

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

II. OBSERVATIONS AND EXPERIMENTS ON A NATURAL INFESTATION

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(With One Text-figure)

INTRODUCTION

FOR some years I have been studying the reactions of various insects infesting a room in an animal house. The two commonest species are the bed-bug, *Cimex lectularius* L., about which some information has been published (Mellanby, 1939), and the cockroach, *Blatta orientalis* L., which forms the subject of the present paper. The remaining arthropod fauna includes small numbers of silver fish, beetles, crickets, flies and woodlice.

The room has been described in detail elsewhere (Mellanby, 1939). It is used for keeping and breeding experimental rats, and racks of cages cover three walls. The main food of the cockroaches falls from the rats' cages. There are windows along the top half of one wall; they admit sufficient light for working, but not direct sunlight, and the intensity of illumination during the day is usually between 30 and 50 metre-candles (1 m.c. equals 0.093 f.c.). The room is also lighted electrically, and so different degrees of illumination can be produced. The floor is covered with concrete and the walls with smooth plaster; during the day the cockroaches live inside the walls, and can enter and leave by the spaces around the steam heating pipes. The temperature is usually between 20 and 25° C.

The animal house under consideration contains a number of rooms, but I have only made an extensive study of one of them. There does not appear to be a great traffic of cockroaches between the rooms (all are infested), but there may be some. In those experiments in which the room was kept illuminated for periods of several days, some of the cockroaches normally infesting it may have migrated to other parts of the animal house and so been subjected to different conditions. For this reason certain conclusions expressed here must be accepted with some caution.

Trapping was done using ordinary "Demon" cockroach traps. It was found that equally large numbers of insects were caught if no bait was used, so the traps were not baited. On a large number of occasions the traps were left in the room

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from about 5 p.m. G.M.T. until about 9 the next morning. On other occasions they were examined at 3-hourly intervals, when the traps were removed from the animal room, emptied and returned within 5 min. without switching on any light.

During the course of this work I have been in touch with Dr D. L. Gunn, who has been studying the daily activity of the cockroach in the laboratory. He has made a number of valuable suggestions for further experiments in the animal room. Some of his results are given in this *Journal* in the paper immediately preceding this, and in both our papers the laboratory experiments and the observations made on the natural infestation are compared. The fact that there is so much agreement in the final conclusions is gratifying.

NORMAL PERIODICITY

No healthy cockroach was ever seen in the animal house during the day; occasionally a moribund individual was found which had apparently been unable to crawl back to shelter. If the light was switched on at any time between 10 p.m. and midnight, hundreds of the insects were seen all over the room. When the light was put on they all ran rapidly, first to the area partly shaded by the cages and then into the cracks in the walls. The open floor was always clear of cockroaches within half a minute of switching on the light.

The results obtained by making catches over 3 hr. periods on 12 nights spread over 9 months are given in Fig. 1. The total cockroach population varied during the period of the experiment, and the catches made during these nights ranged between 127 and 17 individuals; the average figure was 48 (s.e. mean \pm 8). This includes adults and all stages of nymphs, for analysis of the figure shows no significant differences between the behaviour of the different stages. To make the results comparable, the figures for each 3 hr. period are given as a percentage of the night's total catch.

It will be seen from Fig. 1 that the cockroaches were most active during the first half of the night, and that fewer were caught during the second half although it was still equally dark. Thus, of the total number, 52.4% were captured before 23.00 hr. (11 p.m.), and only 5.6% were captured after 2 a.m. Activity appears normally to take place only during darkness. In summer, when the nights were short, activity started soon after sunset, but in winter it had been dark for some hours before full activity was exhibited. Both in summer and winter there was practically no activity during the later hours of darkness.

Changes in temperature are indicated for all occasions in Fig. 1, and fluctuations of humidity are also shown in the majority of cases. There appears to be no direct correlation between cockroach activity and either of these climatic conditions. The temperature was always such as to allow activity to take place (see Gunn, 1934), and whether it rose or fell during the night activity took place at approximately the same time. The humidity varied approximately inversely with the temperature, a rise in temperature having little effect on the absolute humidity and thus causing a fall in the relative humidity (this could also be measured as an increase in the saturation

