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Studies on the Diurnal Rhythms of the Housefly, *Musca domestica* L., in a Dry Tropical Environment.*

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I. Activity under Normal Diurnally-Fluctuating Conditions.

Little of the extensive literature on diurnal rhythms in the animal kingdom has been concerned with houseflies. SHINODA & ANDO (1935), however, noted the times of day at which *Musca domestica* and related species could be collected in largest numbers in Japan, and ILSE & MULHERKAR (1954) investigated diurnal fluctuations in the frequency of the mating reactions of *Musca domestica nebulo* in India. Observations in the latter country have also been made by DEORAS & RANADE (1957), who studied the times of oviposition, hatching and emergence of the same subspecies. Finally, HAMMER (1941), working in Denmark, recorded fluctuations in the numbers of *Musca autumnalis* present on cattle at different times of day.

The present investigation was carried out in the hot dry climate of Khartoum, Sudan. In this locality the *Musca domestica* population, a sample of which was kindly identified by Dr. H. E. PATERSON of the South African Institute for Medical Research, is evidently a hybrid one, resulting from the intermixture of *M. domestica curviforceps* Sacca and Rivosecchi with, probably, *M. domestica calleva* Walker. Representatives of this population were kept in a shaded out-door position on a well-ventilated verandah, and their various activities over the course of the day were recorded. Attention was directed primarily to diurnal fluctuations in the amount of locomotory activity, but the numbers feeding and attempting to mate, and the times of oviposition and emergence from the pupa, were also investigated.

* This investigation was carried out in the Zoology Department of the University of Khartoum, Sudan, and I am indebted to Professors H. Sandon and J. L. Cloudsley-Thompson, past und present heads of the Department, for facilities granted to me there. Financial assistance was kindly provided by a grant from the University Research Funds.

Material and Methods.

Flies on which observations were to be made were captured in and around the University buildings, and immediately after their identification had been checked, transferred to the shaded verandah mentioned above. Here, they were enclosed either in an observation box, in the transparent tube of an aktograph, or in a cage of mosquito netting. Along with the flies was enclosed a small receptacle containing cotton wool soaked in diluted fresh boiled milk, which provided food and water.

Details of the apparatus are as follows:

(a) *Observation box.*

This measured 12 cm. by 17 cm. by 22 cm. The side facing the observer was of transparent perspex, while the opposite side, together with the floor and the roof, was lined with white paper. The remaining two sides were of mosquito netting. The interior of the box was therefore well ventilated, and the flies inside it were clearly visible to the observer.

(b) *Aktograph.*

This apparatus was based on a design described by D'AGUILAR (1952), and is shown diagrammatically as seen from above in Fig. 1. It consisted of a transparent celluloid tube (A), the ends of which were closed with mosquito netting. This tube was suspended centrally by a pin (B) from a transverse beam consisting of a drinking straw (C). Through the ends of this straw passed two further pins (DD), the points of which rested on ground glass surfaces (EE) and acted as pivots. When flies were placed inside tube A, any movements they made along its long axis imparted to it a pitching motion; this motion was recorded by a delicate pointer (F) on a smoked drum (G) which took one week to complete a revolution. To avoid movement of the tube by draughts, the whole apparatus was enclosed in a glass tank, the open top of

