# THE DAILY RHYTHM OF ACTIVITY OF THE COCKROACH, *BLATTA ORIENTALIS* L.

## I. AKTOGRAPH EXPERIMENTS, ESPECIALLY IN RELATION TO LIGHT

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(With Five Text-figures)

## I. INTRODUCTION

In the last few years there has been an increasing interest in animal rhythms. Various aspects of the subject have been reviewed by Szymanski (1920), Fox (1923), Hoffmann (1926), Richter (1927), Amirthalingam (1928), Stein-Beling (1935), Scott (1936), Gunn *et al.* (1937), Piéron (1937) and Kalmus (1938*a*, *b*). This paper is concerned with the daily rhythm in the locomotory activity of the cockroach, *Blatta orientalis* L. Those who are familiar with this insect in its natural haunts are agreed that it comes out and is active only at night. Can this rhythm of nocturnal activity be reproduced under experimental conditions and can it be controlled experimentally? Szymanski (1914) and Wille (1920) showed that it could be reproduced but they did not attempt to control it.

## II. APPARATUS AND METHODS

Szymanski (1914) designed several kinds of apparatus, which he called *aktographs*, for recording animal activity automatically on a smoked drum. I have used two practically identical aktographs, one of which has been described in detail (Gunn & Kennedy, 1936). The animal chamber is 20 cm. long and 10 cm. wide; when the animal walks *along* the length of the chamber, the chamber tips and an attached lever makes a nearly vertical mark on a smoked drum (Gunn, 1937, Fig. 5). Movements of the animal *across* the chamber are not recorded, so that one complete vertical mark on the record represents a walk of at least 20 cm. but probably not usually as much as 30 cm. A spiral drum was used, rotating once a day, so that about 4 days' records came on to one drum paper. A time marker showed hours.

In the principal experiments, only recently moulted adult cockroaches were used. Nymphs were kept until they moulted, so that prolonged experiments could be carried out with individual animals before they died of old age. Only males were used. With certain specified exceptions the work was done in a constant-temperature room at 25·5° C., the normal variation being a short cycle of about ±0·5° C. This is a suitable temperature for behaviour experiments on this species (Gunn, 1934).

In all the experiments, beneath the perforated zinc platform on which the animal walked there was moist common salt, which has an equilibrium relative humidity of 75%. About 30 g. of fresh carrot was put in for food every 3–5 days. This enabled experiments to be carried on with single individuals for as long as 15–20 weeks but, of course, the humidity was disturbed by the carrot. It would naturally be higher near the carrot than elsewhere, and probably higher before the carrot had dried than later on.

When the carrot was renewed, the animal was removed from the chamber, the excess salt solution and faeces pipetted away and more salt was added. The animal was led gently during this exchange and not agitated, and after a few weeks it walked into the removal tube and back into the aktograph, when the time came, in most docile fashion. A few individuals made a temporary escape and had to be handled roughly, but that only occurred early in their case histories.

Thus, apart from the isolation from its kind which was suffered by the cockroach during these experiments, the living conditions were good. I believe that an adult life as long as 22 weeks (19 November 1938 to 24 April 1939) at 25° C. has not previously been recorded for *Blatta orientalis* (see Rau, 1924).

All the apparatus was roofed in and curtained off in a corner of the constant temperature room, and lighted by its own 40 W. electric lamp. This lamp gave a light intensity of about 20–30 metre-candles (1 f.c. = 10·76 m.c.) inside the aktograph, with a narrow shadow at one end and another behind the carrot. This light was controlled by a clockwork switch kindly given by Mr Robert McDowell, and it could thus be automatically turned on and off regularly at pre-determined times. When this light was off, it was too dark for the dark-adapted human eye to read the scale of the light meter. In the main room, daylight was always excluded and a 200 W. ceiling lamp was on day and night.

Thus the temperature was uniform and the light on the aktograph was kept uniform or varied at will. The humidity varied, but with a rhythm of 3–5 days as the carrot dried up and was replaced, and with no daily rhythm. The external factor which was not controllable was mechanical stimulation-pressure change, noise and vibration in general. The stands of the aktographs rested on 4 cm. of sponge rubber on a slate slab built into the wall, so gross vibrations must have been rare. The results obtained show that vibration was not a factor of overwhelming importance. The chamber had a glass lid sealed on with vaseline, so draughts were completely absent, and any chemical stimulation from outside must have had a 3–5 day period.

