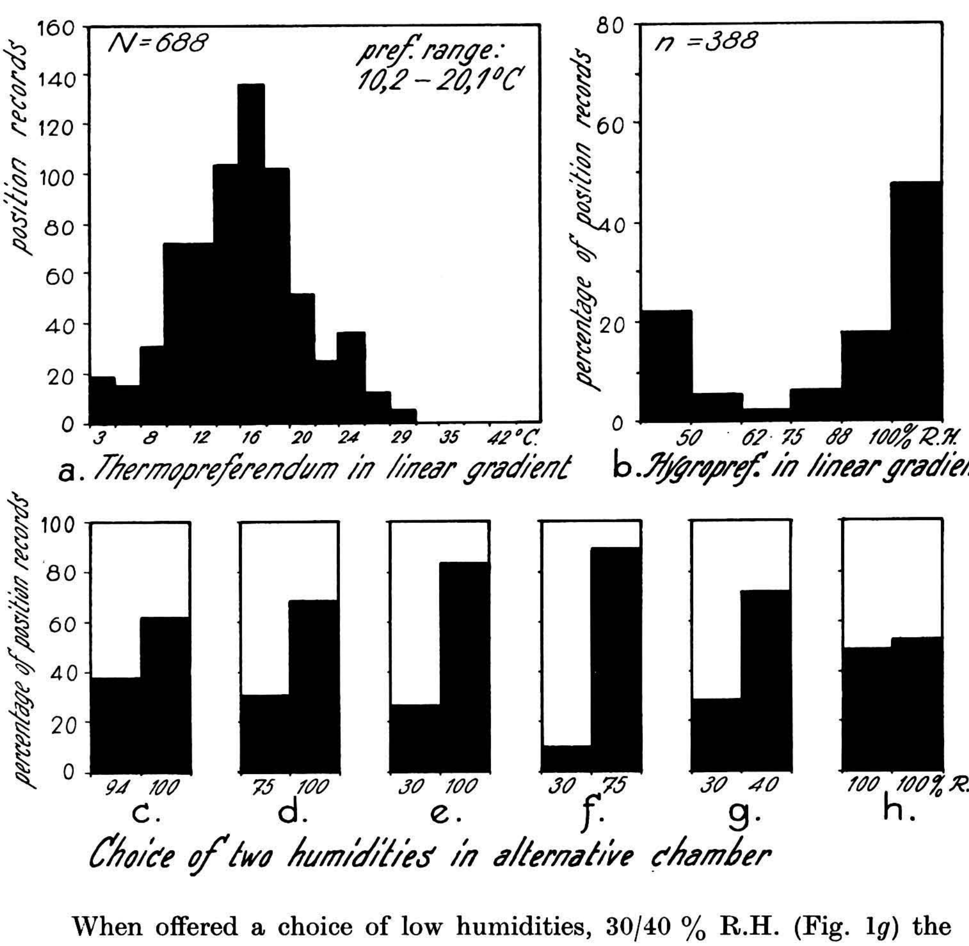
The beetles could easily be caught by means of flower-pots dug into the soil with their tops flush with the surface.

5. *Results.*

Carabus nemoralis shows a definite T.P. of 10.2—20.1° C. average 15.2 ± 0.2° C. This is low compared with the other 3 species tested, except *Abax ater*. (Fig. 1*a*). *C. nemoralis* does not show any avoiding reaction for low temperature, probably because the temperature in the gradient apparatus was not low enough. For high temperature a strong klinokinesis has been recorded for 35° C. In the humidity gradient a hygropreferendum for 100 % R.H. has been observed. (Fig. 1*b*). When tested in the alternative chamber, although the greater number of the insects were gathered in the moister zone, the results were not always significant when a choice was offered of 100 and 94 % R.H. and of

100 and 75 % R.H. (Fig. 1*c*, *d*). A small deviation was observed in the case of a choice of 30 and 75 % R.H. (Fig. 1*f*) where a more intense reaction was initiated than when a choice was offered of 30 and 100 % R.H. (Fig. 1*e*); it may be suspected that a certain difference in physiological condition of the insects was the cause.

