TEMPERATURE AND LOCOMOTION IN PLANARIA.

By WILLIAM H. COLE.

(*From the Biological Laboratory of Clark University, Worcester.*)

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I.

In order to secure further information on the temperature characteristics of vital processes, as determined by the equation of Arrhenius,[1] $\log_e \frac{\text{velocity at } T_2}{\text{velocity at } T_1} = \frac{\mu}{2}\left(\frac{1}{T_2} - \frac{1}{T_2}\right)$, the rate of locomotion of *Planaria maculata* Leidy has been studied at temperatures from 7° to 30°C. inclusive. The observations have been made while the worms were creeping over the bottom of a Petri dish (136 mm. diameter) which rested on two glass rod supports suspended from the sides of a white enameled cylindrical jar (327 mm. diameter; 250 mm. deep). The jar was filled with water, the temperature of which could be regulated by withdrawing or adding water through appropriate outlet and inlets. The surface of the water was 60 mm. above the bottom of the Petri dish. A glass rod stirrer, reaching to within 10 mm. from the bottom of the jar and rotated by a small motor, aided diffusion of the hot and cold water, so that thermal equilibrium could quickly be established. Immediately beneath the Petri dish was placed a circular cardboard of the same diameter, ruled off into 10 mm. squares, and held in place between two glass plates resting on a glass cylinder. The bottom plate was provided with two vertical glass handles reaching well up above the water level, so that the position of the cardboard could be adjusted to make its lines parallel to the direction of creeping of the worms. At the side of the jar away from the observer and slightly above were placed two 25 watt electric lamps, 150 mm. apart, with reflectors 210 mm. diameter. Over the rim of each reflector was stretched thin

[1] See papers by Cole, 1924–25; Crozier, 1924–25, *a, b;* Crozier and Federighi, 1924–25, *a, b, c;* Crozier and Stier, 1924–25, *a, b, c, d,* 1925–26; Glaser, 1924–25, 1925–26, *a, b;* Hecht, 1925–26; and Orr, 1924–25, listed at the end of this paper.

brown paper to render the emergent light diffuse. The center of each paper cover was 190 mm. from the center of the Petri dish, affording an illumination of about 620 meter candles at the latter point.[2] No other light fell upon the animals. When placed on the bottom of the Petri dish at the side nearest to the lamps, the planarians were forced by their negative phototropism to creep away from the source of light and towards the observer. Being illuminated from both sides the animals usually followed a straight path. As the anterior end of the worm crossed over the successive lines on the cardboard, time was taken with a stop-watch to the nearest 0.1 second. When the worm reached the opposite side, the dish was rotated sufficiently to restore the same position relative to the lights. The animal then turned through 180° and crept again towards the observer. Only occasionally did animals creep onto the vertical wall of the dish making handling by a pipette necessary.

Observations on a single animal were begun at the lower temperatures after the water had maintained its temperature to within 0.1° for 5 minutes. If successive times for creeping 10 mm. were nearly the same, five readings were taken, but when considerable variation in the times appeared ten or more readings were recorded. The temperature of the bath was then raised 1.0° or more, a 5 minute interval for thermal adaptation was allowed, and other observations were made. This procedure was repeated until the higher temperatures had been reached. During actual observations the stirrer was stopped, to prevent any mechanical stimulation of the worm. This period of time was usually about 5 minutes, during which the temperature of the bath did not vary more than 0.1°.

The isolated experimental animals were kept in small battery jars containing tap water, two small stones, and branches of the water plant Mryiophyllum. Illumination of the jars was of low intensity and diffuse. The food of the worms consisted of all the fresh beef liver they would eat, administered not oftener than once in 2 weeks.

[2] The intensity of the light was measured by means of a grease spot photometer using a Hefner lamp. The candle power obtained was multiplied by 0.9 to convert to international candles, and the meter candle value was calculated from the formula $\text{m.c.} = \frac{\text{c.p.}}{d^2}$ where d is expressed in meters.

Under these conditions the worms remained normal and healthy in every visible respect. Over a period of 3 months not a single animal died out of a total of 123.

II.

