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SHORT COMMUNICATION

FALLING TEMPERATURE STIMULATES ACTIVITY IN THE SLUG *ARION ATER*

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Dainton (1954) showed that activity was stimulated by falling temperature below 22 °C in the slug *Deroceras reticulatum* (*Agriolimax reticulatus*) and that this response could account for the timing of the activity observed in the field. Runham & Hunter (1970) state that Lewis (1967) was unable to repeat this result on *Arion ater*. Experiments described here show that this slug does respond to falling temperatures below 22 °C by becoming active and that the time between the onset of the stimulus and the appearance of the activity is related to the rate of fall.

The apparatus consisted of a stirred water bath of uniform temperature which could be lowered at controlled rates by regulating the influx of iced water. Immersed in the bath were six air-filled glass chambers, the floor of each of which was lined with wet filter paper which served the dual purpose of saturating the air with water vapour and providing the slug in the dish with a wet surface from which it could absorb water and so replace that lost in mucus production during locomotion (Dainton, 1954). Each chamber contained one slug and even after 5 days (more than twice the duration of any experiment) all slugs were in excellent condition.

Before the experiments slugs were kept in glass dishes, fed on vegetables and subjected to the diurnal changes of temperature (16–22 °C) and light intensity of the laboratory, when feeding and locomotion occurred only at night. Introduction of the slugs into the apparatus during the day stimulated a short period of activity never exceeding 1 h, and no experiment was begun until activity had ceased. About half the experiments were performed on slugs which had been in the apparatus overnight. There was no difference in the results obtained on the first or second day in the apparatus.

A thermistor inserted through a glass chimney into the experimental chamber registered the same temperature as that of the water bath, and its time-dependence was also the same except at the higher rates of fall. These calibration data were used to give the corrected temperature at these higher rates.

Key words: Temperature, activity, slug, *Arion*.

When resting, the slug withdraws its tentacles and their extension is the first sign of activity and is followed by locomotion. Since Lewis' work involved the automatic recording of movement (Lewis, 1969*a*,*b*), the experiments described here refer to locomotor activity. This condition was determined by observing the muscular waves of contraction along the sole of the foot unless these were invisible because of the position of the slug in the chamber, in which case the slug was recorded as locomoting if the tip of the tail was seen to be moving in a forward direction. Head waving movements were not recorded as activity.

Thirty-nine experiments each involving five or six slugs were performed in which the temperature of the water bath was lowered at varying rates and observations of the slugs were made at 5-min intervals. An example of one of these experiments is shown in Fig. 1. The time between the start of the temperature fall and the first observation of locomotion was noted for each slug and the average rate of fall in temperature calculated for this period. Two hundred and twenty-four observations were made and only three slugs did not respond. These were subsequently found to be either moribund or parasitized. Slugs subjected to the same rate of falling temperature showed variation in the time for response and the variation was greater at the lower rates of fall. The results were grouped according to the rates of fall in intervals of 1 °C. In Fig. 2 the mean time of response for each group is plotted against the median rate of fall in temperature for that group and

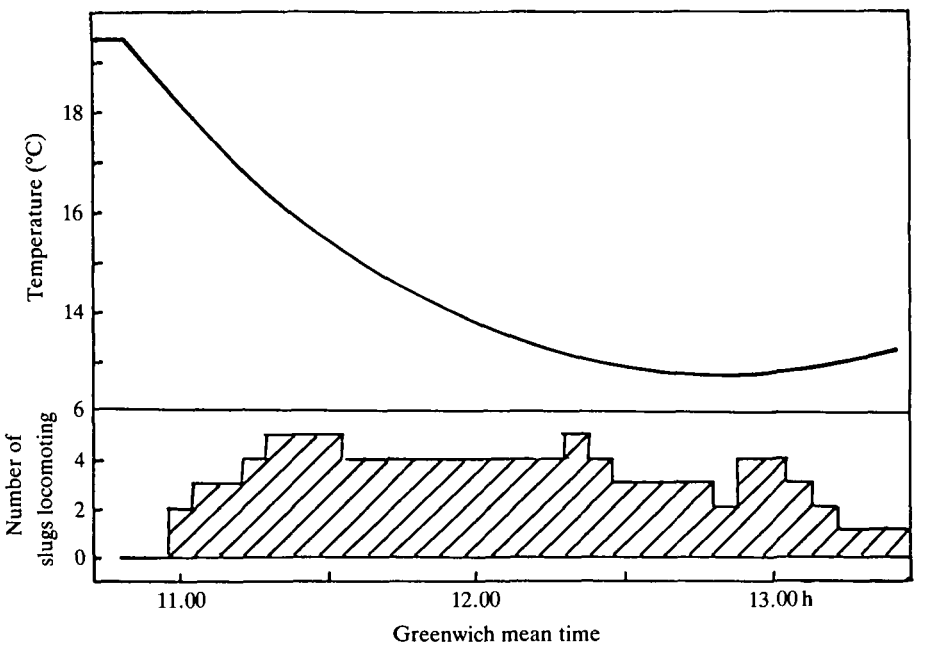

Fig. 1. The stimulation of activity by falling temperature. One of the 39 experiments on which the results summarized in Fig. 2 are based. Six slugs, one in each experimental chamber were subjected to a controlled fall in temperature. The slugs responded by becoming active and the activity persisted as long as the temperature was falling and fell off when it began to rise. For detailed explanation see text.