The only other factor which might have affected the activity of the cockroach was the presence of the experimenter and of occasional visitors; these potential disturbances occurred only during the solar daytime, and the complete inversion of rhythm obtained experimentally shows that they were not important. The apparatus normally required no more than a few minutes attention each day, with an hour or so each fourth day.

## III. TOTAL ACTIVITY PER DAY

In summarizing the results, the records of complete journeys along the aktograph chamber were counted for each hour of each day; parts of journeys were either ignored or reckoned as whole journeys, according to their length. Two animals gave very long experimental records. They were supplied from Sheffield by Dr Kenneth Mellanby as nymphs, kept at a variable temperature about 25° C. in normal daylight and darkness until their last moult, and then used in these

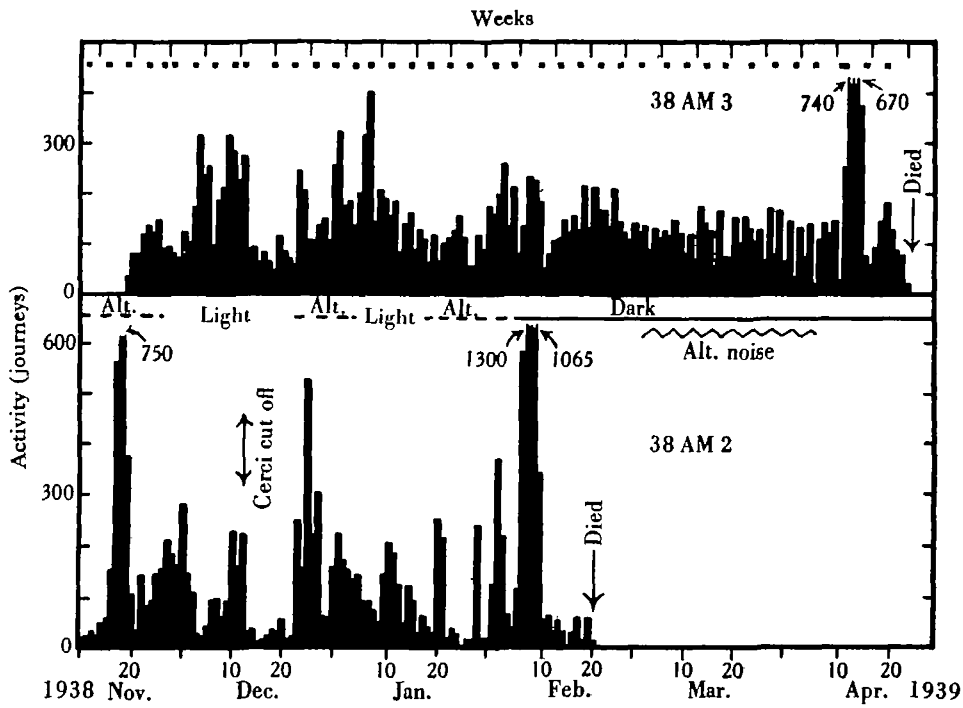


Fig. 1. Daily activity, measured with the aktograph, of two cockroaches from just after the last moult until death. Indications for both parts of the figure: Alt. = alternating light and darkness, 12 hr. each per day; Alt. noise = rattling noise for 12 hr. per day, in continuous darkness; Light and Dark = continuous light and darkness respectively; the spots near the top of the figure indicate the dates on which the food was changed, etc.

experiments. The distance they walked in a day varied from six to 1300 journeys, with an average of about 150, corresponding very roughly to $1\frac{1}{2}$–300 m. per day (average about 40 m. per day). Fig. 1 shows the relation of this daily activity to the age of the animals and the conditions of light.

It is easy to read several long-period rhythms into these two records, but such rhythms do not coincide for the two animals, and in any case cannot be correlated with any external changes. There are, however, two points of resemblance: for about a week after the cerci of the two cockroaches were cut off (12 December) both animals were rather inactive; in the second place, in each case impending death was signalized by a few days of tremendous activity about a fortnight before death.

It is surprising to find that light had little, if any, effect on the total activity per day. Thus, for these two animals, omitting the periods which were exceptional because of amputations or approaching death, the average number of journeys per day for the whole period was 146 (4876 hr.). The average for alternating light and darkness was 156, for continuous light for periods of upwards of a fortnight at a time it was 158 and for continuous darkness it was 125 journeys per day. The figure for continuous darkness is for one animal only, and that towards the end of its life. For the first month in continuous darkness the average is 145 journeys per day, so it would not be proper to conclude that continuous darkness has any depressing effect.