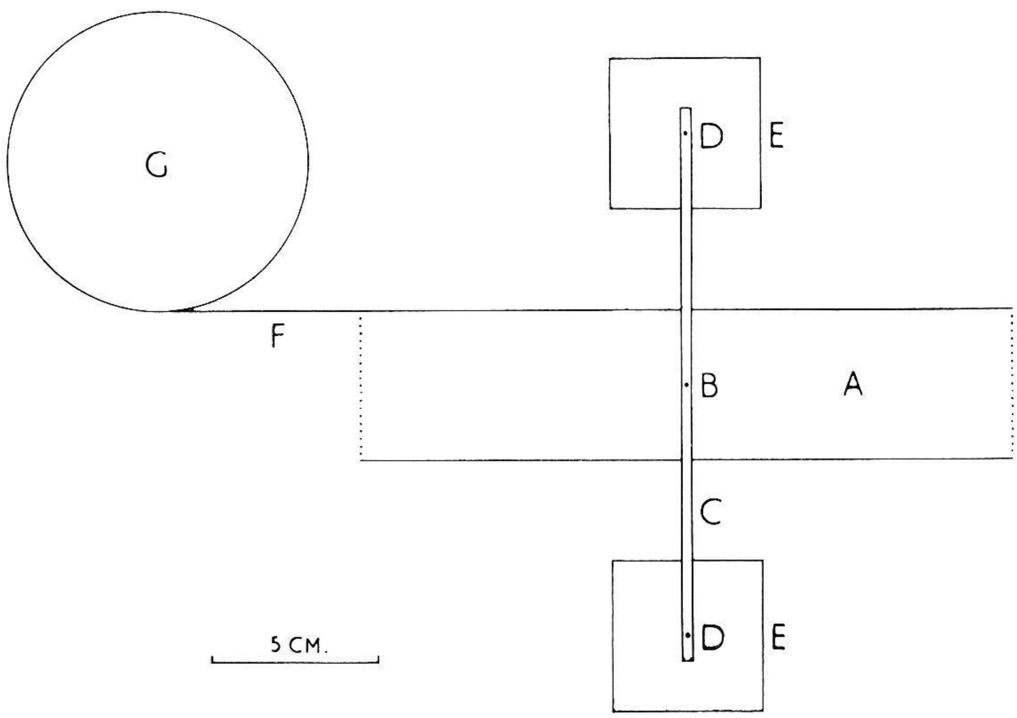

Fig. 1. Aktograph apparatus as seen from above. For explanation see text.

which was covered with white poplin, and the walls of which, except on one side, were covered with white paper. Thermohygrograph readings showed that, within this glass case, diurnal fluctuations in temperature and humidity were almost as wide as immediately outside it, i.e. the differences in range were within 1.5°C and 3% R.H.

(c) *Mosquito-netting cages.*

These measured 31 cm. by 39 cm. by 51 cm., and one side was in the form of a sleeve. They were used to contain the relatively large numbers of flies needed for observations on the time of oviposition. The site of oviposition was always the dish of milk-soaked cotton wool included in each cage.

The supply of pupae needed to make observations on the emergence rhythm was obtained by transferring some of the eggs laid in the cages described above to glass jars in which, following the rearing method of HAFEZ (1948), there was a further supply of milk-soaked cotton wool. These rearing jars were kept on the same shaded verandah as the adult flies, and in them development proceeded right through to the adult stage.

Observations and recordings extended over the period September, 1958, to July, 1960. They were always carried out on bright days when the sun was unobscured by cloud, but direct sunshine never fell onto the standard position on the verandah occupied by the pieces of apparatus described above. Temperature and humidity were recorded continuously by a thermohygrograph placed immediately adjacent to the apparatus being used; when the aktograph was used, the thermohygrograph was placed inside the same glass tank as this apparatus.

Further technical details can more conveniently be described in the sections to which they are particularly relevant.

Movement in General.

Under this heading are included all movements that resulted in a displacement of the position of the insect.

Males and females present together.

Variations in the degree of locomotory activity of male and female flies that had free access to each other were investigated both by direct observation and by the use of the aktograph. In the former case the movements of eight flies (four males, four females) that had been placed in the observation box the previous day were watched for 10-minute periods at standard intervals from shortly before sunrise to shortly after sunset (i.e. from the time when it was just light enough to see the flies to the time when it was no longer possible to see them). The actual times of these observation periods were such that their mid-points occurred at the following times: 20 minutes before sunrise; sunrise; sunrise plus ½ hr., plus 1 hr., plus 2 hrs., plus 4 hrs., plus 6 hrs.; sunset minus 4 hrs., minus 2 hrs., minus 1 hr., minus ½ hr.; sunset; sunset plus 20 minutes. During each 10-minute observation period, counts of the numbers moving were made at 15-second intervals, and at the end of the 10-minute period the 40 readings thus obtained were added together.

