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The Temperature Preferendum of Certain Insects

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THE TEMPERATURE PREFERENDUM OF CERTAIN INSECTS¹

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(With Plate 9 and 10 Figures in the Text)

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1. INTRODUCTION

ALTHOUGH much work had been done on the optimum temperature for various insects, and the maximum and minimum temperature necessary to maintain life, relatively little has been done on their preferred temperature. In fact, at the time the present work was started only one worker in England had ever published on this subject.

In order to avoid any possible confusion between optimum and preferred temperatures it might be well to define them before going further. Although it is realized there are many definitions of the optimum temperature of an insect, for the purpose of this work it is taken to mean the temperature at which the greatest number of insects are reproduced in a given period of time. In other words, it is the temperature at which the relation between the number of eggs laid, the length of life and the mortality is such that the largest numbers of individuals survive after a given time. The temperature preferendum, on the other hand, is the temperature to which an insect moves if given its choice of a temperature gradient.

¹ Part of a Thesis presented to the University of London for the Degree of Ph.D.

The term 'preferendum' was proposed by Dr C. B. Williams while in Egypt, in 1922, although he never published on this subject himself. Since then various workers have adopted the term in one form or another. Herter has used 'thermische Indifferenzzone' and 'thermotaktisches Optimum'. Bodenheimer & Schenkin used 'Vorzugstemperatur'. More recently Gunn has suggested the term 'eccritic' temperature.

Temperature preferendum work may be approached from three different angles. (a) A comparative study of the temperature reactions of a large number of representative insects from various orders. (b) A comparative study of such factors influencing the temperature reactions as: age (larvae and adults), sex, insects tested with and without food, insects previously kept at room and at a constant high temperature, and the environment or natural habitat of the insect (those inhabiting soil, water, stored products, and also parasitic insects, etc.). (c) A detailed physiological study of one species to determine why it prefers a certain temperature or why it reacts as it does. Obviously this latter work could not be undertaken until (a) and (b) had been at least partially investigated. Because of a time limit, as much of the present work as possible was done under the first two groups.

The writer wishes to thank in particular Dr C. B. Williams for suggesting this problem and for his always unflinching help and advice; also the other members of the Entomology Department of Rothamsted Experimental Station for the helpful atmosphere found there.

2. PREVIOUS LITERATURE

As stated above, the first to carry out work on the temperature preference of insects was Williams in 1922 in Egypt. However, this early work was never published and the only reference to it is Kirkpatrick (1923) in his work on the Egyptian cotton-seed bug (*Oxycarenus hyalinipennis*). Kirkpatrick states: 'The resting bugs were found, by means of an apparatus devised by Mr C. B. Williams, to be thermotropic to a temperature of 36° C.'

Herter (1923 *a* and *b*, 1924, 1925) carried out some preferendum studies on insects. His apparatus ('Temperaturorgel') consisted of a cage 61 cm. long, 10 cm. high and 3 cm. wide, with an aluminium floor, a cardboard roof and glass sides. The metal floor was heated at one end with a gas flame and the heat lost to the opposite end caused a gradient to be set up. Thermometers were projected through the cardboard roof. The difficulty with this apparatus was that, owing to the lack of insulation, the temperature gradient within the cage varied with the room temperature. In his work with wood-ants (*Formica rufa*) Herter showed that the temperature of the environment from which the insect was taken influenced its preferred temperature. Figures were quoted which suggested that with an increase in the initial temperature there was a corresponding increase in the preferendum, i.e. that the preferendum varied directly with the temperature of the insect's previous habitat.

Parker (1924), in his work on the clear-winged grasshopper (*Camnula pellucida*), placed fifty first and second instar nymphs on a covered glass plate which was heated in the centre by an electric lamp from below. The temperature ranged from 60° C. above the lamp to 18° C. at the edge of the glass. The grasshoppers arranged themselves in a definite circle around the central area at a temperature of 37–38° C. The experiment was repeated several times. In connexion with an insect's preference for *radiant heat* mention should be made of the early work of Lodge (1918). In working on the sense reactions of house-flies it was observed that they congregated in large numbers round a lighted bunsen-burner and arranged themselves in a very definite circle, the size of which varied according to the distribution of heat. The temperature of this circle was 42–44° C. Heat distribution was controlled by placing larger or smaller pieces of asbestos over the flame, when the flies arranged themselves in larger or smaller circles respectively. If the gas was turned off the flies ceased to sit in a ring, but came closer to the base of the burner.

Kirkpatrick (1925), working with mosquitoes (*Culex pipiens*), provided them with water in troughs on top of a bar of aluminium heated at one end. The water varied from 14 to 36° C. and the females showed a decided preference for water at temperatures of 21–23° C. for oviposition.

Bodenheimer & Schenkin (1928) repeated Herter's early experiments with several insects. They found that the flour weevil (*Tribolium confusum*) had a preferendum of 24·760–26·568° C. if previously kept at a temperature of 15–18° C. However, beetles kept for a month in a constant temperature of 25° C. preferred a zone between 9·118 and 10·740° C. They also found that the average preferred temperature of nymphs of the house cricket (*Gryllus domesticus*) was 20·40° C. in Palestine; while Herter gives 26·512° C. to be its preferendum for Germany. As will be noticed the temperature readings were made to the third decimal place; this seems unjustified since, in most cases, the insect's preferred zone covered several degrees.

Fulton (1928), working independently, devised a preferred temperature apparatus based on an entirely different principle. A trough filled with wet sand was packed in ice at one end, while the opposite end was heated by electric lamps. The wet sand conducted the heat sufficiently well to form a temperature gradient although the changes were greater near the ends. Insects were placed in a glass tube which was imbedded in the sand leaving only the top exposed. Thermometers were pushed into the sand in a slanting direction so that the bulbs were under and in contact with the glass tube. Using adult click beetles (*Melanotus communis*), Fulton found that 57 % came to rest within the range of 26–29° C. The larvae showed no marked preference for any temperature between 17 and 29° C.

Bodenheimer's (1929) work on the desert locust (*Schistocera gregaria*) comprised all stages of the insect. In the development of the young there was a progressive increase in preferred temperature from 29·4° C. for the first stage

nymphs to 36.7° C. for the fifth stage nymphs. Bodenheimer concludes that this rise in the preferred temperature is connected with physiological changes in the insect during development, and also suggests that it is possible that this is connected with the water contents of the insect's body.

Grossman (1929) describes the results of his experiments with the Mexican cotton boll weevil (*Anthonomus grandis*). For this work he employed an apparatus which consisted of a 3 ft. length of $\frac{1}{2}$ in. glass tubing placed within a slightly shorter tube 2 in. in diameter. The space between the smaller and larger tubes was filled with water and sealed off with a cork at the ends. By heating the water at one end of the apparatus and chilling it at the other, a temperature gradient extending from 9 to 60° C. was obtained in the inner tube. In these experiments the weevils only reacted by avoiding temperatures above 49° C.

Bodenheimer & Klein (1930), working with ants, arrived at the conclusion that the preferendum of each species remains practically constant in different months regardless of the differences in the environmental temperatures. Hertzner (1930), working on the behaviour of the Argentine ant (*Iridomyrmex humilis*), used a rather crude temperature apparatus. It consisted of a galvanized pan, 3 ft. long, the bottom covered with soil, with a jar of ice at one end and an electric lamp at the other. The temperature gradient ranged from 13 to 50° C. Using worker-ants with pupae he found that the ants would settle down with their young between 21 and 27° C.

In further illustration of an insect's previous environment affecting its preferred temperature the work of Bodenheimer (1931) may be cited. He suggested that the humidity of the air in which insects are kept before an experiment has an effect on their preferred temperature. For instance, the Tenebrionid beetle, *Adesmia clothrata*, when kept in moist air before an experiment, preferred a temperature of 39.4° C., but when previously kept in dry air, preferred 36.6° C. Gunn (1931) obtained similar results using the cockroach (*Blatta orientalis*). Fahmy (1931) constructed a replica of the original temperature-preference apparatus used by Williams in Egypt. Working with *Ptinus tectus* he found that they preferred a temperature varying from 22 to 25° C. with an average of 23.5° C.

Uvarov (1931) has reviewed the literature on insect preferendum. He states that temperature preferendum 'is probably one of the most potent factors influencing the ecological distribution of insects and their movements', and suggests that the preferendum should be determined for each stage of every insect of economic importance. Nieschulz (1933, 1935) gives a useful discussion on the subject of optimum and preferred temperatures. He investigated the reactions of *Stomoxys calcitrans* to various temperatures. The average optimum was found to be 27.7° C. for the female and 28.8° C. for the male. The relative humidity of the atmosphere was said to be of negligible influence. This optimum temperature was about the same as that at which the normal activity started

to increase. It was found the results were not affected by atmospheric humidity, sex, age, amount of feeding, or egg maturation. The preferred temperature of *Stomoxys calcitrans* was found to average 29.4° C. for freshly captured females and 25.9° C. for males. For females of *Culex pipiens* that had hibernated in a cellar the temperature preferences was 8.9° C.

The following is a comparison of the results obtained by Nieschulz on the reactions of *S. calcitrans* to temperature:

Optimum temperature °C.		Preferred temperature °C.	
Males	Females	Males	Females
28.8	27.7	25.9	29.4

The preferred temperature for the males is almost 3° less than their optimum temperature, while for the females it is 1.7° more than their optimum temperature. These facts are pointed out here since so few investigators of preferred temperature have ever conducted experiments on optimum temperature so that comparisons might be made. Experiments were also carried out by Nieschulz with *Musca domestica* and *Fannia canicularis* similar to those with *Stomoxys calcitrans* above. Optimum temperature for *M. domestica* showed an average of 33° C. for females and 34.2° C. for males. The optimum for both sexes of *F. canicularis* was 23.7° C. A comparison of these results with those for *S. calcitrans* shows that all three flies have typical optimum temperatures that are peculiar to the species.

Martini & Teubner (1933), working with mosquitoes, found the preferred hibernation temperatures were 6–8° C. for *Anopheles maculipennis* var. *messeae* and 10–13° C. for *A. maculipennis* var. *atroparvus*. In the field the former also appeared to avoid high temperatures and high saturation deficiencies more than the latter. Here there was a considerable difference in choice of temperature even between two varieties of the same species. In 1934 Nieschulz carried out further experiments on the temperature preferred by *Stomoxys calcitrans*, the results of which confirmed those published the previous year.