Over 2000 observations were made on 14 animals, but not all of these could be analyzed because of variations in behavior. Five individuals consistently gave unreliable results due to the following types of behavior: (1) creeping with the anterior or posterior end of the body held at an angle above the substratum; (2) frequent crawling movements like those of earthworms (*cf.* Pearl, 1902–03, and Mast, 1903–04); (3) irregular locomotion, describing variously curved paths; and (4) frequent periods of quiescence during which the body was almost maximally contracted. All records in which any such behavior appeared were discarded. The other 9 animals gave reliable results which are presented in this paper.

Subjecting *Planaria* to different temperatures between 7° and 30°C. shows clearly that the velocity of locomotion increases with the temperature. Below 12° the body is more or less contracted, movement is sluggish, and the velocity varies at constant temperature. Up to about 21° the velocity increases gradually to its highest value, when the animal's body is stretched along its longitudinal axis to a length about 25 per cent greater than at 10°. Above 21° the locomotor rate is not always constant, and sometimes shows no increase over that at 20–22°. When an increase appears it is always smaller proportionally than between 13° and 21°. Around 30°, the worms become quiescent.

Comparison of the individual records is easily made by plotting the logarithm of the velocity of locomotion (velocity = 100 × reciprocal of the time in seconds required to traverse 10 mm.) against the reciprocal of the absolute temperature. If the points tend to form a straight line or band the equation of Arrhenius may be applied, and the value of the constant μ may be calculated from the slope of the line which best fits the points (Crozier and Federighi, 1924–25, *a*). The plots will also reveal any critical temperatures at which the value of μ suddenly changes. This treatment of the data showed that between 13° and 21° the locomotion of animals which had been from 2 to 14 days without food exhibited a fairly constant temperature characteristic. These animals, whose records are given in Table I, will be considered first. In Fig. 1, eight individual plots from worms numbered 1, 2, 3, 6, 8, 10, and 11 have been spaced along the vertical axis to facilitate comparison. This is legitimate since it is the slope of the lines which is important for our consideration. The vertical logarithmic scale is of course identical for all the plots, the unit of distance being 0.2. The points are separate observations at different tempera-

TABLE I.

Values for μ at Intermediate Temperatures Obtained from Animals Which Had Been from 2 to 17 Days without Food.

No. of animal.	Days after feeding.	μ
1	14	11,300
2	14	11,650
3	14	11,600
6	2	10,650
6	3	10,800
6	7	11,000
6	11	10,900
8	4	11,450
8	5	11,300
9	3	10,900
10	10	11,100
11	10	10,900
Average..........		11,129 ± 61
6	17	14,750
9	16	14,500
11	14	14,600
12	15	14,600
Average..........		14,612 ± 30

tures. In some cases successive readings were identical, so that fewer than five points sometimes appear at one temperature. The lines have been drawn by inspection through the high and low extremes between 13° and 21°, and from the slopes of the lines the values of μ have been calculated. The critical temperatures are clearly 13° and 21° in the vicinities of which the value of μ suddenly changes. But within this region the temperature characteristic, as determined