1. Carabus nemoralis

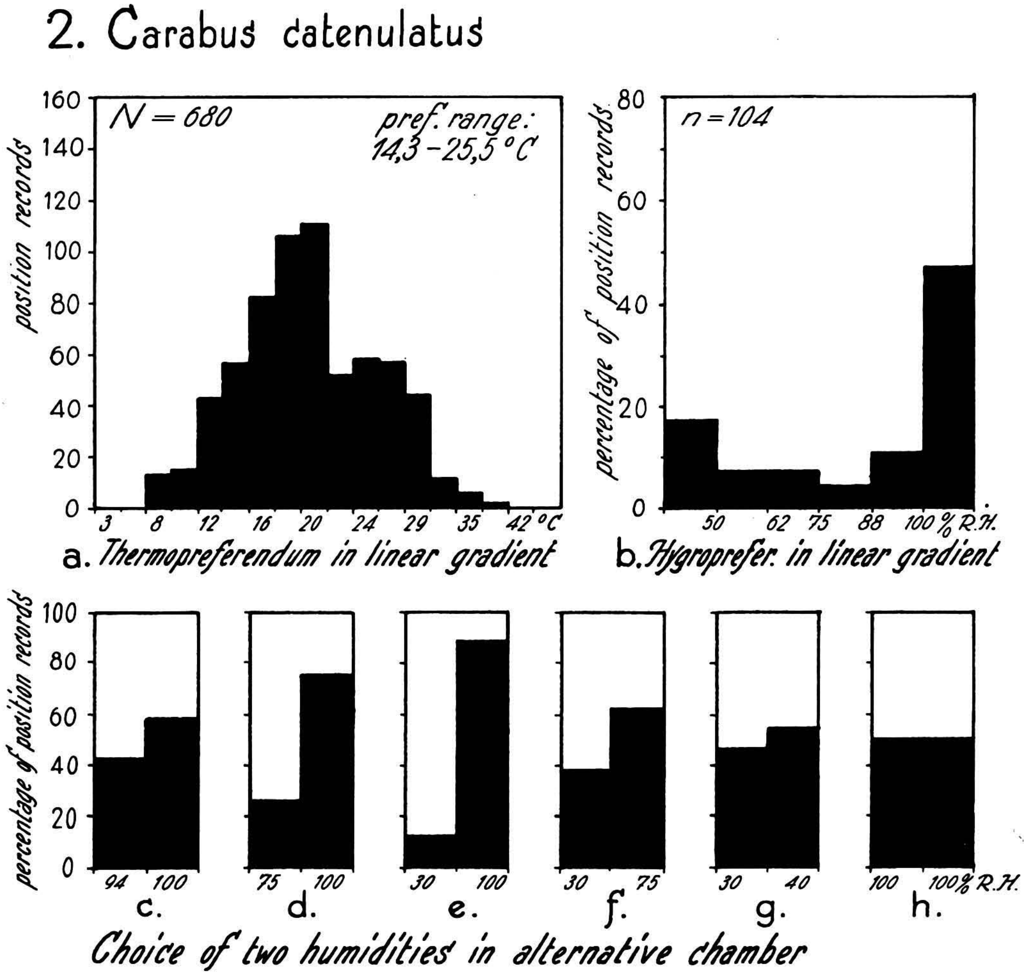


When offered a choice of low humidities, 30/40 % R.H. (Fig. 1*g*) the beetles still give a rather clear (though not quite significant) reaction to the moister side. A control gives a near 50/50 distribution (Fig. 1*h*).