The most exact study of preferred temperature is found in the work of Gunn (1934) on the cockroach. In his experiments he used a temperature-gradient apparatus in the form of a copper trough electrically heated at one end and cooled by ice at the other. The entire trough was well insulated, so that a constant gradient could be maintained irrespective of the room temperature. With this apparatus it was found that the preferred temperature range of an adult male *Blatta orientalis* was 20–29° C., and that this temperature range was not affected by changes in the air humidity.

Herter, in his later work (1934, 1936), used a modified form of his original apparatus in which he inserted thermometers into the aluminium bar, or floor of the gradient. With this apparatus he found the preferred temperature

(which he calls thermotactic optimum) for the flea, *Archaeopsylla*, to be 34.4° C., and for *Cimex*, 35.7° C. These figures are said to agree well with the surface temperature of the insect's hosts. Hertex also experimented with small mammals. Using mice and bats it was found the smaller forms had the higher temperature preference. Results with long-eared bats indicate that the ear perhaps plays a role in temperature perception and so indirectly is a factor in determining the animal's preferred temperature or 'thermotactic optimum'. Herter also recorded the frequency with which orientation occurred with the head toward the cool or heated end of the apparatus.

Nicholson (1934), in working on the influence of temperature on sheep blow-flies, determined the preferred temperature in a different way. The number of flies on the corks of the observation jars at various temperatures was recorded, and it was observed that this number was greatest near the extremes of temperature. Because of their low conductivity the corks probably felt warmer at very low temperatures and cooler at high temperatures, thus being less uncomfortable than the rest of the jar. In these experiments the greatest number of insects gathered on the corks at temperatures below 20° C. and above 35° C. Thus the range between 20 and 35° C. was considered to be the preferred temperature.

Continuing his work on the cockroach, Gunn (1935) made a comparison of the temperature preference of three different species. He found the upper limit of preferred temperature for *Periplaneta americana* and *Blatella germanica* to be 33° C., while for *Blatta orientalis* it was 29° C. The lower limit was not so sharply defined and it was suggested that further work be done before it could be regarded as significant.

Thomsen & Thomsen (1937, 1938) determined the preferendum of certain Dipterous larvae in their natural habitat. The temperature gradient apparatus used allowed the larvae to move freely in dung with a temperature range from 9 to 50° C. This overcame two serious weaknesses of the usual preferred temperature experiment: (a) the insects were in their natural medium and had access at all times to their food, (b) the relative humidity was fairly uniform throughout the apparatus. Larvae of *Musca domestica* in horse dung showed a definite temperature preference, which varied with their age. Larvae that were feeding preferred temperatures between 30 and 37° C., while those ready to pupate preferred temperatures below 15° C. The preference shown by feeding larvae corresponded to that found in their natural habitat in a fermenting manure heap. Within the manure a temperature as low as 15° C. cannot be obtained, hence pupae are to be found in the earth nearby. The optimum temperature for the development of house-fly larvae was shown to be 34° C. Supplementary experiments indicated that the attraction of the larvae to a given zone of the dung layer depended not solely on its temperature, but also on a chemical change therein. This chemotaxis was particularly marked only during the second day of larval life. The authors conclude that

the vertical distribution and movements of the larvae in natural conditions depend chiefly on their temperature preference and to a lesser degree on chemotaxis, negative phototaxis, hygrotaxis and thigmotaxis.

Larvae of *Stomoxys calcitrans*, which live in litter containing cow dung at 20–30° C., had a preferendum between 23 and 26° C. Comparing the temperature preferences of the larvae of these two species with those obtained above by Nieschulz for the adults it will be seen that the same differences hold. Namely, *Musca domestica* prefers a higher temperature in both the larval and adult stages than does *S. calcitrans*.

The first attempt to determine the preferred temperature of soil insects was made by Campbell (1937) in his work on wireworms. A modified form of Fulton's temperature-preference apparatus was constructed in which wet sand was used for the conductivity of heat and cold. The preferendum for these insects was lowest (17–23° C.) in the period February and March. During the summer the preferendum rose until the high point (27° C.) was reached in September, and then dropped in the latter part of September and October. In general, the experiments indicated that the preferred temperature varies with the season, being higher in the summer and autumn than in the winter and spring. It was also shown there is a lag behind the natural soil temperature, indicating that the preferendum does not change until the wireworms have been subjected to the higher or lower temperatures for a month or more.

Thomson (1938) used an alternative chamber to determine the reactions of mosquitoes, *Culex fatigans*, to temperature and humidity. This apparatus was roughly of the same principle as that used by Gunn & Kennedy (1936) to determine the reactions of insects to humidity. The maximum difference of temperature between each side of the chamber was only 10° C. All stages of the mosquitoes showed a strong avoidance of high temperatures. This was strongest in the hungry females, less strong in the blood-fed females and those with mature ovaries, and least strong in the newly emerged females. Gunn & Cosway (1938) tested cockroaches for their preferred temperature at two different humidities—moist and dry. In general, the average preferred temperature of these insects was higher in moist air than in dry. Individual cockroaches which did not react to humidity at a constant temperature likewise ignored the humidity in a temperature gradient. However, individuals which did react to humidity at a constant temperature also reacted to it in a temperature gradient by going to a lower temperature in dry air than they did in moist.

The only work on the reactions of aquatic animals to a temperature gradient is a recent paper of Doudoroff's (1938) on fishes. An apparatus is described whereby a steep horizontal temperature gradient can be maintained without the presence of vertical gradients in the water. Several species of marine fishes, chiefly *Cirella nigricans*, showed a marked selection for temperatures which were relatively high in comparison with the normal environment of the

fishes. While acclimatization was found to influence selection, the effect was slight and only temporary, the selected temperature being, to a large extent, independent of past experience. It was concluded that selection is indicative of the relative stimulative or detrimental effects of given rapid changes of temperature, while the common view that such selection indicates the nature of 'optimal' conditions or habitat preference is not tenable.

3. DESCRIPTION OF TEMPERATURE GRADIENT APPARATUS

Since the various pieces of apparatus used in the present work are new, or modified, a brief description is necessary. It should be mentioned that all were made in the Rothamsted workshop and were relatively inexpensive. The total cost of the two most expensive items, the linear brass gradients, was under £2 each.

(a) *Williams's early apparatus*

Plate 9A is a photograph taken by Dr C. B. Williams of his original temperature-preferendum apparatus. When the present work was started, the first temperature gradient to be constructed and tried was a replica of this. It consisted of a glass tube $1\frac{1}{2}$ in. in diameter and 40 in. in length, supported at each end by a retort stand with clamps. 'Compo' tubing, $\frac{1}{4}$ in. in diameter, was tightly coiled in a spiral fashion about the glass tube and looped down at one end with a small gas flame on the steep slope. At one side both ends of the compo tubing were joined to a Y tube, which in turn was joined to a glass funnel by means of rubber joints. This funnel was for filling the coils with water. In order to prevent air locks no water was used in the coils which had not previously been boiled. Compo tubing of a low melting point, which cannot be passed directly into a flame, should be immersed in a hot water bath which in turn may be heated by a bunsen burner. For taking temperatures a thermometer, with a thread tied to each end, was inserted into the glass tube and the strings allowed to hang free at the ends. The thermometer could thus be pulled along in either direction and the temperature recorded at any position in the apparatus where insects were gathered. The ends of the glass tube were plugged with cotton wool.

By heating the water at one point and setting up a circulation through the compo coils, a gradient could be maintained from a high temperature (about 35° C.) at one end of the apparatus down to room temperature at the opposite end. Inversely, if the compo loop were cooled instead of heated a gradient could be made from a low temperature at one end up to room temperature at the other end.

The great advantage of such an apparatus was that an insect had at all times a choice of a series of gradients. Each space between two compo coils offered a small independent gradient. Above the preferred temperature the insects tend to group in the cooler space between the coils, and below the preferred temperature in the warmer area on the coils. After a few trials, this apparatus was abandoned in a search for one which offered a complete gradient from a low to a high temperature.

(b) *Brass trough with ice-box* (Pl. 9B and Fig. 1)

This apparatus was made in the form of a trough built up from solid brass strips $\frac{1}{2}$ in. in thickness. The inside depth was 1 in., the inside width 2 in., and the overall length 4 ft. The trough was blocked off $3\frac{1}{2}$ in. from each end by soldering in place a brass piece of the same thickness as the sides.

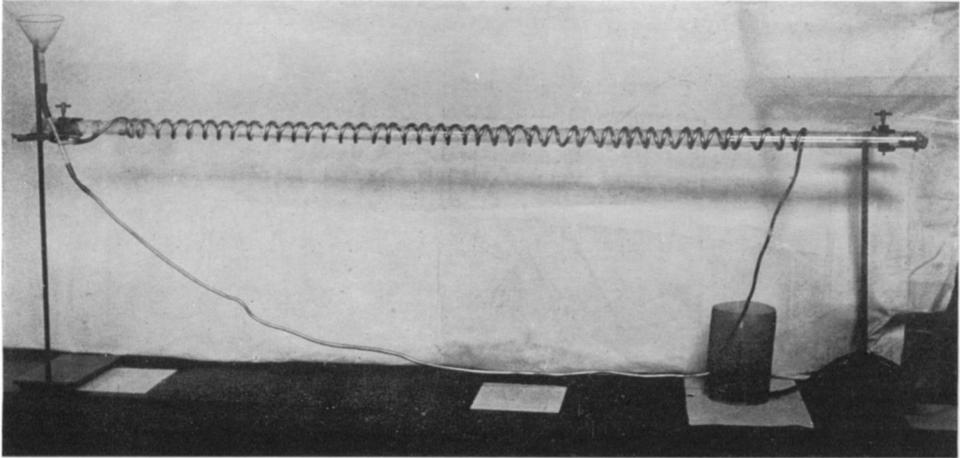


Photo A. Apparatus used by Williams in 1923.