It can be stated, however, that prolonged illumination under these experimental conditions has no great depressing effect on activity. Neither did the onset of continuous light have any observable effect (Fig. 1). The rise in activity on one of the two occasions when continuous light was replaced by alternating light and darkness can be correlated just as well with recovery from the depressing effect of cercal amputation. Light, then, appears to have no effect on total activity per day but, as is shown below, daily variations in light certainly have a great effect on the time of day at which the activity occurs.

In passing, it may be placed on record that in these experiments one animal walked very approximately 3½ km. (14,500 journeys) in 100 days and the other 5½ km. (22,000 journeys) in 155 days.

## IV. DAILY RHYTHM OF ACTIVITY

Each of the two animals dealt with above was first tested in alternating light and darkness, with darkness between 18 and 06 hr. G.M.T. Fig. 2 (*a*, *d*) shows that high activity did not occur at all parts of the day indifferently, but that in this experiment it was concentrated into the hours of darkness. The average figures shown in the graph fairly represent the results for the separate days, except that a few isolated bursts of activity during the period of illumination do not show.

Similar tests were carried out with the dark period lasting for 12 hr. after 11 and 04 hr. G.M.T. daily (Fig. 2, *b*, *c*, *e*, *f*); in these cases the animals had been kept in continuous light for at least a fortnight before the new rhythm of light was started. In all six experiments (Fig. 2) there was one continuous period of high activity each day and the greater part of this period occurred during the hours of darkness.

The average figures shown fairly represent the individual days' records. Thus in Fig. 2*e* high activity is shown as starting between 08 and 09 hr., about 3 hr. before the light was turned out; this actually occurred on 7 out of the 11 days, while on 2 of the other days activity increased 1 and 2 hr. respectively before darkness fell.

In general, high activity started during the first hour of darkness. There were, however, two exceptions to this in the six tests; in one (*e*) it started 2–3 hr. before dark and in the other (*d*) there was no great increase of activity until the third hour in darkness. At the other end, it was usual for activity to reach a fairly low level several hours before the light came on again. That is to say, activity is brought to an end by some cause other than the change from darkness to light, and it does not necessarily start when darkness begins. Nevertheless there is a clear correlation

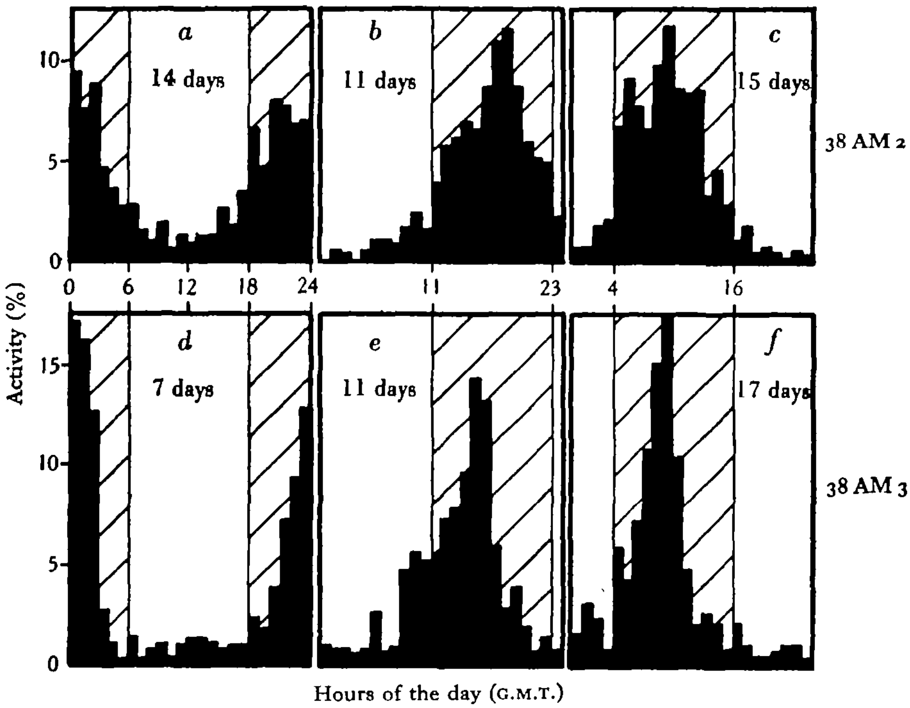


Fig. 2. Hourly activity of two cockroaches in alternating light and darkness (12 hr. each per day). The hours of darkness are indicated by diagonal lines. In order to reduce the six parts of the figure to uniform size, for each experiment the average number of journeys was worked out for each hour of the day, for the 7–17 days, and each average was expressed as a percentage of the sum of the averages.