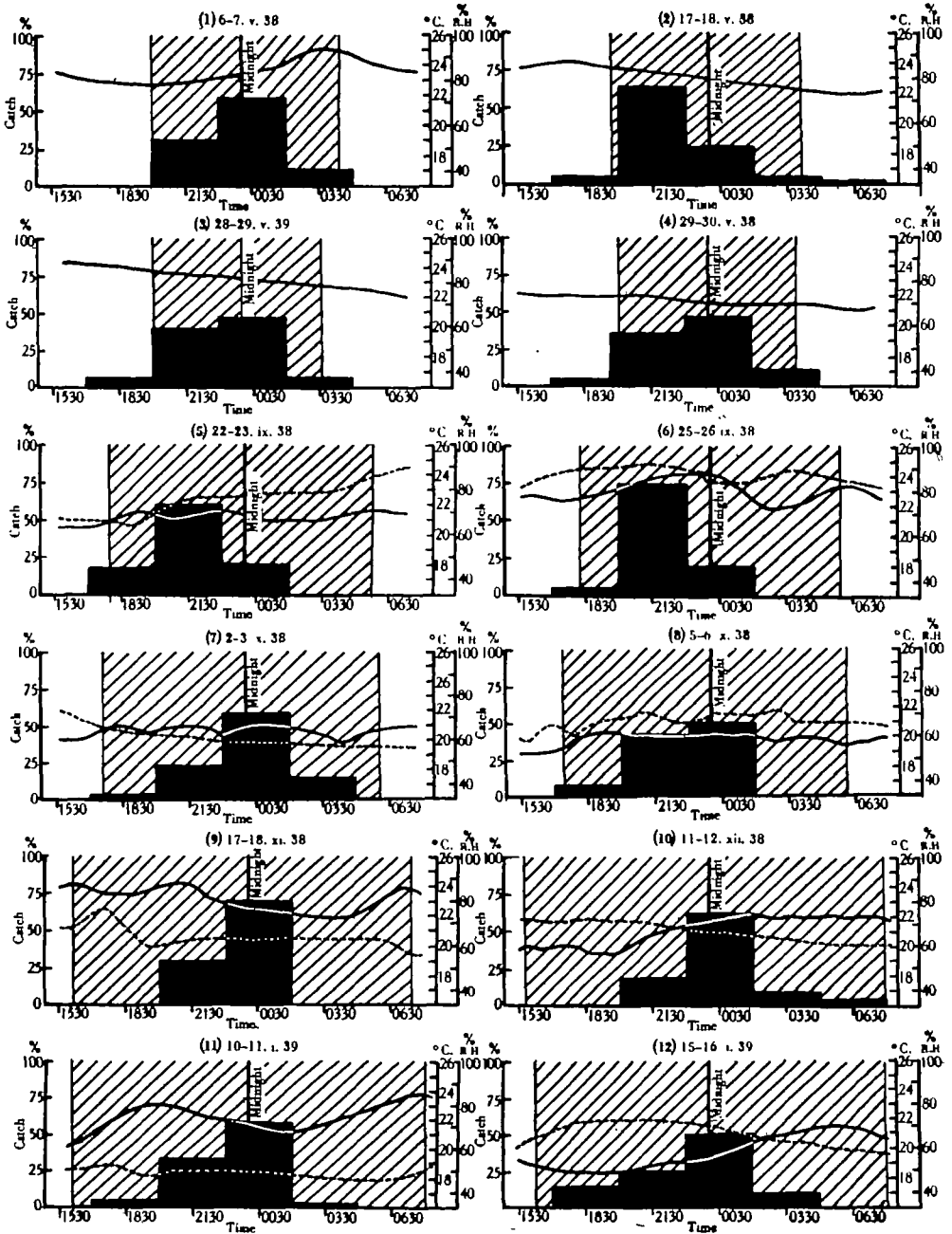


Fig. 1. Numbers of cockroaches captured in traps examined at 3-hourly intervals, each diagram showing results obtained over one 24 hr. period. Black area represents the number of cockroaches. Period from sunset to sunrise (G.M.T.) shaded diagonally. Continuous line=temperature. Broken line=relative humidity. In each diagram the horizontal scale gives the time, the vertical scale on the left the percentage of the total catch of cockroaches at any period, and the scales on the right the temperature ($^{\circ}$ C.) and relative humidity (%) respectively.

deficiency). Therefore if the activity of the insects is not correlated with the changes in temperature, it could hardly be expected to be correlated with humidity either. Activity seems to take place at approximately the same time at all seasons of the year, independently of fluctuations of temperature and humidity, and of changes in the length of day.

It is interesting to compare these results with those which Gunn obtained in experiments where conditions of illumination simulated those of night and day (see p. 270). His results bear a striking resemblance to mine—maximum activity during the earlier hours of the “night”, and little during the later hours of the night or during the “day”.