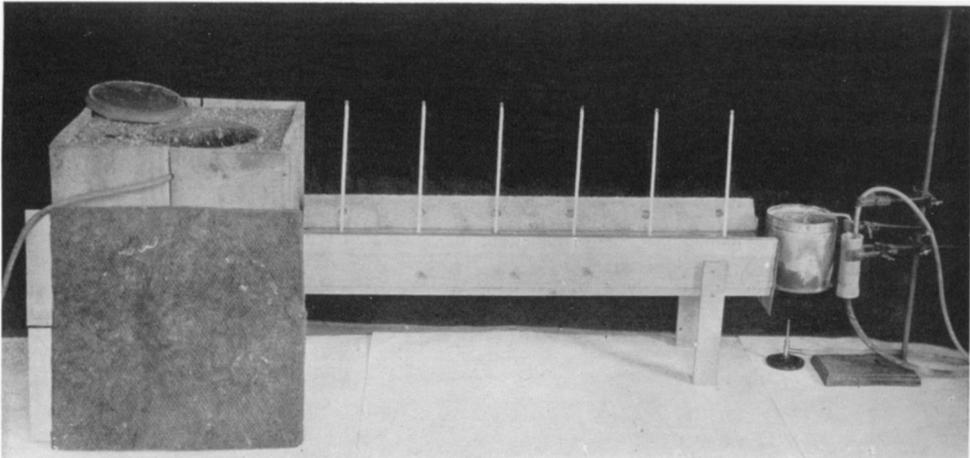


Photo B. Gradient apparatus with hot bath and ice-box. (Thermometers 6 in. apart.)

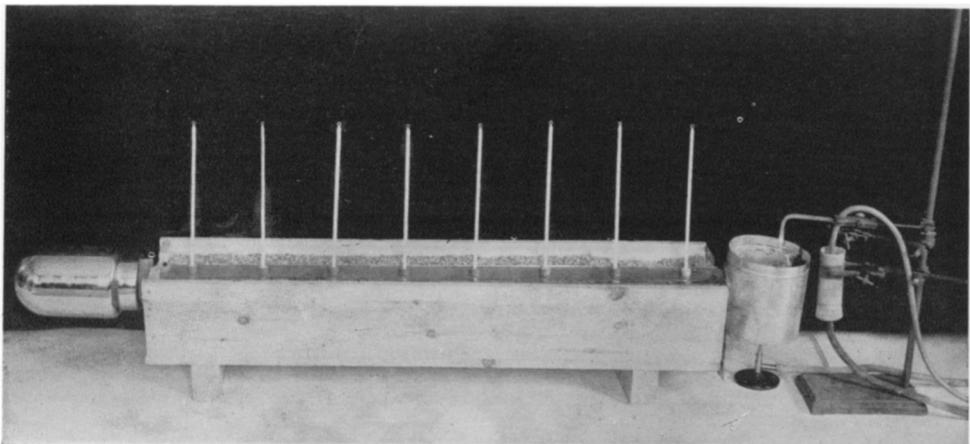


Photo C. Gradient apparatus with hot bath and Thermos jar. (Thermometers 5 in. apart.)

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A circular tin 6 in. in diameter by 6 in. in depth was secured and a hole made into one side 2 in. from the bottom. The trough was projected through this opening into the tin for a distance of $3\frac{1}{2}$ in., and the tin soldered tightly about the brass end-piece. This was to serve as a hot water bath for heating the hot end of the gradient.

For the other end of the trough a larger tin was secured (a 28 lb. honey pail), 8 in. in diameter by 12 in. in depth, and with a tightly fitting cover. A hole was made in the can 2 in. from the bottom and the free end of the trough projected into the tin the same distance as for the opposite side, and soldered in a like manner. Since this honey pail was to store the ice for the cold end of the gradient good insulation was necessary. First it was wrapped with cotton wool. Then a wooden box, 18 by 18 in. and 21 in. deep, was built around it so that the top of the tin was just level with the top of the box. The box was filled with granulated cork, which was firmly packed about the tin. Near the top of the tin was fitted an overflow outlet so that the water from the melting ice could drain off. The entire box was then covered with a square of thick felt as used for covering bee hives, and over this was a wooden lid.

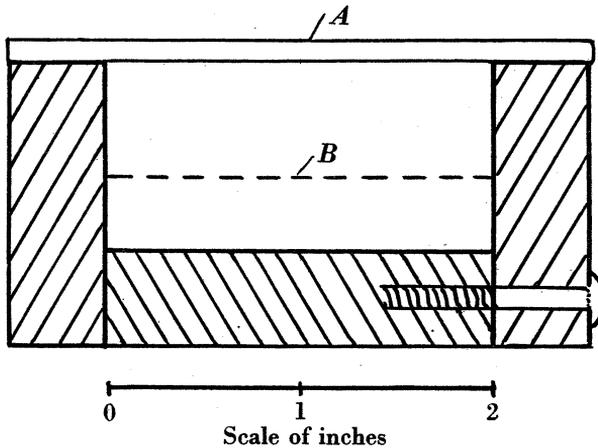


Fig. 1. Cross-section of linear apparatus. *A* = glass top. *B* = false floor of organdie.

There was thus left an actual run-way in the trough of $37\frac{1}{2}$ in. for the insects. (Notice that $3\frac{1}{2}$ in. of the gradient which ran from the ice chamber to the outside of the insulation box was lost for experimental work.) In order to prevent temperature loss from the metal gradient it was also lagged in the same way as was the ice container. First with cotton wool and then with granulated cork. To hold the cork a wooden trough 8 in. wide and 4 in. deep was built to fit about the entire exposed length of the brass channel. At the cold end this trough fitted flush with the ice-box, while at the hot end it was covered with tin-plate to protect it from the bunsen burner.

The cover to the gradient consisted of six glass plates each $6\frac{1}{2}$ in. long, 3 in. wide, and $\frac{3}{8}$ in. in thickness. The ends of each plate were ground so as to fit tightly to the next and a hole was drilled in the centre of each to admit a thermometer. The glass covers were then sealed in place with vaseline. The rubber stoppers used to hold the thermometers in position were first 'weathered' out of doors for 3 months. This was to avoid any toxic emanation from the new rubber as discussed by Mellanby & Buxton (1935). A piece of wall board $\frac{1}{2}$ in. thick, 3 in. wide, 38 in. long and with holes bored to allow for the thermometers to project through was then placed over the glass. The primary purpose of this cover was to darken completely the experimental chamber whenever this was desired. However, it was also

beneficial in serving as additional insulation. A 95 cm. rule was placed alongside the trough for determining the position of the insects.

The hot water bath was kept at a uniform level (about 1 in. from the top of the tin) by means of a constant level apparatus (Fig. 2). This was held in place by a retort stand and was supplied with a constant stream of water from a nearby tap with an overflow to the sink. The heat for the water bath was supplied from a micro bunsen burner which was fitted to burn night and day.

With this apparatus a temperature gradient over a 3-day period (the length of each experiment) averaged from about 10° C. at the cold end, when cooled with ice and salt, to 35° C. at the hot end. There was but little variation from hour to hour except at the cold end, which fluctuated between 5 and 10° C. The temperature gradient was approximately a straight line allowing the insects a choice of about 1° C. in every 4 cm.

(c) *Brass trough with Thermos vacuum flask* (Plate 9 C)

This apparatus was also of brass and was constructed in practically the same way as the above gradient. The only difference being that the ice for the cold end was contained in a 1 gallon Thermos vacuum flask instead of a lagged ice-box. One end of the trough was projected through the flask's cork for 4 in. and the cork sealed in place about the trough with marine glue. The flask could then be filled with ice and salt and slipped on and off the cork at the end of the gradient.

By using the vacuum flask, and thus eliminating the large amount of lagging, an additional 2½ in. of the trough were made available for experimental purposes. This gave a run-way of 40 in. instead of 37½. To cover this trough eight pieces of glass, 5 in. in length (and eight thermometers), were used instead of six as in the previous gradient (Fig. 3).

Ice remained in the flask for a period of 24 hr. However, when the ice was not in actual contact with the brass bar the temperature immediately went up at the cold end of the gradient. To avoid this a larger Thermos would probably be of advantage. Otherwise the gradient obtained was about the same as when an ice-box was used.

The chief advantages of this apparatus were as follows: (a) light in weight—easily moved about by one person, (b) compact, took up less space, (c) used a minimum of ice. This gradient machine was not constructed until near the end of the preferendum work and no results from it are included in this paper.

4. TECHNIQUE OF EXPERIMENTS

(a) *Apparatus and working precautions*

So far as I am aware only one previous worker on thermo-preferendum has ever made any attempt to distinguish between floor temperature and air temperature in the gradient. Most have taken the air temperature by projecting thermometers through the top, or sides, of the apparatus while the insects remained in contact with a metal floor. In the present work it was decided to test the gradient for any possible differences in temperature within the apparatus itself. The following are the average results of twenty readings

taken at three different positions along the linear gradient, i.e. at 85 cm. the cold end; 55 cm. the centre of the gradient; and 10 cm. the hot end:

Position in gradient	Floor	Centre	Roof
85 cm.	6° C.	11° C.	11° C.
55	20.5	21	21
10	44	36	36

The average room temperature was 20° C. 'Floor' indicates that the thermometer was lying flat on the floor but the bulb was not in metallic contact with it. 'Centre', the thermometer bulb was projected through the glass cover, to about midway in the apparatus, in the same position as when experimental temperature readings were taken. 'Roof' indicates that the thermometer was propped tightly against the inside of the glass roof. All three thermometers (i.e. floor, centre and roof) were placed in tier one above the other at each of the three positions shown above.

As can be seen at the cold end the floor was 5° colder than the centre and roof. In the centre the floor, centre and roof temperatures were all about the same. This was more or less expected, since the temperature here was approximately the same as that of the room. At the hot end the floor was 8° hotter than the air above it or the roof. In no single reading was the difference between either the centre or air temperature and the roof ever more than 0.5°, the average being the same for both.