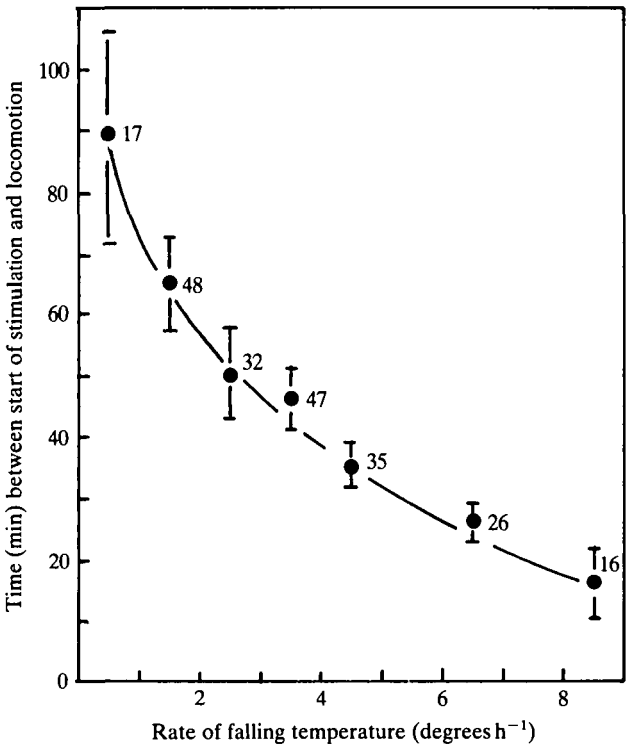

Fig. 2. The relationship between rate of falling temperature below 22 °C and the time between the onset of the fall and the appearance of locomotory activity in *Arion ater*. The points are the means of the number of observations stated in the figure and they are plotted against the median rate of fall for that group. Standard errors are indicated by the bars.

this shows that there is a clear inverse relationship between the time of response and the rate of temperature fall.

The stimulus to which the response was obtained was falling, and not low, temperature. Even with temperatures as low as 8 °C the slugs remained inactive if the temperature was not falling. From the results so far obtained it is not possible to ascertain whether the stimulus to which they were responding was the rate of fall or some actual fall of about 2–2·5 °C. The results as indicated in Fig. 2 suggest that the latter might be the case except at very low rates of fall when it appears to be less. The slowest rate of fall attempted was 0·2 ° h^{-1} and all slugs tested at this rate responded in between 2·5 and 3·5 h.

Immediately the cold water inflow was turned off the temperature in the tank began to rise and the locomotory activity subsided (Fig. 1). The speed with which this happened depended on the rate of rise and figures for this will be published elsewhere.

It is clear from these results that contrary to the statement of Lewis (1967) quoted by Runham & Hunter (1970), *Arion ater* responds to falling temperature below 22 °C by becoming active. The response is shown to rates of fall as low as

$0{\cdot}2\,^{\circ}h^{-1}$. Slugs experience falling temperatures of this order or greater in their daytime resting places after nightfall and following some showers of rain by day. It is on these occasions that slug activity is observed in the field. Significantly, slug activity does not occur on continuously wet days when there is no such fall in temperature.

Lewis (1969*a*,*b*) states that locomotory activity in *Arion ater* subjected to a 12:12 h light:dark regime occurred largely within the dark period. However his data show that activity does not begin until a period of time after the onset of darkness which is entirely consistent with stimulation of activity by a fall of temperature following extinction of even a fluorescent light. Thus, direct measurement showed that a fall of temperature of $1\,^{\circ}h^{-1}$ was maintained for 2 h following such extinction in a small room. The results obtained by Sokolove, Beiswager, Prior & Gelperin (1977) on *Limax* can be interpreted in the same way. Moreover, Beiswanger, Sokolove & Prior (1981) found that removal of the eyes in *Limax* did not affect the time of onset of activity and he also noted that the activity began up to 2 h after the onset of darkness. Newell (1968) claimed that he could not explain his results on surface activity in *Deroceras* in terms of temperature responses but he was not always observing his slugs at 100 % relative humidity. Hogben & Kirk (1944) demonstrated that slugs in non-saturated air are cooled by loss of water by evaporation.

Using a mechanical method of recording locomotion Dainton (1954) found that when *Deroceras* was kept in a thermostatically controlled constant temperature room in continual darkness the activity became evenly spread over the 24 h in 4 or 5 days. When such slugs were reintroduced into a diurnally varying temperature, but still in continual darkness, the activity was confined to the period when the temperature was falling. It seems that the entraining factor for the circadian rhythm of activity and rest is temperature and not light in both *Deroceras* and *Arion*. The work has now been extended to other pulmonates, some of them with shells, and it may be that this is a general characteristic of land pulmonates. In their normal daytime resting places beneath soil or stones they would not be aware of the onset of darkness. Moreover the occasional daytime activity is also explicable in terms of a response to falling temperature. This response is an effective behavioural adaptation ensuring that the slug is only active in damp conditions. The appropriate temperature fall only occurs in the slugs' resting place when the humidity at the surface is very high (B. H. Dainton, unpublished observations).

Kerkut & Taylor (1956), using a preparation of the pedal ganglion of *Limax maximus*, recorded an increase in output from the ganglion in response to a fall in temperature from 18 °C. This result appears to be in agreement with the behavioural responses of slugs to falling temperature.

Above 22 °C, *Arion ater* responds to rising temperature by becoming active. Such temperatures only rarely occur in daytime resting places on exceptionally warm summer days. This behaviour, which was also described by Dainton (1954) in *Deroceras*, is clearly an escape reaction enabling the slug to avoid potentially desiccating conditions.

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