When the aktograph was used, the movements of four flies (two males, two females) were recorded continuously from the time when they were first placed in the apparatus to 48 hours later. A record of activity which included two complete nights and the full daylight period between them was thus obtained. The times between sunrise and sunset, and between sunset and sunrise, were then each divided into twelve equal periods, and the smoked-drum tracings were analysed by measuring the area cleared by the pointer during each of these approximately hourly periods.

The results of six sets of direct observations are shown in Fig. 2, and the results of 18 aktograph recordings in Fig. 3. In the latter figure, results are shown only for the periods during which there was daylight, i.e. from the beginning of the period immediately before sunrise to the end of the one immediately after sunset. During the night hours, activity was recorded on only three occasions, when it rated only one or two units on the scale adopted.

Activity was thus virtually confined to the hours of daylight. Within this period, both figures show that, soon after activity commenced, it rose to a small morning peak. It then dropped, and later rose again to a high level of activity in the afternoon; this

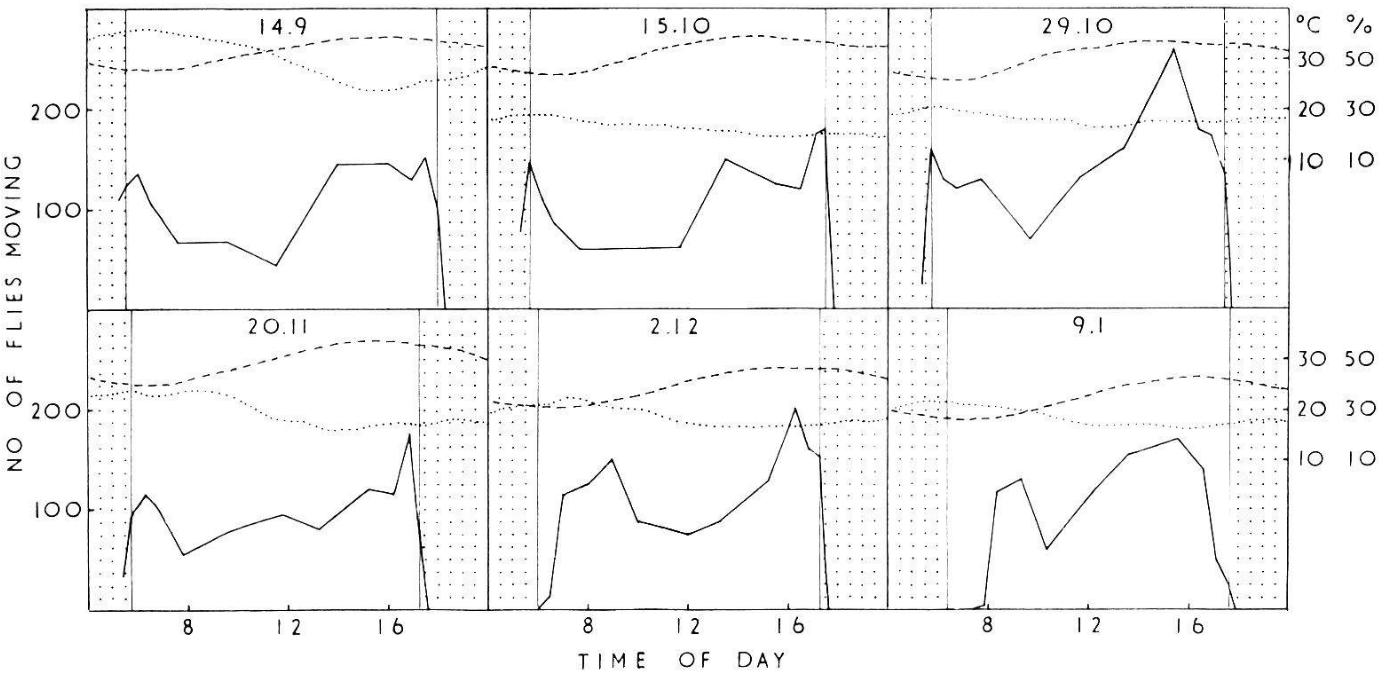

Fig. 2. Diurnal fluctuations in the movement in general of *M. domestica* adults (both sexes), as indicated by direct observations on the dates shown. Broken lines: temperature; dotted lines: relative humidity; stippled areas: periods before sunrise or after sunset.