between the rhythmical occurrence of darkness, whenever that starts during the day (04, 11 or 18 hr.), and the rhythm of high activity. In fact, by suitable adjustment of the time of darkness, the high daily activity of the cockroach can be made to occur when one pleases. Mellanby (1940) has obtained a similar result in a study of cockroaches in a natural infestation. Fig. 3*a* shows that this rhythm starts without delay as soon as continuous light is replaced by alternating light and darkness (see below).

## V. ABOLITION OF THE RHYTHM

Since the activity rhythm is related to the rhythm of light and darkness, it might be expected that in continuous light the activity rhythm would disappear. Practically speaking, it does, but not at once (Fig. 3*b*). The rhythm previously established by alternating light and darkness persists for a time but, within the first few days, complete hours of the active period pass with no activity at all, while bursts of activity occur increasingly frequently at other times. The process of averaging the results from several experiments conceals these effects (Fig. 3*b*), but they can be seen clearly in the record of a single test (Fig. 4). Continuous darkness (Fig. 4) has much the same effect as continuous light.

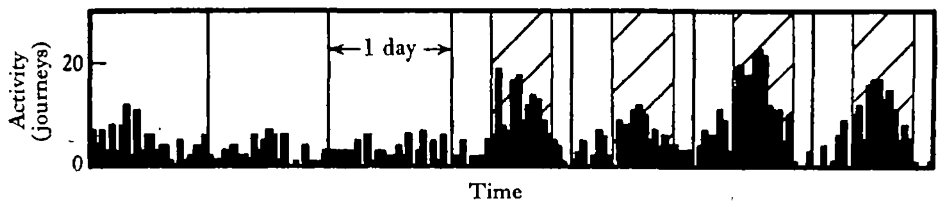


Fig. 3*a*. The initiation of rhythmic activity immediately the alternation of light and darkness begins. Average number of journeys in each hour in four experiments which were put together irrespective of the time by the clock; the onset of darkness (diagonal shading) on the fourth day was made to coincide for the four experiments.

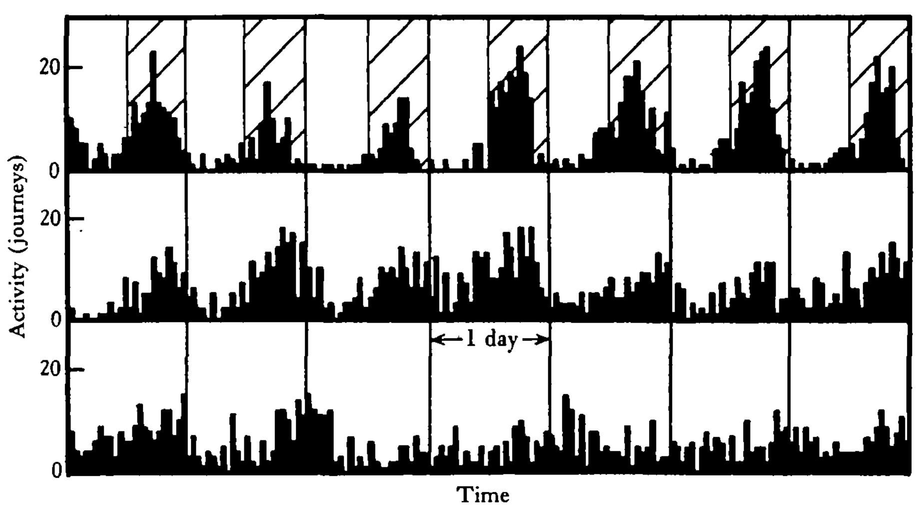


Fig. 3*b*. The slow disappearance of the daily rhythm of activity in continuous light. In the first week shown there was an alternatior of light and darkness. Average of four experiments put together as in Fig. 3*a*. Diagonal lines indicate the dark periods.

After several weeks in continuous light or continuous darkness, the record of a single day's activity no longer gives any indication of the previous rhythm. Even so, the averaging of the daily records of one individual long kept in constant light or darkness reveals some trace of rhythm (Fig. 5). In a selected group of 12 consecutive hours averaged over a fortnight the activity may be twice as great as in the other 12 hr.; but in the proper rhythms, such as are shown in Fig. 2, the difference is of a different order, the journeys in the active period usually numbering at least six times as many as those in the inactive period.