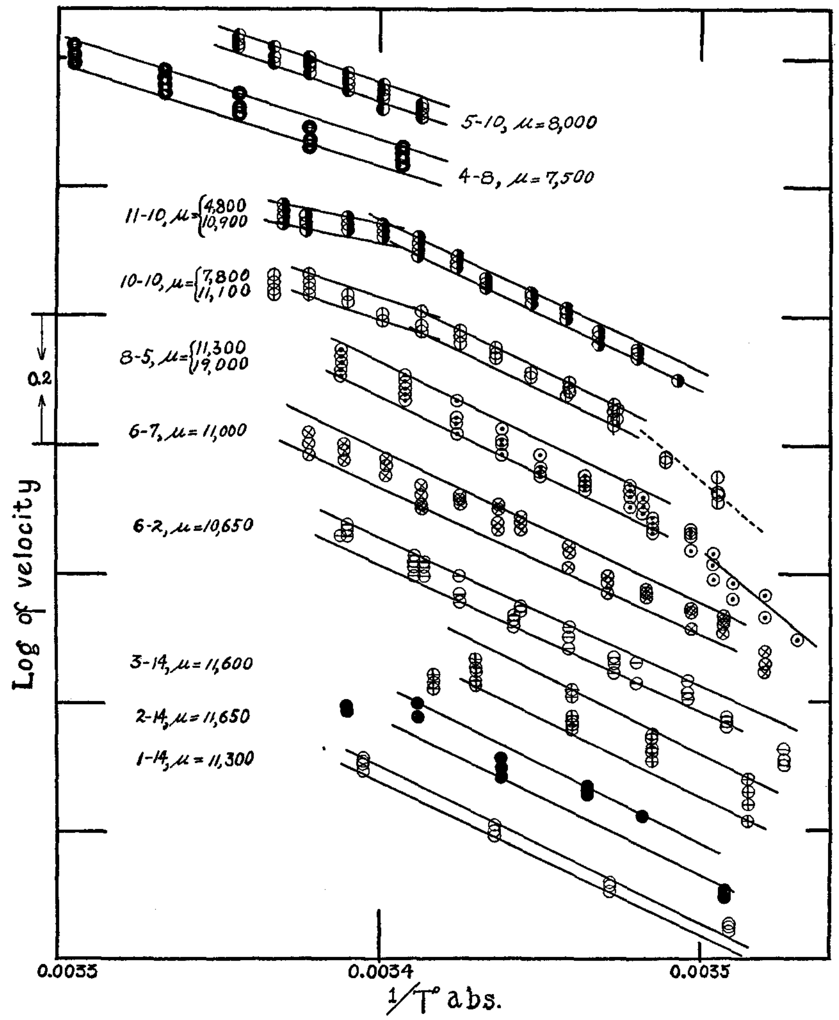

FIG. 1. Plots of observations from 10 individuals which had been from 2 to 14 days without food. The first number identifies the animal, and the second indicates the number of days after feeding. The logarithm of the velocity of locomotion is plotted against the reciprocal of the absolute temperature. Each point represents a single observation, except where two or more successive observations were identical, and the lines have been drawn by inspection through the extreme variates between 13° and 21°. The values of μ have been calculated from the slopes of the lines. For the sake of comparison, the plots have been spaced along the vertical axis with a uniform logarithmic scale the unit of which is 0.2.

by the slope of the lines, varies only from 10,650 to 11,650, the average being 11,129 with a probable error of the mean of 61. It is to be noted that this is similar to the value found in other animals where the determining reaction is supposed to be a catalyzed oxidation (*cf.* Crozier, 1924–25, *b*).

Above and below the critical temperatures regularity in the locomotor velocity disappears. Animal 8, as shown in Fig. 1, gave the best series of observations below 13°. The other worms showed consider-

TABLE II.

Values for μ at Low and High Temperatures Obtained from Animals on the Day of Feeding and on Subsequent Days.

Low temperatures.			High temperatures.		
No. of animal.	Days after feeding.	μ	No. of animal.	Days after feeding.	μ
6	$\frac{1}{6}$	18,750	4	8	7,500
6	1	19,300*	5	10	8,000
6	2	19,400	6	$\frac{1}{6}$	7,610
6	3	16,150	9	$\frac{1}{8}$	8,300
6	6	22,000*	9	2	8,700
8	4	18,000	10	10	7,800
8	5	19,000	11	10	4,800
9	$\frac{1}{8}$	14,700			
9	$1\frac{1}{4}$	17,600*	Average................		7,530
9	3	18,400*			
10	10	19,200*			
Average..................		18,409			

* Values obtained from a small number of plotted points.

able variation in their rates at constant temperature in this range, but in no case was the rate greater than at 13°. Similarly, at the higher temperatures consistently regular results were not obtained. Many worms showed no increase in rate at all above 21°, and not a few remained quiescent. A few records were obtained, however, and when plotted, the points fell fairly regularly within parallel straight lines, as shown in Fig. 1, Nos. 4, 5, 10, and 11. This condition is to be contrasted with that found at the lower temperatures, where the scattering of the plotted points prevented accurate representation by parallel lines. In Table II appear the values of μ which were obtained from the high and low temperatures. The former are probably much more reliable than the latter, and give a mean value of 7,530. If Animal 11, which shows a value (4,800) widely differing from the others, be omitted the corrected mean becomes 7,985. This is very close to the value found by Crozier, and by Glaser (*loc. cit.*) for other kinds of activities at higher temperatures. The much higher value at low temperatures, although perhaps not so accurate, also corresponds roughly with what has been found in other processes at similar temperatures. The results obtained from the low temperatures lead to suggestions only, since they are insufficient for a complete interpretation.