The temperature preference of *Carabus catenulatus* amounts to 14.3—25.5° C. average 19.9 ± 0.2° C. (Fig. 2*a*). Klinokineses are shown for 5—8° C. and 35—42° C. Compared with *C. nemoralis*, this species has a more extensive and somewhat higher T.P., though they are very similar in size and biotope. In the humidity gradient there is a significant hygropositive reaction (Fig. 2*b*). When tested in the alternative chamber the majority tend to congregate at the moist side of the apparatus.

(Fig. 2*c*, *d*, *e*, *f*). At a choice of 30 and 40 % R.H. only a weak reaction may be recorded, but the intensity of the reaction grows with increasing difference of humidity. Controls give an exact 50/50 distribution (Fig. 2*h*).

Abax ater again has a more confined range of temperature preference: 9.7—20.6° C. average 15.1 ± 0.2° C. (Fig. 3*a*), the lowest of the four



species concerned. A few (not all) individuals show an avoiding reaction for 5° C. At the hot side a klinokinesis is observed for as low a temperature as 29° C. A hygropreferendum for 100 % R.H. is shown in the linear humidity gradient. (Fig. 3*b*). The reaction in the alternative chamber is very definite, only the choice of 30 and 40 % R.H. being insignificant. (Fig. 3*c*, *d*, *e*, *f*, *g*). A near 50/50 distribution is obtained in a uniform chamber, (fig. 3*h*).

Finally, *Geotrupes sylvaticus* shows a 11.9—26.9° C. thermopreferendum with an average of 19.3 ± 0.3° C. thus covering a wide range. (Fig. 4*a*).

TABLE 1
Carabus nemoralis

Choice of % R.H.	W/D	excess perc.	W	W_{th}	$\sigma = \sqrt{\frac{1}{4} n}$	t	P
100/94	1.6	23.5	21	17	2.91	1.35	0.1—0.2
100/75	2.2	37.5	33	24	3.46	2.60	ca. 0.01
100/30	5.0	66.6	30	18	3.0	4.00	< 0.001
30/100	5.0	66.6	30	18	3.0	4.00	< 0.001
30/75	9.0	80.0	36	20	3.16	5.06	< 0.001
30/40	2.6	44.4	26	18	3.0	2.66	0.001—0.01

TABLE 2
Carabus catenulatus

Choice of % R.H.	W/D	excess perc.	W	W_{th}	$\sigma = \sqrt{\frac{1}{4} n}$	t	P
100/94	1.3	15.0	23	20	3.16	0.95	0.3—0.4
100/75	3.0	50.0	36	24	3.46	3.46	< 0.001
100/30	7.3	76.0	44	25	3.54	5.36	< 0.001
30/100	7.3	76.0	44	25	3.54	5.36	< 0.001
30/75	1.7	25.0	25	20	3.16	1.58	0.1—0.2
30/40	1.2	8.0	27	25	3.54	0.56	0.5—0.6

TABLE 3
Abax ater

Choice of % R.H.	W/D	excess perc.	W	W_{th}	$\sigma = \sqrt{\frac{1}{4} n}$	t	P
100/94	3.2	52.4	32	21	3.24	3.42	< 0.001
100/75	5.0	66.6	40	24	3.46	4.62	< 0.001
100/30	5.9	71.0	41	24	3.46	4.91	< 0.001
30/100	5.9	71.0	41	24	3.46	4.91	< 0.001
30/75	8.6	78.1	43	24	3.46	5.50	< 0.001
30/40	1.5	20.0	18	15	2.74	1.94	ca 0.05