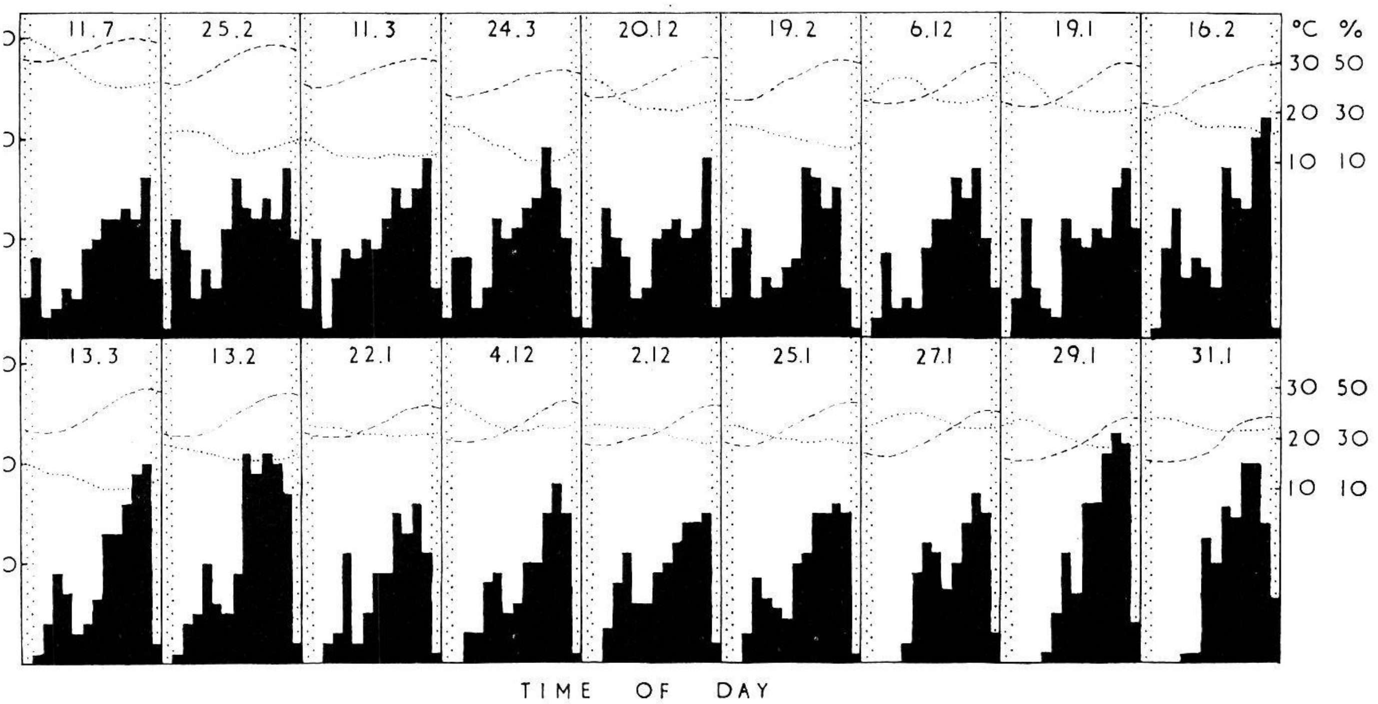

Fig. 3. Diurnal fluctuations in the movement in general of *M. domestica* adults (both sexes), as indicated by aktograph recordings on the dates shown. Conventions otherwise as in the previous figure.

second high activity phase tended to be more prolonged than the morning peak, and always reached a higher maximum.