It appears from these experiments that the thermal increment from about 13° to about 21° for locomotion in *Planaria* which have been without food for from 2 to 14 days, is 11,100. Below 13° it becomes much larger, showing considerable variation from 15,000 to 22,000. Above 21° the thermal increment decreases, and seems to lie between 7,500 and 8,000. In both these extreme regions the value of μ does not appear to be changed as a result of feeding as is the case at intermediate temperatures.

III.

Planaria which were tested soon after feeding revealed quite a different ratio of increase in locomotion at the intermediate temperatures. An attempt was made to study this modification of the thermal increment. Observations were made on animals a few hours after feeding, and frequently thereafter up to 2 days. During this period it was very difficult to secure regular and concordant results. The worms were very sluggish, showed much indefinite creeping, and frequently came to rest. Only 2 of them, Nos. 6 and 9, gave results which could be analyzed. Their records are given in Table III. The critical temperatures within 4 hours after feeding seem to be around 18° and 25°; after 24 hours they are at 15° and 25°, and after 48 hours they have shifted to 13° and 21°. At the lower temperatures μ is not much changed, but over the median range it increases from around 7,000 to near 11,000. At the higher temperatures the values are not clear, since the worms usually showed no increase in rate. These suggestions are merely tentative, in view of the small number of cases.

There can be little doubt, however, that immediately after feeding and for at least 48 hours thereafter the thermal increments for locomotion in *Planaria* are quite different at the intermediate temperatures than subsequently. It has been reported by Willier, Hyman, and Rifenburgh (1925) that during the first few hours after feeding rather striking changes in the food and in the intestinal cells take place. These are followed by a slow digestive process which ends at about the 5th day. Thereafter up to 6 weeks the fat and protein content as well as the histological appearance remain unchanged. It is probable that profound metabolic changes occur soon after feeding and during digestion, and that these might shift the velocities of the reactions underlying the locomotor activity so that control passes from one process to another. After 2 days, and up to 14 days, there is no change of control, indicating perhaps a rather uniform metabolic state.

TABLE III.

Changes in the Constant, μ, As Produced by Feeding.

No. of animal.	Hrs. after feeding.	High temperatures.	Median temperatures.	Low temperatures.
6	4	25–30°:3,600	18–25°: 7,600	9–18°:18,750
9	3	25–30° 0	18–26°: 8,300	13–18°:14,700
6	24	25–30° 0	15–25°: 9,800	10–15°:19,400
9	30	25–30° 0	15–25°:10,100	12–15°:17,600
6	48	25–30° 0	10–22°:10,850	
9	48	20–25°:8,700	13–20°:16,100	10–13°:18,400

Animals 6, 9, and 11, which had previously given values for μ of about 11,000, showed an increase to 14,600 when tested 17, 16, and 14 days after feeding respectively. No. 12, an animal not tried before, yielded a similar value (see Table I). It appears in the three former cases that the temperature characteristic has changed again, although the reason is not clear. It is not likely that this new value is the result of faulty technique or inaccurate observations, because the tests were performed in the same way as all the others, and when repeated on 2 of the worms gave almost identical results. Other cases of association between temperature characteristics, 8,000 and 11,000 with an occasional appearance of 14,500 have been reported by Crozier and by Glaser (*loc. cit.*). The modification of μ, as by feeding in the case of *Planaria*, coincides with the conception of experimental control of μ as advanced by Crozier and Stier (1924–25, *a*).

IV.

SUMMARY.

A consideration of the temperature characteristics or thermal increments for locomotion in *Planaria* shows that they agree essentially with those reported for certain activities of other animals (Crozier, and Glaser[1]). A process with the lowest increment ($\mu = 7{,}000$ to $8{,}000$) assumes control of the locomotor rate at temperatures above 20–22°; that with the highest increment ($\mu = 18{,}000$ to $22{,}000$) controls below 13°; and one with an intermediate value ($\mu = 11{,}100$) is in command at the intermediate temperatures (13–21°). Another reaction with increment $\mu = 14{,}600$ may, under certain conditions (*e.g.* 2 weeks after feeding), control the series over the median range. Excepting the latter, these increments are typical of catalyzed oxidative reactions (Crozier 1924–25, *b*) so that when these are in control it may be assumed that respiration is the fundamental process determining the rate of locomotion. Feeding produces a modification of the increment throughout the median range of temperatures, up to 2 days afterward.

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