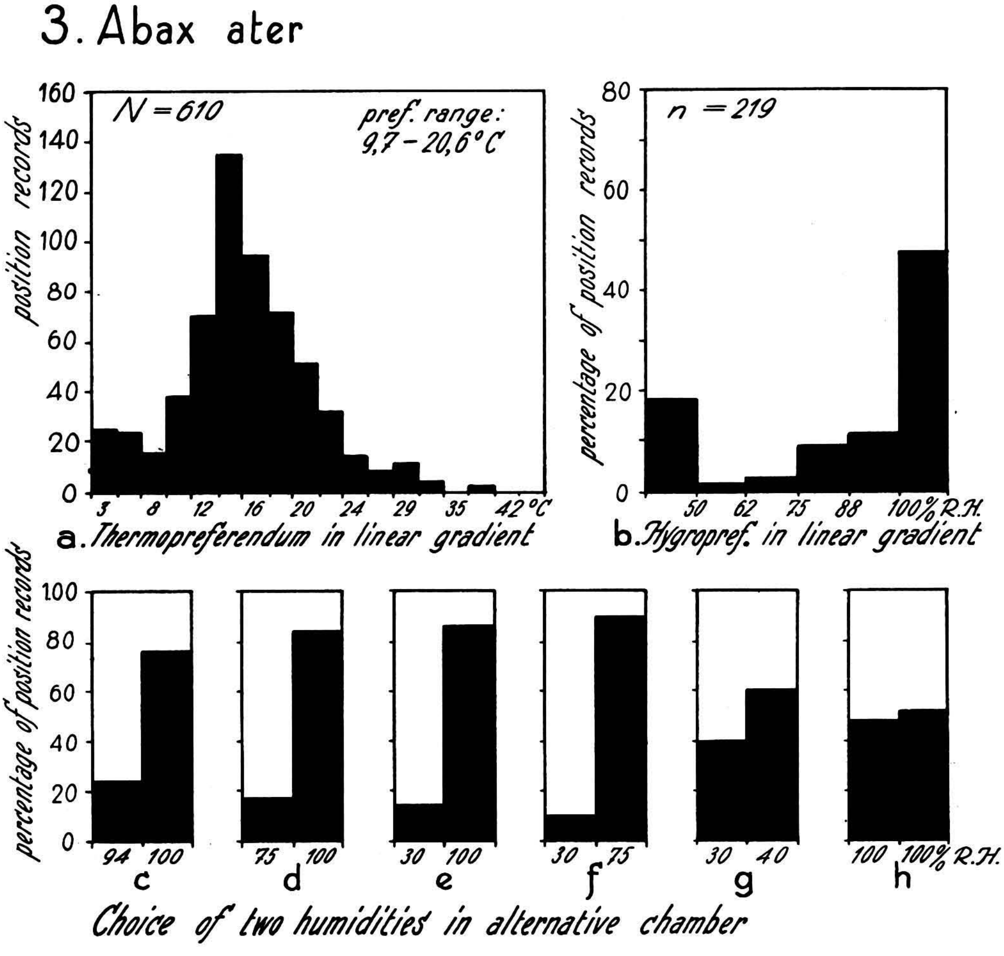
TABLE 4
Geotrupus sylvaticus

Choice of % R.H.	W/D	excess perc.	W	W_{th}	$\sigma = \sqrt{\frac{1}{4} n}$	t	P
100/94	2.6	45.0	29	20	3.16	2.84	0.01—0.001
100/75	2.6	45.0	29	20	3.16	2.84	0.01—0.001
100/30	4.6	64.3	46	28	3.74	4.81	< 0.001
30/100	4.6	64.3	46	28	3.74	4.81	< 0.001
30/75	2.2	38.2	38	27.5	3.71	2.83	0.01—0.001
30/40	1.2	8.7	25	23	3.39	0.59	0.5—0.6

W = number of insects on wet side; W_{th} = number of insects in case of even distribution ($= \frac{1}{2} n$).