In both figures the results are arranged in order of decreasing minimum temperature, and it will be seen that provided this temperature was below a certain level, there was a close relationship between it and the time at which activity started in the morning. Thus, Fig. 3 shows that at minima of 22.5°C and above, activity started in the period before sunrise, while at 22.0°C and down to 20.5°C, activity started during the next period. From 18.5°C to 20.0°C activity was delayed by a further period, while at 15.5°C to 16.5°C it did not commence until the fourth period after sunrise. This correlation of activity with minimum temperature did not result from a certain temperature having to be reached before activity could begin, for the temperature at the time that activity actually started varied from 20.5° to 22.0°C when movement started during the first period after sunrise, to 15.5-17.5°C when movement began during the fourth period after sunrise. A similar relationship between minimum temperature and the time of onset of activity is apparent in Fig. 2.

Although there was a consistent tendency for a small activity peak to occur in the morning, and a larger, less well-defined one in the afternoon, it will be seen from Fig. 3 that the actual periods in which highest activity occurred during the morning and afternoon varied considerably on different days, even within groups of recordings in which activity started at the same time of day. The question thus arose as to whether these differences were also related to variations in climatic conditions. Of these variables, temperature (apart from the effects of low minima) showed no consistent correlation with activity, and neither did relative humidity; the same was found to be true if the figures were converted to saturation deficiencies. Barometric pressure varied within a range of 8 millibars diurnally, and of 19 millibars over the whole period of the observations, but these variations, again, bore no apparent relationship to recorded variations in the activity pattern. A variable that might be expected to have been of greater importance is the light intensity cycle. Activity recordings were always made on days when the sun was at no time obscured by cloud, but since the aktograph was in a constant position on a shaded verandah, the pattern of this cycle varied with seasonal variations in the position of the sun in the sky. Some attempt to assess these variations was made by measuring the light falling on the aktograph at twelve equal intervals between sunrise and sunset in the middle of each month in which aktograph recordings were made. These readings, which were taken from a Weston exposure-meter pointed in standard directions from the position normally occupied by the aktograph, indicated that the time of maximum light intensity varied from approximately one hour after true noon in December and January, to approximately one hour before noon in March and July; in February the highest readings were obtained at noon precisely. There was not, however, any consistent relationship between these seasonal differences and the variations in the activity patterns shown in Fig. 3; indeed, there were sometimes considerable differences between activity patterns recorded only a few days apart.

It appears, therefore, that the only day-to-day or seasonal variable to have exerted a clearly defined effect on activity was temperature when it dropped below a certain value. Other physical variables doubtless influenced the activity cycle in some degree, but these effects are not discernible from the data available.

Males and females separated.

An attempt to determine the extent to which each sex contributed to the activity patterns described above was now made by recording the movements of males and females separately. Both sexes were tested on the same day, four males being placed in the tube of one aktograph, and four females in the tube of another.