In order that the air surrounding the insects should be as nearly as possible at the same temperature as that recorded on the thermometers, and in order to avoid any controversy on the subject, a false floor was placed in the apparatus. This floor was of finely woven 'organdie' cloth and was held in place, half-way between the brass floor and the cover, by adhesive zinc-oxide plaster. This plaster had no apparent odour and was superior to all other sticking substances in preventing even the smallest insects from working their way beneath the cloth. It was later discovered that this false floor had the following additional advantages: (a) it was easy to see the insects against a white background, (b) the insects could easily get a foothold, (c) if any insects got on to their backs they could readily right themselves.

Thermometers were placed at 10, 25, 40, 55, 70 and 85 cm. In the early experiments temperature readings were taken every 30 min., but since there was little variation in the temperature the readings were reduced to one each hour in the later work. At each temperature reading a record was also taken of the room temperature. Since most of the insects experimented with had a preferred range of several degrees all temperature readings were taken to the nearest degree only, never to fractions.

It is impossible to have a temperature gradient without also having an inverse gradient in relative humidity, i.e. the relative humidity will be the lowest at the warm end of the gradient and highest at the cool end. The only

way to maintain a constant relative humidity in a temperature gradient would be by completely drying the air or by keeping it saturated. Since neither of these alternatives appeared feasible it was decided to measure and record the relative humidity each day. In this linear gradient it varied from 10 to about 45 %. However, as will be shown later, it was possible to keep an approximately uniform relative humidity when the experimental trough was filled with food for certain stored product insects.

Since the space above the false floor was only $\frac{1}{2}$ in. in height and 2 in. in width the relative humidity had to be taken with a very small instrument. For this purpose four Edney paper hygrometers were selected as used by Gunn & Kennedy (1936). These are watch-like instruments, 2 in. in diameter and about $\frac{1}{4}$ in. in thickness, and give a direct reading of relative humidity. They were placed in the apparatus at night, after the insects had been removed, and the relative humidity recorded the following morning. They thus had ample time to reach equilibrium before the readings were taken. The hygrometers were always placed at 0, 30, 60 and 90 cm. along the gradient. Each week the hygrometers were calibrated with a wet and dry bulb sling psychrometer. In addition, during the day, when not in use, they were kept in separate desiccators in which the relative humidity was controlled by known concentrations of sulphuric acid as described by Buxton & Mellanby (1934). Each hygrometer had a number, and the one used at the dry end of the gradient was kept at a low humidity (about 10 %); the one used at the moist end was kept at about 75 % relative humidity and the remaining two at intermediate humidities.

In very few of the papers on thermo-preferendum has the humidity ever been measured or even mentioned. Nieschultz (1933) made an attempt to overcome the humidity difficulty by having desiccating agents at the cool end and humidifying solutions at the warm end of the apparatus. Gunn (1934) forced a regulated stream of air of a known dew point into his apparatus. More recently Thomson (1938), working with mosquitoes, determined the humidity range to which they were insensitive and then kept his temperature gradient within this predetermined zone. However, with mosquitoes this was quite easy to do, since all stages were indifferent to a relative humidity between 30 and 85 %.

The hot water bath was kept heated by a gas flame day and night, and the ice-box was likewise kept continually packed with ice. A uniform gradient could thus be maintained continuously over a period of weeks or even months. The advantages of keeping the gradient going over long periods were: (a) one could commence work immediately upon arrival in the morning without waiting for a gradient to form, (b) the hygrometers could be left in the apparatus over night for recording the relative humidity at different positions along the gradient. The ice-box was packed three times a day, morning, noon, and night, with two parts finely crushed ice and one part common salt (sodium chloride).

This mixture gives a theoretical temperature of -18° C. according to Kaye & Laby (1921). An average of about 6 lb. of ice was used at each packing. In order to secure the maximum results from this freezing mixture it was necessary to keep the water level about 2 in. above the brass trough which projected into the ice-tin. The water above this level was periodically siphoned off into the sink. About once a month the salt which caked at the bottom of the tin also had to be cleaned out.

The first experiments were conducted in a laboratory with three south windows. Although the windows were shaded it was quite impossible to keep the light uniform on all parts of the gradient. During the same day the light might change from bright sunshine to cloudiness and at night to artificial light. The experimental trough was therefore kept completely dark by covering it with 'masonite' wall board cut to fit exactly over the glass plates. However, when the cover was lifted for the purpose of making an observation, the insects immediately became restless, and started moving about. After a little preliminary work, all apparatus and experiments were moved to a dark room in the basement. During each experiment only one small shaded light was alight, and this was below the level of the trough. An indirect uniform dim light, which was just sufficient to see the position of the insects, was cast over the gradient. This dark room had an additional advantage in that it was constructed as a constant-temperature room. Although no attempt was made to keep it at a uniform temperature it nevertheless remained between $18-21^{\circ}$ C., night and day, throughout the year.

It should be mentioned that each time work was started with a different species of insect the gradient was thoroughly sponged out with cotton wool and boiling water, and the false floor removed and replaced with a new one.

(b) *Observations*

Each experiment was carried on for a period of 3 days. The number of observations made varied somewhat according to the nature of the experiment, but usually every half-hour the number of insects, and their positions in centimetres, were recorded. When insects were used with food, observations were made after they had been in the gradient for 1 hr., 2 hr., 4 hr., 8 hr., etc. This was to see how long it took the insects to come to their preferred temperatures and if their preference changed with time. After each experiment a control was carried out for 1 day at a uniform temperature. This was for the purpose of getting the random distribution of the animals when there was no gradient. A control often showed an insect to be strongly thigmotropic (for example, the bed-bug), or to have definite end preferences. So far, the Thomsens have been the only experimenters to use a control in connexion with preferendum work.

Thirty insects were usually used in each experiment, five being introduced into each of the six cover openings. Half-hourly observations usually resulted

in twenty-four readings a day, seventy-two in 3 days. Thus there was a total of 720 observations daily or 2160 for the 3 day experiment. The numbers of insects, both experimental and control, were all originally plotted against position in centimetres, and, superimposed upon this, the temperature and humidity were also plotted against position (Fig. 2).

Taking the insects' positions in centimetres rather than recording the number at each temperature had the following advantages: (a) it permitted the rapid recording of observations, and no interpolation between thermometers was necessary; (b) it allowed the plotting of experimental results

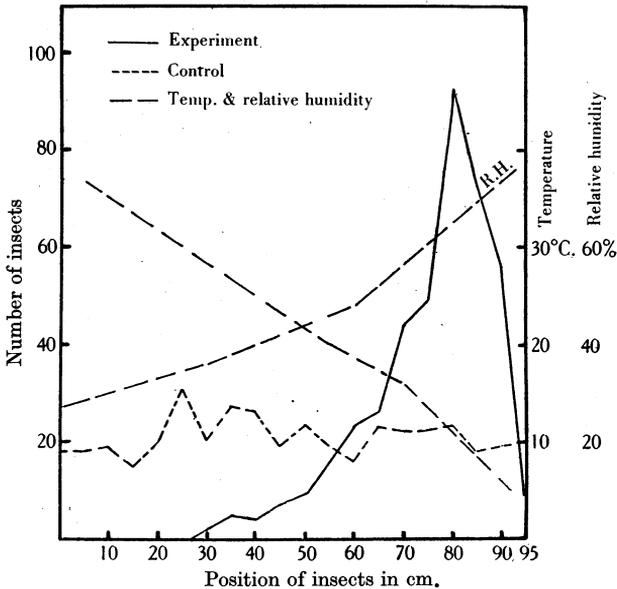


Fig. 2. Temperature-preference curve of adult *Apanteles congestus* (Braconidae, Hym.) arranged according to position in centimetres in the gradient. Each point is the average of not less than forty-two hourly observations on thirty insects previously kept at room temperature (cf. Fig. 3).

against a control—since the control was taken in centimetres at a uniform temperature, positions had to be taken in centimetres; (c) it is easy to convert position into temperature gradient, but more difficult to record the reverse process; (d) some insects may have an end preference which would not show up if positions were taken in °C.; (e) the results lend themselves more readily to statistical treatment; (f) some insects may not respond to a change in the temperature gradient; but if their positions were taken in °C. and the temperature gradient changed, they would appear to be changing their preference—when in reality it would be the temperature changing and not the insects.

If we have insects which distribute themselves evenly (i.e. no preference) in a gradient that is high at one end, low at the other and fairly uniform in the

centre, and if these insects were plotted against position, a straight line would result. If plotted directly against temperature, a curve would be obtained with a central mode, apparently indicating that these insects had a temperature preference for the centre of the apparatus, merely because a longer space at each temperature would be available in the middle. It would not show the even distribution of the insects nor that just as many per centimetre were at the hot and cold ends as were in the centre.

The difficulty of showing all results in this form is that each experiment requires a separate graph. When they are converted into numbers of insects against temperature this resulting graph is as shown in Fig. 3. This form has been used for a selection of results, as a larger number can be illustrated in a small space.

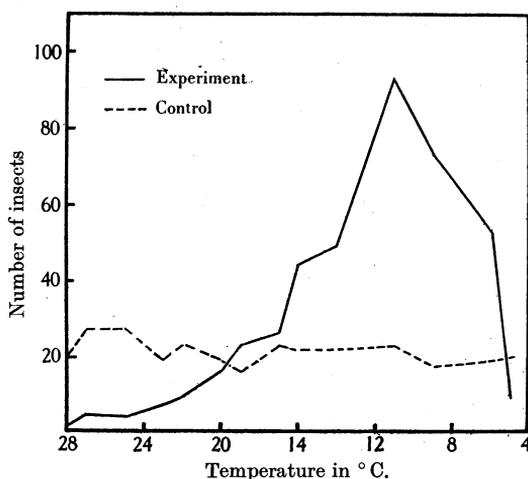


Fig. 3. Temperature-preference curve of adult *Apanteles congestus* (Braconidae, Hym.) arranged according to temperature in gradient in °C. (cf. Fig. 2).

The original records were taken in the manner shown in Table 1. It is impossible to print all of these; but the original records are deposited at Rothamsted Experimental Station, where they can be consulted.

(c) *Insects used*

A total of twenty-three species of insects from six orders has been tested for their temperature preferendum. These have included insects of widely different environments and habits, such as the following: stored product insects, leaf-feeding insects, plant-sucking insects, human parasites, insect parasites, and soil insects. During the winter months work was done on stored product insects (mainly beetles), while in the warmer months insects from out of doors were used. The summer insects included such pests as ants,

wireworms, sawflies, earwigs, etc. The following is a detailed list of the species used.