$$\sigma = \sqrt{\tfrac{1}{4} n} \; ; \; t = \frac{W - W_{th}}{\sigma}.$$

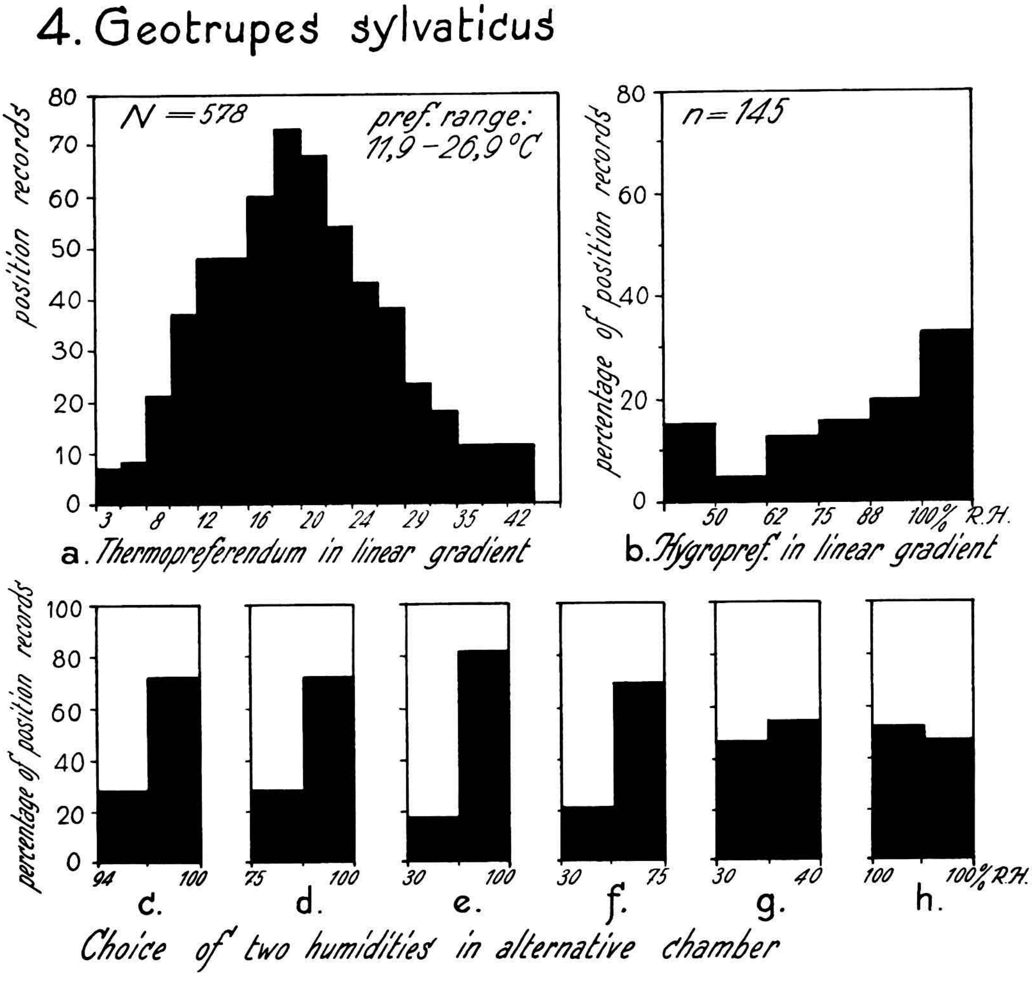
A klinokinesis at the hot side only, could be observed for 45° C., which may be considered fairly high. The humidity reaction in the linear humidity gradient is weak compared with that of the 3 Carabid species, (Fig. 4b) the reaction being altogether definite and statistically significant. The area occupied by these dung beetles, however, is less well-defined



than in the Carabids. In the alternative chamber too, reactions are less definite (Fig. 4c, *d*, *f*) only the choice of 30 and 100 % R.H. being really significant. (Fig. 4*e*). Nevertheless, an excess percentage of records on the drier side has never been observed. When a choice is offered of 30 and 40 % R.H. a near 50/50 distribution was recorded, quite similar to the control reaction, (Fig. 4*g*, *h*) so apparently at low R.H. no distinction is made between small differences of humidity.