EFFECTS OF CONSTANT ILLUMINATION

When the room was illuminated by a 60 W. electric bulb, the intensity of light in the open varied between 12 and 6 m.c., but below the cages it was less than half a metre-candle. In a total of 28 nights under these conditions, on 22 no cockroaches were captured, and on the remaining 6 nights a total of only 8 individuals was trapped (the average figure for 42 catches made in darkness in the period covered by this experiment was 65). On numerous occasions when I entered the illuminated room between 10 p.m. and midnight, I never saw a single cockroach. The few that were caught probably ran along to the traps in the shadow under the cages (two of the traps were actually in this shadow). Even after several days of constant light, no activity was observed among the cockroaches. It was thought that perhaps the light might not be so much preventing the insects from leaving their holes as diverting them into other parts of the animal house. To get over this, all the rooms were illuminated for a period of 8 days. Even after this no cockroaches were observed in any of the rooms. It is, of course, not known how active they were inside the walls, or whether they found any food there. If it were possible, it would be interesting to continue this experiment for a longer period (many weeks), until the insects in the walls would be suffering from extreme starvation. Various circumstances make it impossible for me to do this.

Some experiments were made to find whether a very dim light might be left burning without preventing the activity of the cockroaches but still sufficiently bright to allow the insects to be observed. As the cockroach population was fluctuating, it was impossible to express the results of the various illuminations upon the activity other than in a rather rough manner. With a 15 W. lamp, which gave an illumination of 2.5 m.c. in the middle of the room, few cockroaches were caught (about one-tenth the number captured in darkness). A smaller light which gave an intensity of only 0.6 m.c. in the middle of the room, and of only one-twentieth of this under the cage racks, affected the activity of the insects less. On four nights during one week, on two occasions when the room was in darkness the catches numbered 113 and 211, and on two occasions with the small lamp burning the catches were 55 and 39. These figures show that further laboratory experiments under more carefully controlled conditions might yield valuable results, but that

it is impossible to leave a lamp burning which gives sufficient light to allow observation of the insects without affecting their activity, for even with an intensity of illumination of 0.6 m.c. it is difficult to study the cockroach's activity.

Gunn (1940) has found that constant light of an intensity higher than that produced by the 60 W. lamp in the animal house still allows the cockroach to exhibit activity in the laboratory. In his experiments the insects were unable to move out of the light, and for a time they then exhibited periodic activity not unlike that observed in alternating light and darkness. In the animal house when it was possible for the animals to choose between the darkness (inside the walls) and the light (in the room), they chose to remain in the dark, though perhaps they were very active inside the walls during the normal period.

EFFECTS OF CONSTANT DARKNESS

It was possible to darken the animal room during the day by means of shutters fitted over the windows. As the rats had to be fed, it was never possible to keep the room permanently darkened for more than 48 hr., but on one occasion during 4 days the light was only put on for about half an hour on each morning.

When the room was darkened earlier than usual, provided that during the previous night normal conditions of darkness had existed and the room had not been artificially lit up, no effects on the cockroaches were observed. They began their activity at the same hour as they would have done had the room only become dark after sunset. This was observed on a number of occasions when the room was darkened at noon, and even when it was kept dark for 48 hr. no effects were observed. It is possible that further darkness might have upset the rhythm, but because of the rats it was impossible to maintain such conditions.

Darkness at an abnormal time following abnormal illumination had a marked effect on cockroach activity. When the room had been illuminated for 8 days, during the whole of which period only 4 cockroaches had been trapped, and was then darkened at 12.50 (p.m.), 40 cockroaches were captured within 2 hr. As mentioned above, darkening the room at this time after a night of darkness did not make the onset of activity any earlier. Then when the room was kept illuminated until 04.30—by this time all activity would normally be over (see Fig. 1)—and then darkened for 4 hr., 42 cockroaches were captured. These experiments seem to indicate that there was little movement of the cockroaches into the other rooms, and that they were being prevented from coming out of the walls by the light. In fact they almost appear to have been "waiting" there for suitable conditions for activity, i.e. darkness.

It has been noted that darkness following abnormal illumination may reveal an upset in the normal rhythm of activity of the cockroach. But as soon as normal conditions of illumination by day and darkness by night return, these insects appear to revert to their original periodicity, and thereafter early darkening of the room has little effect. After a period of several days of constant illumination, 3 days of normal illumination occurred, and then the room was darkened at mid-day. Only 3 cock-

roaches were caught before 17.00, 11 before 20.00, and 75 were captured during the night. The darkness was maintained for a further 24 hr., and no cockroaches were trapped up to 17.00 hr., 8 were trapped before 20.00, and 76 after this hour. These figures indicate not only that a few days' exposure to normal conditions practically re-establishes the activity rhythm of the cockroach, but also suggest that under conditions of constant darkness the rhythm may establish itself further. That this really does happen is further suggested by some observations made during the period of 4 days' darkness after constant light lasting 8 days. During the first 24 hr. of darkness, the majority of the cockroaches (64 %) was captured before 20.00 (8 p.m.), and only 36 % after that hour, though normal activity is confined to this later period. During the remaining 3 days of the experiment, although irregular activity was noticed, more than 60 % of the cockroaches were captured during the period in which activity is normally manifested under natural conditions of illumination.