Order	Family	Species
Dermaptera	Forficulidae	<i>Forficula auricularia</i> Earwigs
Hemiptera	Cimicidae	<i>Cimex lectularius</i> Bedbug
	Pyrrhocoridae	<i>Dysdercus howardi</i> Cotton stainer
Lepidoptera	Tineidae	<i>Tineola biselliella</i> Common clothes moth
Coleoptera	Elateridae	<i>Agriotes</i> sp. Wireworms
	Bruchidae	<i>Acanthoscelides obtectus</i> Bean weevil
	Ptinidae	<i>Ptinus tectus</i>
	Anobiidae	<i>Lasioderma serricorne</i> Tobacco beetle
		<i>Sitodrepa panicea</i> Biscuit weevil
	Curculionidae	<i>Calandra granaria</i> Granary weevil
		<i>Calandra oryzae</i> Rice weevil
		<i>Dermestes vulpinus</i> Leather beetle
	Dermestidae	<i>Anthrenus verbasci</i> Carpet beetle
		<i>Tenebrionidae</i>
	Tenebrionidae	<i>Gnathocerus cornutus</i> Horned flour beetle
		<i>Tenebrio molitor</i> Meal worms
		Cucujidae
<i>Laemophloeus turcicus</i>		
Hymenoptera	Tenthredinidae	<i>Pteronidea melanaspis</i> Saw-flies
	Braconidae	<i>Apanteles congestus</i>
Diptera	Formicidae	<i>Acanthomyops</i> sp.
	Sepsidae	Sepsid flies

With many of the insects, both the immature and adult stages were tested separately and the results compared in an effort to find differences, or similarities, in their preferendum. With others the sexes were experimented with independently to see if sex could be in any way related to choice of temperature.

All species experimented with were kept at room temperature. As stated above this remained at 18–21° C. in the dark room. In addition to these, a number of insects were also kept at a high temperature (27° C.) to see if this would alter their preferendum. A constant temperature oven, thermostatically controlled to keep at 27° C., was used for this purpose. Some soil insects were

also kept at low temperatures (freezing) before being tested. A comparison was then made between those previously kept at room temperature and those kept at freezing point.

The technique of previous workers has been to place insects in a preferendum apparatus without food, in a strange environment and often in bright or changing light. (Thomsen & Thomsen (1937), who worked with maggots in dung, are an exception.) In an endeavour to determine if insects react to a temperature gradient in the same way with food as they do without it, several stored product pests were tried. The experimental trough was filled with their usual food (rice, bran, wheat, fish meal, etc.) and the insects distributed in the normal way. The glass cover to this linear trough was cut into six sections of 16 cm. each. This was a great advantage in removing insects with food, or with soil, since only two 8 cm. sections needed to be uncovered at a time. All twelve sections of food were removed at one time and placed in separate Petri dishes. This was to avoid any movement of insects, due to a change of temperature, when the apparatus was opened. This same technique was used for determining the position of soil insects along the gradient.

Since the thermometers projected directly into the food material, quite an accurate temperature record was obtained of the insect's actual habitat. An additional advantage in using food was that an almost uniform humidity was maintained over the period of the experiment (3 days). However, it is likely that if the food were allowed to remain in the gradient for a longer period a humidity gradient would have finally been set up.

In selecting specimens for an experiment, only the most active and healthiest ones were chosen. Those that were crippled, deformed or appeared abnormal in any way were thrown out. Each experiment was always carried through to its completion with the same individuals originally selected. For example, if one or two insects died, were lost or killed in the middle of an experiment they were not replaced by fresh ones. This accounts for the total number of observations not being the same in certain of the experiments. After the last observation was made at night the insects were removed from the apparatus and fed in a container separate from the stock supply. In transferring the insects to and from the gradient, they were always handled with a camel-hair brush in order to prevent any injury to them.

An equal number of insects, usually five, was introduced into each of the six thermometer openings. After each observation was recorded the insects were disturbed to see if they would return to a similar temperature. No attempt was made to direct them in any particular direction but just to start them moving. Two methods were used for this. The first was to have within the trough a light piece of bent iron wire which by means of a magnet could be used to disturb the insects from outside the glass cover, as used by Gunn & Cosway (1938). Secondly, insects that were not sensitive to the wire and magnet were disturbed by a thin copper wire, well protected with rubber.

5. RESULTS

(a) *Stored product insects* (Table 2)

The flour beetle (*Tribolium confusum*), when kept at room temperature, showed a definite temperature preference for 25 to 30° C. and gradually diminishing down to 10° C. (Fig. 4). In a separate experiment the beetles

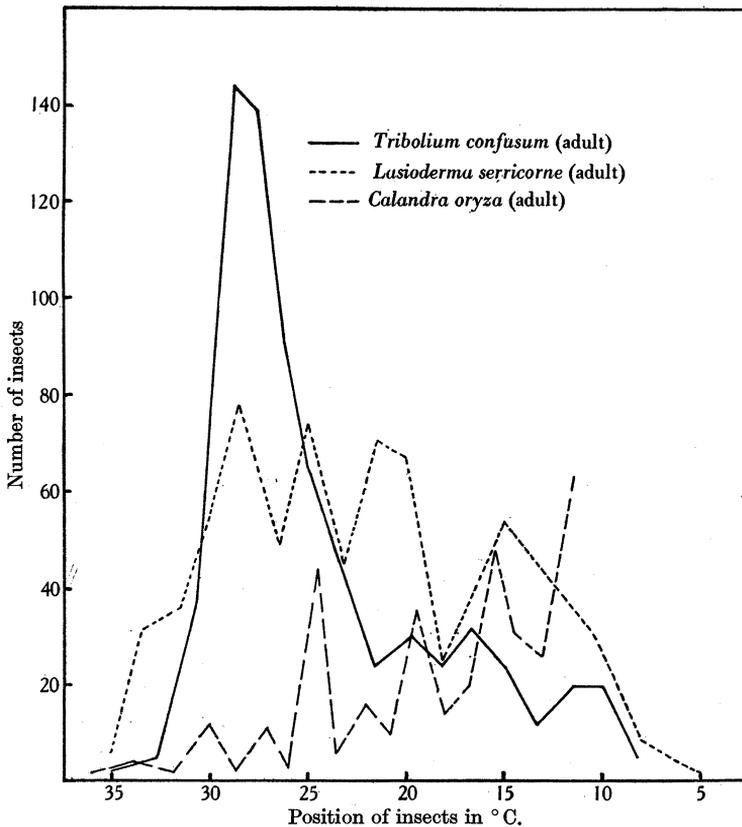


Fig. 4. Temperature-preference curves of adult insects of various species previously kept at room temperature (without food).

were kept for a month at a constant temperature of 27° C. (their optimum) previous to going into the gradient. These formed a very high peak at the cold end, 14° C., with the exception of a few that distributed themselves irregularly from 30 to 16° C. (Fig. 5). The peak number of insects thus occurred at a temperature 12° lower than when kept at room temperature. In general these results agree with the work of Bodenheimer (1928) on *T. confusum*.

In discussing extremes of temperatures Chapman (1931) makes the following statement: 'it would seem, in general, that the tropical insects, including

those of tropical origin, do not have the capacity for enduring dormancy. This is true of *Tribolium confusum*, which will die in a few weeks at 7° C.' In view

Table 2

Stage	Previous temp.	Food	Preferred temp. °C.	Preferred range humidity	Figure
<i>Tribolium confusum</i> (Flour beetle)					
A	Room	None	25-30	35	4
A	27° C.	None	(14)	60	5
A	Room	Bran	10-(25-30)	38	6
<i>Lasioderma serricorne</i> (Tobacco beetle)					
A	Room	None	15-32	40-55	4
A	Room	Rolled oats	8-32	45	6
A	27° C.	None	(15) and (27)	40-60	5
<i>Calandra oryzae</i> (Rice weevil)					
A	Room	None	10-20	40-60	4
A	27° C.	None	(14)-23	40-60	5
A	Room	Rice	8-(17)-25	60	6
<i>Calandra granaria</i> (Grain weevil)					
A	Room	None	(14)-25	20-60	—
A	27° C.	None	(14)	60	—
A	Room	Wheat	9-(20)-30	60	—
<i>Dermestes vulpinus</i> (Leather beetle)					
A	Room	None	(30)	60	7
L	Room	None	(30)	60	—
L	Room	Fish meal	20-30	55	—
A	Room	Fish meal	(7)-(16)-(25)	30-36:45	8
<i>Gnathocerus cornutus</i> (Horned flour beetle)					
A	Room	None	13-(20)-35	23-70	—
L	Room	None	13-(20)-35	23-70	7
L	Room	Bran	12-30	35	8
<i>Plinus tectus</i>					
A	Room	None	(8)	80	—
A	Room	Fish meal	(8)	55	—
<i>Tenebrio molitor</i> (Mealworms)					
L	Room	None	13-(19)-20	25-42	7
L	Room	Bran	13-(19)-20	60	8
<i>Oryzaephilus mercator</i>					
A	Room	None	15-(24)-(28)	—	—
<i>Oryzaephilus surinamensis</i>					
A	Room	None	15-(24)-(28)	—	—
Replicate of above two					
A	Room	None	(10)-(28)	40-70	—
<i>Anthrenus verbasci</i> (Carpet beetle)					
A	Room	None	8-(12)-25	40-45	—
<i>Acanthoscelides obtectus</i> (Bean weevil)					
A	Room	None	13-30	15-40	—
<i>Sitropeda panica</i> (Biscuit weevil)					
A	Room	None	14-(21)	20-40	—
<i>Laemoploeus turcicus</i>					
A	Room	None	14-(17)-(21)-28	30-60	—
<i>Tineola biselliella</i> (Clothes moth)					
L	Room	None	14-(17)-20	30-40	—

A = adult; L = larva.

of the above the insects going from a previously high to the lowest possible temperature could hardly be associated with going to a more favourable habitat.