6. *Discussion.*

It has been proved that the populations of four kinds of Coleoptera, living in the forest: *Carabus nemoralis*, *C. catenulatus*, *Abax ater* and *Geotrupes sylvaticus* have a preferred temperature which is lower than that of those insects, which live in exposed places (e.g. flies, earwigs) or in stored products (e.g. *Tenebrio*, *Dermestes*). In addition the preferred humidity of the four species has been recorded and certain conclusions have been drawn from a comparative study of these data.



It is evident that the temperature and humidity preferences of these beetles show a marked relation to the corresponding factors in their natural surroundings. Moreover, the thermopreferendum of these 4 species is very low if compared with, for example, *Musca domestica:* 33.5° C.; *Stomoxys calcitrans:* 28° C.; *Musca vicina:* 33° C. (according to NIESCHULZ, 1933—'35); *Culex pipiens* 31° C. (BUETTIKER, 1948), insects living in drier places e.g. *Forficula auricularia:* 26—33° C., (VAN HEERDT, 1946) or those, living in stored products e.g. *Tribolium confusum:* 29° C.

Dermestes vulpinus 30° C. (DEAL, 1941); *Tenebrio molitor:* 32° C.; *Anthrenus verbasci:* 32° C.; *Ergates faber:* 35° C., (according to HERTER, 1943).

Their humidity preferences, on the other hand, tend to be higher than in the groups of Insects previously mentioned: *Anopheles maculipennis* var. *messeae:* 40 % R.H. (BUETTIKER, 1948); *Blatta orientalis:* when offered a choice of 20 and 90 % R.H. prefers 20 % R.H. (GUNN and COSWAY, 1938); *Tenebrio molitor* choice of 94 and 100 % R.V. prefers 94 % R.H.; *Carabus auratus:* choice of 55 and 86 % R.H. prefers 55 % R.H. (LECLERCQ, 1947).

Carabus nemoralis, C. catenulatus and *Abax ater* are insects which live throughout the year in the damp layer of fallen leaves of a Querceto-betuletum. The temperature of their biotope never rises higher than about 25° C. even in hot summertime. The relative humidity, which during the day tends to fall considerably, however, rises again at night and soon reaches 100 % R.H. when the temperature drops after sunset. Owing to its hygroscopic abilities, the desiccated upper layer of dead leaves absorbs the humidity of the air and takes up still more water whenever the temperature drops below dewpoint. This water is lost again during the following day, but, as will be easily understood, provides a damp medium, where extreme conditions of heat and drought are never apt to occur. As these beetles are animals of the night, they never show themselves at daytime and, owing to their low temperature and high humidity preferences, they will fit very well into their natural haunts.

Geotrupes sylvaticus, a dung beetle, has a far wider range of temperature and humidity preference. In accordance with these facts, the habits of this insect are quite different from the Carabids previously mentioned. They are often seen at daytime, busily walking about in search of food, which mainly consists of animal droppings. They are not confined to the damp interior of the woods and are more euryoecous than the Carabids.

As a matter of fact a comparative study of the temperature and humidity preferences of the Carabid beetles and of *Geotrupes sylvaticus* reveals a clear difference, the preferences of the former being more restricted than those of the latter.

Comparing the separate results, it can be stated, that *C. nemoralis* shows a lower T.P. than *C. catenulatus*, although both species are about equal in size, behaviour and habitat. Their humidity preferences are much the same, so it is difficult to give a plausible explanation for this phenomenon.

Either of the 4 species, when tested in the linear humidity gradient apparatus (extending from 45—100 % R.H.) shows a humidity preference of 100 % R.H. This preference, generally corresponds with their behaviour in their natural surroundings, the reaction of *Geotrupes sylvaticus* being weaker than of the Carabids. A definite end preference is observed, owing to the strong thigmotactic reactions of these insects.