This residual rhythm, if it may be so called, is not detectable by simple inspection of the records, but appears only when the numbers of journeys are averaged for a week or more. It has been found in all the records for continuous light or darkness. It is characterized by the activity being above average in a series of *consecutive* hours, but only slightly above average. Thus in the four periods in continuous darkness shown in Fig. 5, the selected groups of 12 hr. contained 69, 59, 59 and 64% respectively of the day's activity. This active period was

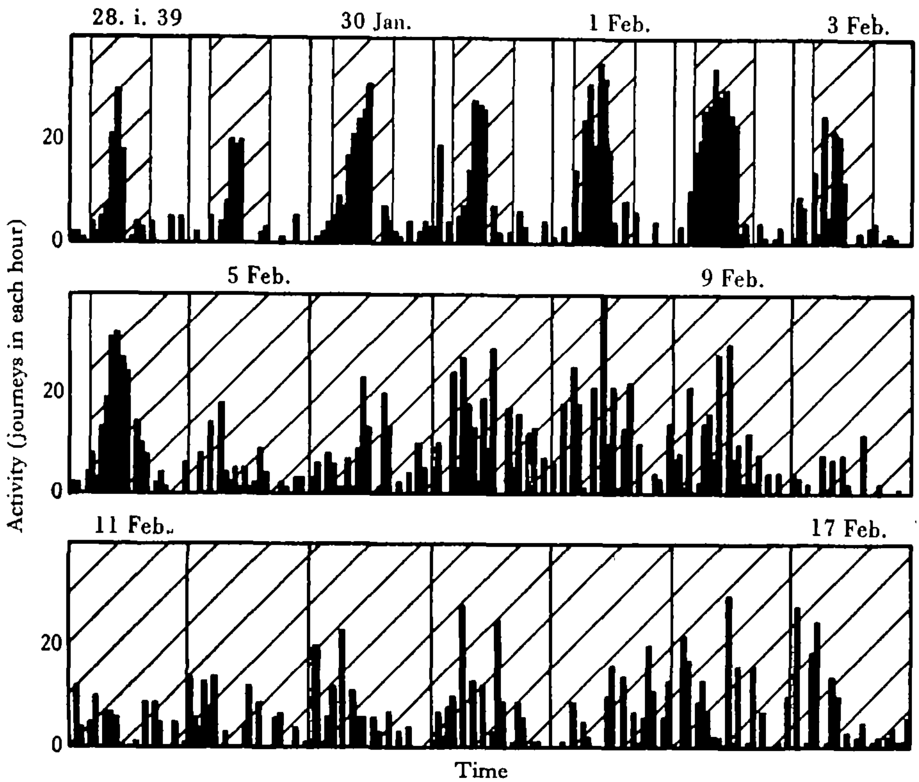


Fig. 4. The disappearance of the daily rhythm of activity in constant darkness. Individual record from animal numbered 38 AM 3. During the first week (top) there was an alternation of light and darkness (12 hr. each) and from 04 hr. on 4 February onwards there was continuous darkness.

between 03 and 15 hr. in the first two and between 12 and 24 hr. in the last two periods. During the latter, there was a motor making a continuous rattling noise between 06 and 18 hr.; but it seems unlikely that this could have affected the animal, for the aktograph was well buffered and the cerci had been cut off. Hair sensilla on the cerci have an auditory function (Pumphrey, 1940).

The excess over 50% shown by the activity during the 12 hr. period of greatest activity is statistically significant. The active period did not tend to fall into the same part of the day in different experiments, but most of the experiments were not carried on for long enough to allow the period of slightly higher activity to

In one experiment lasting 4 days, the 12 hr. darkness was followed each day by only 8 hr. of light, so that darkness came on 4 hr. earlier each day. On the first 2 days activity started 2 hr. after dark, on the third day 4 hr. after dark and on the fourth day 8 hr. after dark. Thus the onset of activity did occur earlier than previously, but it did not shift as much as the onset of darkness.