EFFECTS OF MECHANICAL DISTURBANCES

These experiments were made to see how vibration affected the activity of the cockroaches. After preliminary trials it was found simplest to produce the vibration by walking noisily about the room instead of spending time devising mechanical apparatus.

As mentioned above (p. 279) if the room was illuminated suddenly at 22.00 hr. hundreds of cockroaches were seen running about the floor. If, before switching on the light, I walked about the room for 5 min., then practically all the insects disappeared. However, the cockroaches appeared to "get used to" a disturbance of this kind, for if I walked about the room for an hour instead of 5 min. before switching on the light, then a large number of the insects had reappeared. Trapping experiments confirmed this conclusion for similar numbers were captured between 20.00 and 23.00 hr. whether or not the experimenter walked about the room for the whole period.

Cockroaches are known to be sensitive to air movements (Necheles, 1924), so some experiments were made using an electric fan. When this was pointed at the ceiling, so that all the air in the room was kept moving but there was no considerable draught along the floor, the catch was not affected. When the fan blew directly at the traps some effect was noticed. On six consecutive nights experiments were made. On days 1, 3 and 6, when the fan was not running, 116, 87 and 113 (mean = 105) cockroaches were captured: on the other nights, when the fan was blowing directly at the traps, the catches were 42, 46 and 77 (mean = 55) cockroaches respectively. The air velocity in the neighbourhood of the traps was approximately 10 m. sec., which is considerably higher than these insects are likely to meet normally. If so great a wind only reduced the catch by about 50 %—and it seems probable that it did not reduce the activity of the cockroaches at all, for they presumably were more concentrated in other parts of the room—then it is unlikely that air movements have much effect on the general activity of the insects, though sudden changes may have temporary effects on the behaviour.

All these experiments on the effects of mechanical disturbance show that these factors are certainly of much less importance than light in maintaining or upsetting the activity rhythm of the cockroach.

FURTHER OBSERVATIONS ON THE EFFECTS OF ATMOSPHERIC HUMIDITY

It has been suggested that cockroaches are most active at night, not because it is then dark, but because the humidity is usually higher (Necheles, 1927). The results given in Fig. 1, showing no correlation between normal activity and atmospheric humidity, contradict this view. On several occasions I sprayed and sprinkled water in the animal room in the evening, and by these means produced a practically saturated atmosphere. If the room was then kept dark, a normal catch of cockroaches was obtained, but if the light was left burning the activity of the insects was entirely prevented. Also, on those occasions when the humidity rose considerably during the day, no activity was then found. It appeared unlikely that atmospheric humidity has any important effect on the activity rhythm of the cockroach.

DISCUSSION

The results given in this paper indicate that in a natural infestation under normal conditions of illumination, cockroaches are mainly active during a period of about 6 hr. during the 24, and the peak of this activity occurs shortly before midnight. Provided that the temperature falls within the zone of normal activity, its fluctuations have little effect on the periodicity of the activity. The activity occurs only in the dark, but seasonal changes in the length of day and night have no great effect on the time at which activity starts and stops. The rhythm appears to be controlled in the cockroach by some internal mechanism, as to the nature of which we at present have no knowledge.

It is interesting to compare my results with those obtained by Gunn in the laboratory. Our techniques were entirely different—my results were obtained by trapping a sample of a wild population under more or less uncontrolled conditions. Gunn (1940) worked in each experiment with one insect and he controlled all such conditions as temperature, humidity, illumination and food. Nevertheless our results are strikingly similar, except for the fact that he found that activity continued in the light whereas in my experiments this never happened. This point is discussed above (see p. 281). All the other observations on the periodicity of activity made by the two methods show a striking similarity, and suggest that rhythmic activity is a factor inherent in the cockroach.

SUMMARY

1. Trapping experiments were made to investigate the activity of cockroaches in a naturally infested animal room.
2. Under normal conditions of illumination (light by day and dark by night),

activity only occurred at night, and most activity occurred during the period just before midnight. There was little activity during the later hours of darkness.

3. Artificial illumination of the order of 6 m.c. almost entirely prevented the cockroaches from appearing. Even lower intensities of light greatly reduced the number which appeared.

4. Darkening the room during the day did not cause the cockroaches to appear, unless the room had been artificially illuminated during the previous night.

5. Mechanical vibration and air movements appear to have little effect on the rhythmic activity of the cockroach.

6. The rhythmic activity of the cockroach appears to be controlled by some internal mechanism which we do not yet understand. External factors like light can modify the rhythm and may temporarily abolish it, but under normal conditions it is readily re-established.

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