In the alternative chamber a marked hygropositive reaction in a humidity gradient extending from 30—100 % R.H. and from 30—75 % R.H. was observed in all cases. A similar reaction in a gradient from 100—94 % R.H. and 100—75 % R.H. is, although always positive, much weaker in *C. nemoralis*, *C. catenulatus*, and *Geotrupes sylvaticus*; *Abax ater* being the only case, in which the reaction is really significant. A choice of 30—40 % R.H., however, always proves insignificant, even in *Abax*. In *Carabus catenulatus* and *Geotrupes sylvaticus* a choice of 30 % R.H. in the presence of 40 % R.H. gives a near 50/50 distribution, only slightly different from that shown by controls in a uniform chamber. Still, stress must be laid on the fact that none of the experiments (about 200 in all) ever showed an excess percentage on the drier side.

THOMSON (1938) in *Culex*, PIELOU and GUNN (1940) in *Tenebrio* and WIGGLESWORTH (1941) in *Pediculus* observed that their objects show in general a greater sensivity within the higher range of humidity. For example, the louse shows a striking preference of 92 % R.H. in the presence of 95 % R.H. while the mosquito in this range even reacts to differences of 1 % R.H.

In our case too, the reaction in the higher range of humidity is more pronounced than in the lower range (e.g. in *Abax ater*, a choice of 94 and 100 % R.H. gives significant results, but of 30/40 % R.H. proves insignificant). Moreover, it may be pointed out, that the greater the difference of humidities offered, the stronger the reaction, (e.g. in *Carabus catenulatus*, when offered a choice of 100/94 % R.H., 100/75 % R.H. and 100/30 % R.H., the W/D ratio is steadily increasing: 1,3, 3.0 and 7.3).

As a whole, the reactions of *Abax ater* prove to be the most positive of the 4 species tested, the results of *Abax*, being, however, very similar to those of *Carabus nemoralis*.

The mechanisms of the reactions, to temperature as well as humidity, clearly show the same kind, that is: Klinokinesis. On the entry of an adverse region, the beetles no longer walk straight, but follow a hesitant course. In some cases a directed response has been observed (abruptly turning to the favorable region). An amputation of sense organs has not been made, so no more can be said concerning this subject.

These results show in a very positive way the existance of a relation between thermo- and hygropreferendum and the natural surroundings in Insects. These Coleoptera, living in the cool, damp layer of fallen leaves in the woods, have preferences quite contrary to those of flying, free living species or stored products pests.

Summary.

1. The populations of *Carabus nemoralis*, *C. catenulatus*, *Abax ater*

and *Geotrupes sylvaticus*, 4 species of Coleoptera, living in the Querceto-betuletum (Baarn, Netherlands) have a low temperature- and a high humidity preference, compared with other kinds of insects which live in more exposed biotopes or in stored products.

2. The preferred ranges of the 3 Carabid species are more restricted than those of Geotrupes, which agrees with the euryoecous way of life of the latter.

3. Although the humidity reaction is not always significant, the number of insects observed at the moister side of the alternative chamber, is always more than the number at the drier side.

4. The reactions to differences in humidity are more definite, when a choice is offered of 2 high humidities than of 2 low ones.

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REFERENCES

Temperature preference:

DEAL, J., J. Anim. Ecol., **10**, 324—356 (1941). (Reviews previous literature).
WIGGLESWORTH, V. B., Parasitology, 33, 67—109 (1941).
GUNN, D. L. and B. M. WALSHE, J. exp. Biol., **19**, 133—140 (1942).
HERTER, K., Mitt. d. Gesellsch. v. Vorratsschutz E.V. **18/19** (1943).
HEERDT, P. F. VAN, Thesis (Univ. of Utrecht, Netherlands), (1946).
BUETTIKER, W., Thesis (Eidg. Techn. Hochschule, Zürich, Switzerland) (1948).
BRO LARSEN, E., Kgl. Danske. Vidensk. Selsk, **21**, 1—32 (1949).

Humidity preference:

LECLERCQ, J., Arch. Intern. Physiol. **55**, 93—116 (1947). (Reviews previous literature)
HEERDT, P. F. VAN, Thesis (1946). (As stated above).
BUETTIKER, W., Thesis (1948). (As stated above).