When given bran in which to move about and feed they still showed a marked preference for 25–30° C.; but there were also more insects at the lower temperatures and even a slight rise at the cold end (Fig. 6). *Tribolium*'s temperature preference in these two experiments corresponds quite closely to their optimum, which is 32° C. for reproduction, according to Chapman (1931).

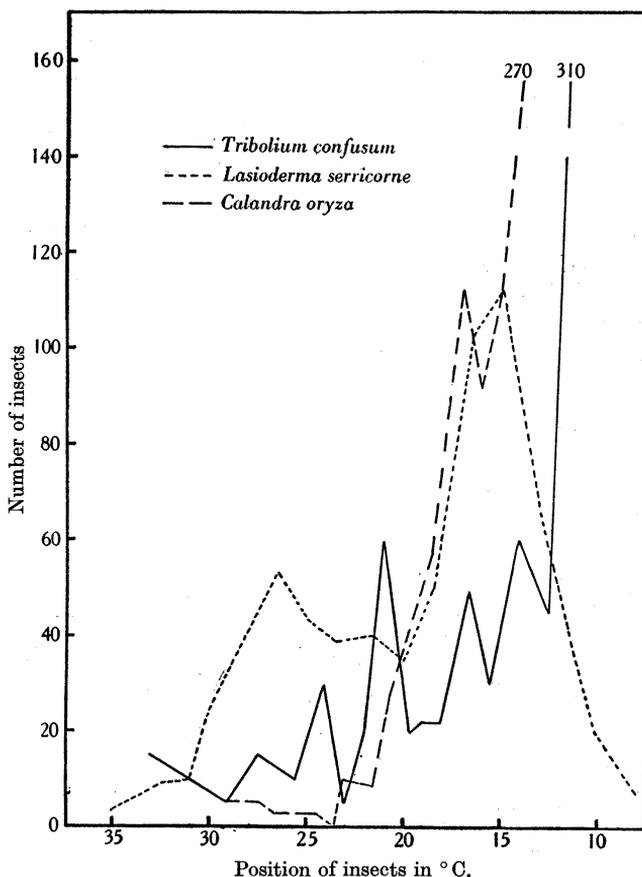


Fig. 5. Temperature-preference curves of insects shown in Fig. 4 but previously kept at a temperature of 27° C. (without food).

The temperature-preference curve for the tobacco beetle (*Lasioderma serricorne*) fluctuates over a zone from 32 to 15° C. (Fig. 4). When given food this zone became even wider, extending all the way from 32° C. to the cold end of the gradient (8° C.) (Fig. 6). However, after being kept at 27° C. for a month the beetle's preference was altogether changed. There was a slight peak at 27° C. and then a very decided one at 15° C. with a complete dropping off at the cold end (Fig. 5). In the first two experiments only about 25 % of the insects were found to be near 32° C.—the temperature given as their optimum

by Powell (1931)—and in the last experiment less than 15 % were near this figure.

Rice weevils (*Calandra oryzae*), previously kept at room temperature, present a violently fluctuating curve rising somewhat at the cool end (Fig. 4). When previously kept at a constant temperature of 27° C. they form a curve beginning at about 23° C. and rising very rapidly at the cool end (Fig. 5). On the other hand, weevils given rice, as a medium in which to choose their temperature, formed a peak at 17° C. which gradually sloped off to 25° C. on one side and 8° C. on the other (Fig. 6). Thus in every experiment these insects were found in greatest numbers at a temperature much below their optimum of 25° C., as given by MacLagan & Dunn (1936).

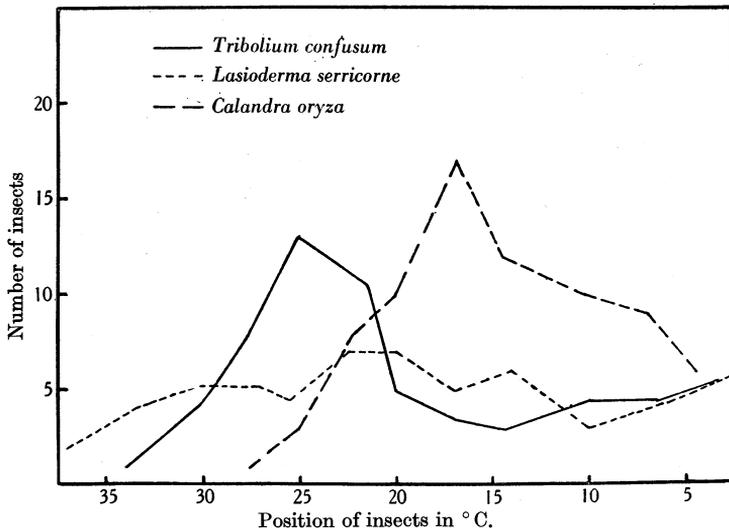


Fig. 6. Temperature-preference curves of insects shown in Figs. 4 and 5 when given food in the temperature gradient.

The temperature preference for the grain weevils (*Calandra granaria*) begins at 35° C., starts to rise at 25° C. and finally makes a very rapid ascent at 14° C., the cold end of the gradient. When the weevils were kept at a constant temperature of 27° C. for a month they gathered in even larger numbers at the cold end. Beginning at about 28° C. the numbers do not increase greatly until the temperature reaches 14° C., then the curve rises almost perpendicularly towards the cool end. When given food, the insects had a definite preference for 20° C., which tapered off to 30° C. on the hot and 9° C. on the cold side. With food, their preference was almost identical to that of *C. oryzae* above. However, in no case were more than about ten insects ever found near 28° C.—their optimum as found by Kunike (1936).

Both larvae and adults of the leather beetle (*Dermestes vulpinus*) behaved similarly in the temperature gradient. After reaching a very steep peak at 30° C. they dropped suddenly and then trailed off in small numbers to 9° C. (Fig. 7). With food the larvae had a rather wide preference zone, extending from 32 to 20° C. with another slight rise at 7° C. Adults with food had three

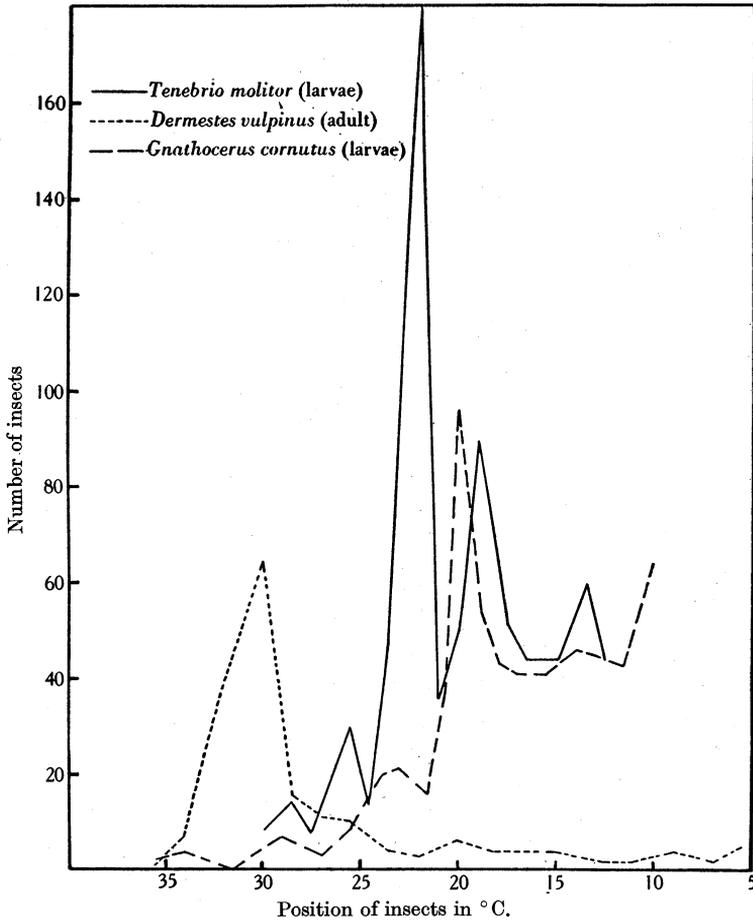


Fig. 7. Temperature-preference curves of certain adult and larval insects previously kept at room temperature (without food).

quite separate and definite peaks; the first one at 25° C., the second at 16° C., and the third at 7° C. (Fig. 8).

There was also a great similarity between the larval and adult temperature-preference curves of the horned flour beetle (*Gnathocerus cornutus*). They both began at about 35° C. and reached their maximum at 20° C., then declined to 13° C. However, the adults rose slightly at the end of the trough. When the larvae were placed in bran they occupied a longer range than before—a range

extending from 30° C. to about 12° C. (Fig. 8). No experiments were conducted with the adults in their food medium.

Both with and without food, *Ptinus tectus* showed a decided preference for the cold end of the gradient—about 8° C. Once, when tested without food, they showed a very weak preference for 25–20° C. *P. tectus* differed from most

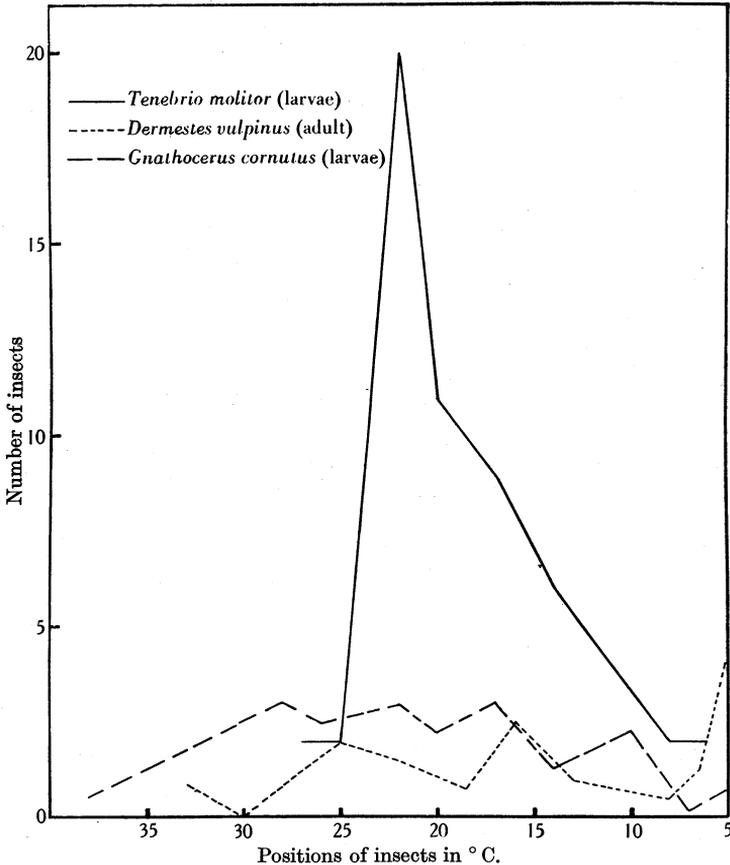


Fig. 8. Temperature-preference curves of insects shown in Fig. 7 but with food in the temperature gradient.

insects which went to a low temperature in that they were active and perfectly able to move about at all times. Most insects had to be removed from the cold end before they regained sensibility and could move about. It appears that this species remained in the cool zone because of preference and not because of being trapped. Also in the controls, at a uniform temperature, *Ptinus* distributed itself evenly throughout the length of the gradient.