A number of individuals were first tested in continuous light (25° C.); of these, three trapped specimens which had been kept in an open dish in an ordinary room did not show any rhythm from the start. Perhaps the rise of temperature to 25° C. upset the internal "clock" of these animals. On the other hand, of seven animals which had been bred from the egg inside a dark oven at 25° C., three showed a clear rhythm in continuous light, two a doubtful one, one none at all, while the remaining animal was quite inactive. No doubt the oven was not quite light proof, while all manipulation during rearing—cleaning, feeding, etc.—was carried out in daylight hours, so these experiments cannot safely be used as evidence about the method of acquisition of the tendency to show a rhythm.

## VII. DISCUSSION

Szymanski (1914) with *Blatta orientalis* and Wille (1920) with *Blatella* (*Phyllodromia*) *germanica* did ten aktograph experiments each, each with one animal at a time and lasting 24 hr. Both found an average of 3 hours' activity, starting at 15.30 hr. at the earliest and ending at 00.30 hr. at the latest. The temperature varied around 20° C. In my experiments at 25° C. the active period lasted longer than this, being seldom less than 6 hr. Szymanski also recorded a short period of activity at about 06 hr. in the morning, and because of this second period he regarded the cockroach as polyphasic (Szymanski, 1920). Truly polyphasic animals, like mice, have many short periods of activity each day. My experiments indicate that the cockroach is really monophasic.

Neither of these authors attempted to analyse the cockroach's activity rhythm. A number of authors, on largely or entirely theoretical grounds, have considered that diurnal changes of temperature and humidity provide both the stimulus for the rhythm and the evolutionary reason for its existence (Picard, 1912; Necheles, 1927; Crawford, 1934). It may be that factors other than light can be used to control the rhythm, but so far light has been found to be potent and other factors impotent in a number of cases (Kalmus, 1938*a*, *b*). I hope to investigate these and other questions at a more suitable time. For example, can rhythms of periods other than 24 hr. be set up? Will a short pulse of half an hour's darkness each day suffice to maintain a rhythm? Would rhythms occur if there were no correlation between danger and light in the life of the individual? What is the internal clock, especially for a persistent rhythm? Does the light act through the compound eyes?

Szymanski (1914) carried out two experiments which are of considerable importance. In one of these, half the aktograph chamber was shaded and half lighted all the time, while in the other, half was warmed and the other half not warmed. In both experiments, during its active period the cockroach walked indifferently in the two halves of the chamber. During this time, the well-known responses to light and temperature seem to have disappeared. Mellanby (1940) found, however, that in a natural infestation—in a less limited space than is available in an aktograph—cockroaches did not emerge into a continuously lighted room. They may have emerged in other rooms nearby or they may have been active inside the cavities in the wall.

Esterley (1917) showed that certain marine plankton copepods tended to come to the top of a long vertical tube in the evening, even though kept in continuous darkness at an even temperature for 2 days. This accentuation of geo-negative behaviour occurred with a diurnal rhythm even in the absence of external clues.

Broadly speaking, it is thus to be expected that many animals which show a diurnal rhythm will behave differently according to the phase in which they are tested. Most of the work on behaviour is done during the daytime, and this work on the cockroach suggests that the nocturnal phase can be investigated without doing more than check experiments at night. In the cockroach, at any rate, the rhythm can be reversed by a suitable alternation of light and darkness and then for a few days the rhythm persists almost in full in continuous light. Experiments on behaviour during the active phase can then be done in the daytime during these few days. In the experiments described here, the institution of a new rhythm was always preceded by a period of continuous light; this may not be necessary.

## VIII. SUMMARY

1. In an aktograph at 25·5° C., at upwards of 75% relative humidity and with food present, the average locomotory activity of the cockroach per day does not depend on whether there is continuous light for weeks, or continuous darkness, or a daily alternation of light and darkness.

2. When temperature and humidity do not vary during the day and other factors are kept as constant as possible, the cockroach's activity can be largely concentrated into any desired half of the day, simply by suitably adjusting the time of onset of the half-day's darkness. A rhythm can thus be set up, so that the main activity occurs at the same hours each day.

3. This activity rhythm persists for some days in continuous light or continuous darkness, but eventually activity becomes much more evenly spread over the whole day, leaving only a slight residual rhythm which is unrelated to the previous conspicuous one. A new conspicuous rhythm can then be started at once by alternation of light and darkness.

4. There are indications that animal responses to physical stimuli may depend to a considerable extent on whether the animal is in the active or the inactive phase of its daily cycle. A method is suggested for making it possible to study the nocturnal phase during the daytime.

*I have enjoyed the pleasure and benefit of discussing this work with* Dr Kenneth Mellanby and of comparing his unpublished results with mine.

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