Meal worms (*Tenebrio molitor*), both with and without food, rose to their highest peak at about 20° C. (Figs. 7 and 8). Without food, they had a minor

peak at 19° C. and another at 15° C. On the other hand, when food was supplied, there was a gradual decline from their maximum to 9° C. at the cold end. It might be suggested that the meal worms tested first left an odour, thus causing those in the second experiment to gather in the same place. This would hardly seem possible, since the first experiment was conducted on 19–21 April and the second on 29 November–1 December 1937. It is rather surprising that even more larvae were not found near the cold end, since they can survive cold much better than heat. Cotton & St George (1929) found that all stages of the meal worms were killed by a 1 hr. exposure to 52° C., while larvae exposed for more than 7 months to a freezing temperature remained alive.

A comparison between experiments with the saw-toothed grain beetles (*Oryzaephilus mercator* and *O. surinamensis*) showed the preference of both species to be almost identical, with two definite peaks. Here the two peaks were quite close together, one at 28° C., while the other was 24° C. The results for *O. mercator* were obtained from experiments conducted 5–7 March, while *O. surinamensis* was not tested until 19–21 March. In the presence of such striking similarities, it was decided to repeat the experiment at a later date. A replicate was started on 11 October, more than 6 months after the first experiment. Again the behaviour of the two species was similar, each showing two peaks. However, the two modes were more widely separated than before, the first being between 25 and 30° C. and the second at about 10° C. In both experiments the maximum peak occurred very near 27° C., the temperature given as the optimum for the most rapid development of *O. surinamensis* from egg to adult according to the investigations of Back & Cotton (1926).

The preference curve for the carpet beetle (*Anthrenus verbasci*) started at 30° C., attained its greatest height at about 12° C. and then suddenly dropped to almost nothing at the cold end. Its choice was thus decidedly within the cold zone, below 15° C., but not against the end of the trough.

The temperature preference for the bean weevil (*Acanthoscelides obtectus*) fluctuated quite violently between 30 and 13° C. All that can be gathered from results of this nature is that the weevils avoided temperatures above 30° C. In the control these insects had a definite preference for the ends. Biscuit weevils (*Sitodrepa panicea*) had one peak at about 21° C. and another at 17° C., with most of the insects in a zone between 21 and 14° C. Here again the insects showed an end preference in the control at a uniform temperature. Adult *Laemophloeus turcicus* presented a rather undecided temperature-preference curve, extending from about 30 to 14° C., with a peak at 21° C. and another at 15° C. Most of the insects were gathered in the zones 28 to 21° C. and 17 to 14° C. The clothes moth larva (*Tineola biselliella*) was the only Lepidopterous insect used. Here a definite preference was shown for the cool zone, 20 to 14° C., with a peak at about 17° C.

The above four experiments were conducted during the early part of this

work in one of the large entomological laboratories where uniform light and constant temperature did not prevail as in the dark room which was used in all other experiments.

(b) *Soil insects* (Table 3)

In all experiments with soil insects the thermometers projected directly into the soil, or other medium, in the same way as when food was used. At the hot end of the gradient moisture was continually condensing on the glass covers and dripping back on to the soil. As a result the moisture content of the soil remained fairly constant throughout. Most of the soil work was done with wireworms because (a) they are a serious agricultural pest in England, and (b) they could be obtained in sufficient quantity.

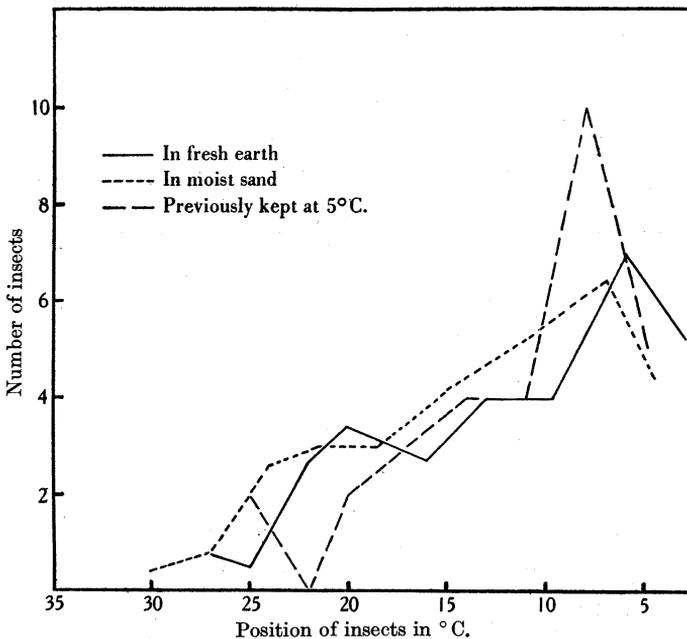


Fig. 9. Temperature-preference curve of wireworms, larvae of *Agriotes* sp. (Elateridae, Col.) under different conditions.

Fig. 9 shows a comparison between the results of wireworms that were placed in fresh earth (i.e. unmoistened) and those placed in well-moistened sand. As can be seen, about the only difference is that those in wet sand make a more gradual decline from a peak at the cold end (8–9°C.) of the gradient. In order to determine if previous temperature had any effect on their reactions a batch of wireworms was kept for 12 days at 5°C. After being placed in the gradient they were allowed ample time, 48 hr. to take up their preferred positions. From Fig. 9 it can be seen that the insects cover about the same range as when kept at room temperature. However, more individuals are

found at low temperatures, and there is a very abrupt dropping off from the cold end.

Ants (*Acanthomyops* sp.) were the second species of soil insects to be tried. They were also given fresh unmoistened earth and allowed to remain for 48 hr. before a reading was taken. In general their preference coincided with that of the wireworms, being highest at the cool end (8° C.) and gradually declining to about 30° C.

It is interesting that in none of the experiments with soil insects were they ever found to be most numerous at the very end of the gradient, their peak always occurring about 5–15 cm. from the cold end of the apparatus.

Table 3

Stage	Previous temp.	Medium	Temp. °C.	Relative humidity	Figure
<i>Agriotes</i> (Wireworms)					
L	Room	Fresh earth	(8)–20	—	9
L	Room	Moist sand	(8)–23	—	9
L	5° C.	Moist sand	(8)–18	—	9
<i>Acanthomyops</i> sp. (Ants)					
A	Room	Fresh earth	(10)–25	—	—
A	Room	None	(14)	30	—
<i>Apanteles congestus</i>					
A	Room	None	(10)–20	20–40	2, 3 and 10
<i>Pteronides melanaspis</i>					
L	Room	None	(11) and (31)	35 and 45	—
A (males)	Room	None	5–20	30–55	—
A (females)	Room	None	5–(8)–15	20–50	—
<i>Dysdercus howardi</i> (Cotton stainer)					
Nymph	Room	None	(12)–(25)	22–50	—
A	Room	None	12–25	22–50	—
Sepsidae (Diptera)					
A	Room	None	(9)	20	—
<i>Forficula auricularia</i> (Earwig)					
A	Room	None	(9) and 25–30	15 and 37–45	—
<i>Cimex lecularius</i> (Bedbug)					
A	Room	None	(12) and (22)	24 and 44	—

A = adult; L = larva.

Other insects (Table 3)

One day some small Braconid parasites were found in a cluster of spider's eggs. These were later identified by the British Museum as *Apanteles congestus* and proved to be one of the insects to give the most interesting results. The average for the 3 day experiment showed the parasites to have a decided preference for a temperature around 10° C. (Figs. 2 and 3). Here again the peak was 15 cm. from the end of the gradient, so one could hardly say that an end preference played a part in their reactions. It appeared that the insects' position shifted from day to day. The results were then plotted for each day separately, as shown in Fig. 10. On each successive day the parasites moved nearer and nearer to the cool end. The daily change in position is so definite that there can hardly be any doubt that they were actually moving to a cooler

region. An explanation as to why they successively moved from a warmer into a cooler region would be very difficult and could be a full-time problem in itself. Undoubtedly the Braconids underwent some fundamental physiological change.

At the same time that the experiment was started, eighteen surplus parasites, from the same egg mass, were placed in a vial and kept at room temperature. These were all dead after $1\frac{1}{2}$ days. After 3 days the experimental parasites, which were alive and quite active, were used in a control at a uniform

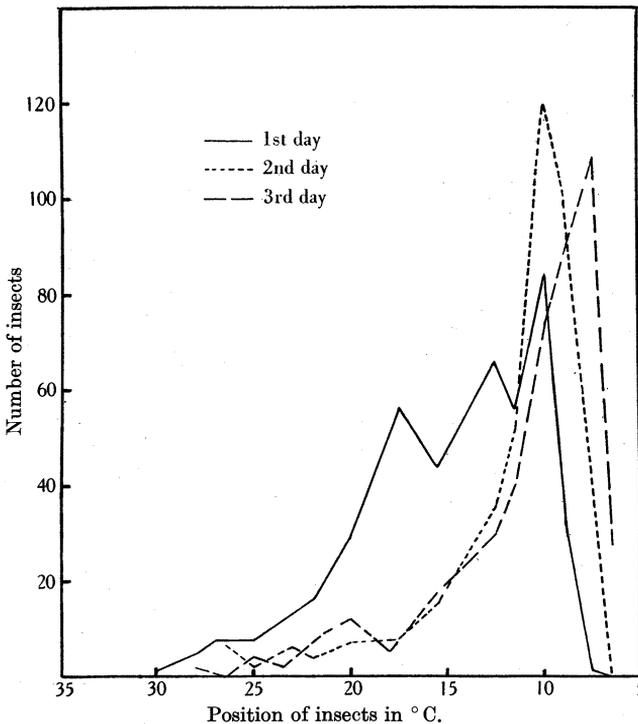


Fig. 10. Temperature-preference curve for *Apanteles congestus* for three successive days, showing the change in position towards the cool end of the gradient.

temperature. They gave a perfect random distribution throughout the gradient (Fig. 2). The methods followed in this experiment were slightly different from the normal. The parasites were not taken out of the gradient for feeding at night, but were allowed to remain in the apparatus continuously day and night. This was for two reasons: (a) the food of the Braconids was not known, and (b) the insects were too fragile to be handled any more than absolutely necessary.

A complete picture may be obtained of the behaviour of the saw-flies (*Pteronides melanaspis*), as the larvae can be compared with adults, and males

with females (Table 3). The larval preference went up very decidedly at 31° C., curved down, and then rose again at the extreme cold end of the gradient (11° C.). This is just opposite to the behaviour of the adult. Although they occupied the same temperature zone as did the larvae they rose in greatest numbers in the centre of the range (15–28° C.), rather than at the extreme temperatures near the ends of the zone. In comparing the differences between the two sexes it can be seen that they both extend over exactly the same range. However, the males are evenly distributed within this range, while the females are decidedly more numerous near the cool end (10–16° C.). The female saw-flies' choice for the second and third day was approximately the same, but for the first day greater numbers gathered at the lower temperatures.

Cotton-stainer nymphs (*Dysdercus howardii*) had a small peak at 29° C. and another at 25° C., but the majority were arranged between 25 and 12° C. The adults had a somewhat similar temperature range. These were tropical insects, imported from the West Indies, and one would expect to find more of them with a high temperature preference. Ants (*Acanthomyops* sp.), when given a choice of the gradient, without earth, repeatedly congregated directly against the cold end (14° C.). Those given soil, although they preferred the cool zone, were not found in large numbers tightly against the end, their peak appearing at least 15 cm. in from the end. Adult *Sepsid* flies present very much the same sort of preference as ants in an empty gradient, i.e. rising very sharply against the cold end (9° C.) of the trough. The end temperature here was about 5° lower than during the previous experiment.

The temperature preference for adult earwigs (*Forficula auricularis*) rises very suddenly at the cold end of the gradient. However, there is also a large number of insects gathered between 25 and 30° C. (Table 3). In this and the previous experiment the insects certainly did not gather at the cool end because of an end preference, as was readily shown by the controls. The bedbug (*Cimex lectularius*) preference, like that for the earwigs, goes up sharply against the cold end and also has a second peak near the centre of the gradient—about 22° C. (Table 3). However, the bedbug was not a suitable insect for experimental purposes, because its very strong thigmotropic tendencies were not easily overcome. The insects were inclined to gather in groups and when disturbed immediately formed another group regardless of temperature, except to avoid the very high temperatures.

6. DISCUSSION

It has been the purpose of this paper to show that, when given their choice of a temperature gradient, certain insects have a preferred temperature. The temperature range of all insects tested is shown and no effort has been made to select species to prove any particular case. It is realized that general conclusions cannot be drawn for insects as a whole from these experiments alone. However, it is believed that one conclusion is justified, namely, that insects

have a temperature preference, but it is a range rather than a point as suggested by some workers. The only preference some insects show is an avoidance of both extreme temperatures, e.g. the adult tobacco beetle when kept at room temperature, and horned flour beetle larvae in bran. On the other hand, they may merely avoid high temperatures and are to be found in all other parts of the gradient, e.g. the biscuit weevil, the bean weevil, rice weevil when kept at room temperature, adult *Dermestes* in food, and *Laemophloeus turcicus*. With insects that went to the cold end of the gradient it was difficult to distinguish whether they went there because of preference, or whether they wandered into the cold zone and were overcome, or trapped, before they could get away. Examples of such insects are the *Tribolium confusum* and *Calandra oryzae* when previously kept at 27° C., grain weevils, from both room temperature and 27° C., *Ptinus tectus* with and without food, ants and bedbugs.

Another rather peculiar preference is presented in the bi-modal curve with a peak near each end of the gradient. Saw-flies and earwigs are examples of this type. It has been suggested that these insects may have a wide range in which they are inactive, and are only active when they go outside of this zone. When they encounter too high a temperature they return to just within the upper limits of their preferred range. The same would happen when they encounter too low a temperature—they would return to just within the lower limits of their temperature zone. This is probably the explanation of a bi-modal curve with widely separate peaks.

In practice this would be what one might expect to find with most out-of-doors insects. It seems that it would be necessary for them to be indifferent to a fairly wide range of temperature in order to survive. Most summer insects must be able to withstand the hot days as well as quite cool nights. It is also not surprising that individuals of the same species sometimes give erratic and conflicting results in the temperature gradient when it is recalled that different individuals of the same insects, in nature, are often found at many different temperatures at the same time. Certain individuals may be in the hot sun while others are in the shade or other cool locations.

It might be said that insects go to a certain temperature in the gradient because they are attracted to the humidity there. The following insects have approximately the same temperature range both without and with food: *Dermestes* larvae, horned flour beetle larvae, meal-worms, tobacco beetles, rice weevils, *Ptinus tectus*, and *Tribolium* when previously kept at room temperature. Of course these are in addition to the soil insects, whose choice was also made independently of the relative humidity. The only insects that may have been trapped at the cold end were the ants.

One theory that may be advanced for insects gathering at the cold end of the gradient is they have *no* temperature preference, i.e. they were just wandering about, went into the cold zone, were overcome by the cold and

trapped there. In any case it is considered much more significant when insects show a preference outside of the cold zone.

No attempt was made to determine why an insect goes to or avoids a certain temperature. However, two theories which are worthy of mention are the classification of the insects' behaviour as follows: (a) behaviour reaction, in which insects receive the stimulus from a high or low temperature through certain receptors and their nervous system; (b) physiological reaction, in which the metabolic activities are speeded up, as when going into a higher temperature zone; or slowed down as when going into a lower temperature zone. In an insect that avoids a high temperature it would be impossible to tell whether it is showing a behaviour or a physiological reaction, without a detailed study of the insect's behaviour. On the other hand, an insect which avoids a low temperature is definitely showing a behaviour reaction. A study of the half-hourly and hourly observations from the daily record sheets shows that when insects leave the hot end of the gradient they invariably remain away from it. (After equal numbers have been introduced into the six thermometer openings.) However, they often move away from the cold end at first but eventually return to it and there remain.

It is possible that this temperature preferendum work may have definite practical applications as well as academic interest. Dr Baird, entomologist in charge of the Insect Parasite Laboratory, Belleville, Ontario, Canada, informs the writer that there all parasites, which are to be reared in large numbers, are tested for their temperature preference. They are then reared at their preferred temperature and much better results are obtained than formerly. It seems that the parasites do better at temperatures lower than those previously thought best for breeding purposes. The work has not yet been published. Temperature preference might also be used to advantage in eradicating insect pests, with a definite preferred temperature, from large warehouses and granaries where the temperature can be controlled. A small room, or other area, could be heated or cooled to the insect's preferendum while the rest of the building remained at an undesirable temperature. After the insects had gathered at their preferred temperature they could then be more easily destroyed.

During the course of the present work many questions and related problems have arisen to which a proper answer can only be given after further work and additional study have been carried out. One of the most important problems in connexion with temperature preferendum work, and one on which a large amount of work may be done, is: Why do insects seek out certain temperatures? What causes them to go to one temperature and not another a few degrees away? Another question almost equally important is: Why do certain insects, after being previously kept at a high temperature, have a lower preferred temperature than when previously kept at room temperature for the same length of time? In the future it is intended to concentrate mainly on the

preferendum of soil and aquatic insects. Here such variable factors as humidity, light and odour can be more readily standardized.

In the present experiment temperature has been considered the major factor in determining the position which the insects have taken up. However, such influences as humidity, odour, thigmotropism and possibly light must also be taken into account.

7. SUMMARY

1. A description is given of three different types of apparatus experimented with before selecting a linear brass gradient which gave a range of temperature from 10 to 35° C. in a straight-line gradient. This allowed the insects a choice of about 1° C. in every 4 cm. The relative humidity in such an apparatus varied inversely with the temperature except where food was used, when it remained practically uniform.

2. The temperature preferendum was tested of twenty-three species of insects from six orders. Insects were chosen to represent different environments or habitats, such as the following: stored product insects, leaf-feeding insects, plant-sucking insects, human parasites, insect parasites and soil insects.

3. Results are based on experiments each carried out for not less than 3 days. In every case a control was also run for 1 day to get the random distribution of the insects.

4. At the cold end of the gradient the metabolic activities of the insects were slowed down to such an extent that many species were trapped there, thus giving an apparent preference for the colder end. As a result when insects went to a warmer zone it was considered more significant than when they went to a cold zone.

5. The flour beetle (*Tribolium confusum*) when kept at 27° C. had a lower preferred temperature than when kept at room temperature.

6. Wireworms kept at 5° C. for a fortnight gave no different reaction from those kept at room temperature.

7. Insects that were given food in the gradient had a narrower preference zone than when not given food.

8. In general the preferences of the immature forms tended to coincide with those of the adults of the same species.

9. With saw-flies (*Pteronides melanaspis*) the males tended to have a wider temperature range than did the females.

10. The Braconid parasites (*Apanteles congestus*) went to a lower temperature on each successive day they were in the gradient and at the end of 3 days were alive and quite active. At the same time a surplus stock kept at room temperature were all dead at the end of 1½ days.

11. Generally speaking, all the insects experimented with have shown a definite temperature preference but the preference has been for a fairly wide range of temperature and not a point as has been suggested by some workers.

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