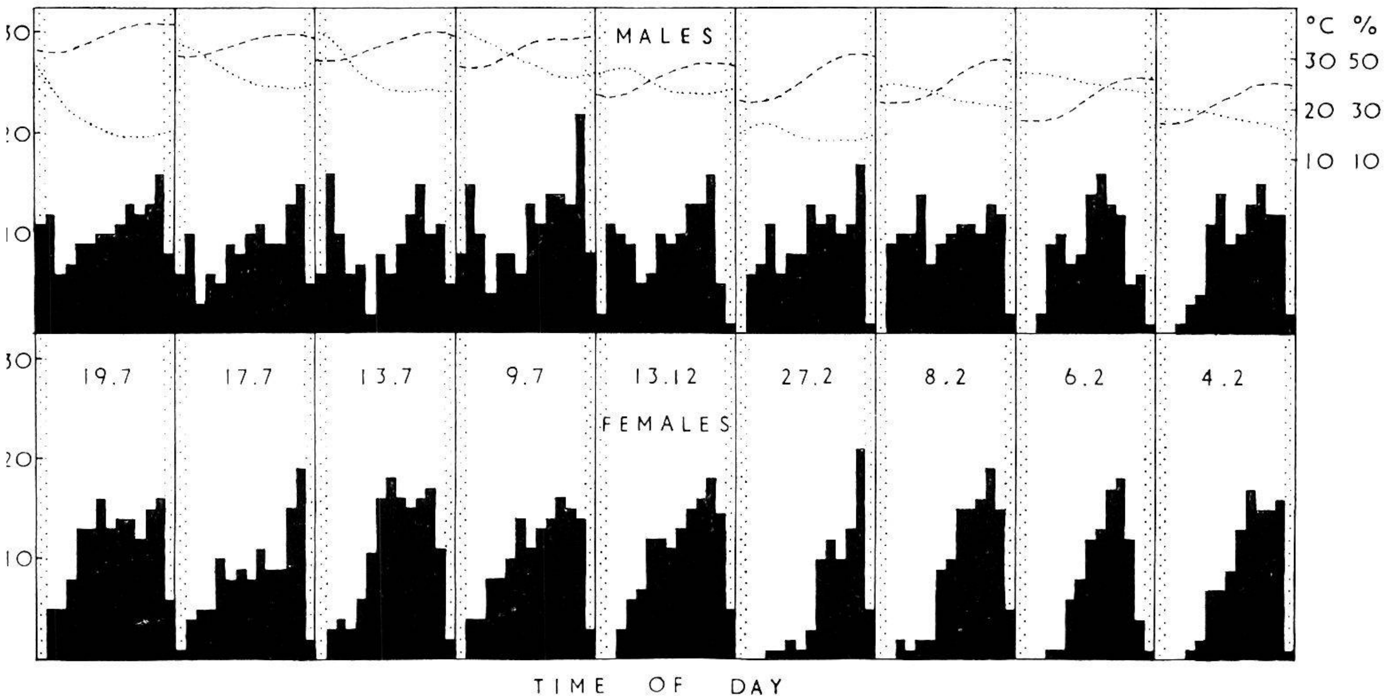

Fig. 4. Diurnal fluctuations in the movement in general of male and female *M. domestica* separated from each other but tested on the same days, as indicated by aktograph recordings. Conventions otherwise as before.

Both pieces of apparatus were placed in the same glass tank, and the procedure was in other respects exactly as before.

The results are shown in Fig. 4, from which it will be apparent that the activity of the males followed a similar pattern to that of both sexes together in so far as there was a rapid rise to a morning peak, then a distinct drop, followed by a second period of high activity during the afternoon. The second high-activity period, though more prolonged than the first, did not, however, invariably reach a higher maximum, and in this respect the results differed from those obtained when both sexes were present. The activity of the females followed a quite different pattern. It almost always started later in the morning (by either one or two periods) than that of the males, and rose fairly gradually to a high level, the maximum reading being obtained during the afternoon. In both sexes the time of onset of activity was again correlated with the minimum temperature (more closely in the males than in the females), but the actual times at which maximal activity occurred varied considerably, and these variations bore no consistent relationship to the climatic differences recorded.

Although the activity of males and females allowed free access to each other obviously cannot be regarded simply as the sum of the activity of the two sexes when separated, there seems little doubt that the early morning peaks shown in Figs. 2 and 3 were caused primarily by the movements of the males. Direct observations indicated that these movements disturbed the females, so this sex must also have contributed to the morning peaks, though probably only to a minor degree. The less well-defined but larger afternoon peaks presumably resulted from the combined high activity of both males and females.

Feeding Activity.

Preliminary observations showed that the activity rhythm was profoundly affected by the presence or otherwise of the diluted milk normally provided for the flies. Thus, when this supply was removed from the aktograph early in the afternoon, movement continued up to midnight or even later. The following morning, activity restarted at the usual time, and continued until mid-day or shortly afterwards, by which time all the flies were either dead or too weak to move. When, instead of diluted milk, only water was supplied, the flies were similarly but less rapidly affected i.e. movement was prolonged less far into the night and death occurred several hours later than when neither milk nor water was present. This indicated that the diluted milk was important both as a source of food and of water.

The problem of whether there was any regular rhythm of feeding activity when food was continuously available was investigated by direct observations on the same flies as were used to obtain the results shown in Fig. 2. Counts of the numbers feeding on the di-

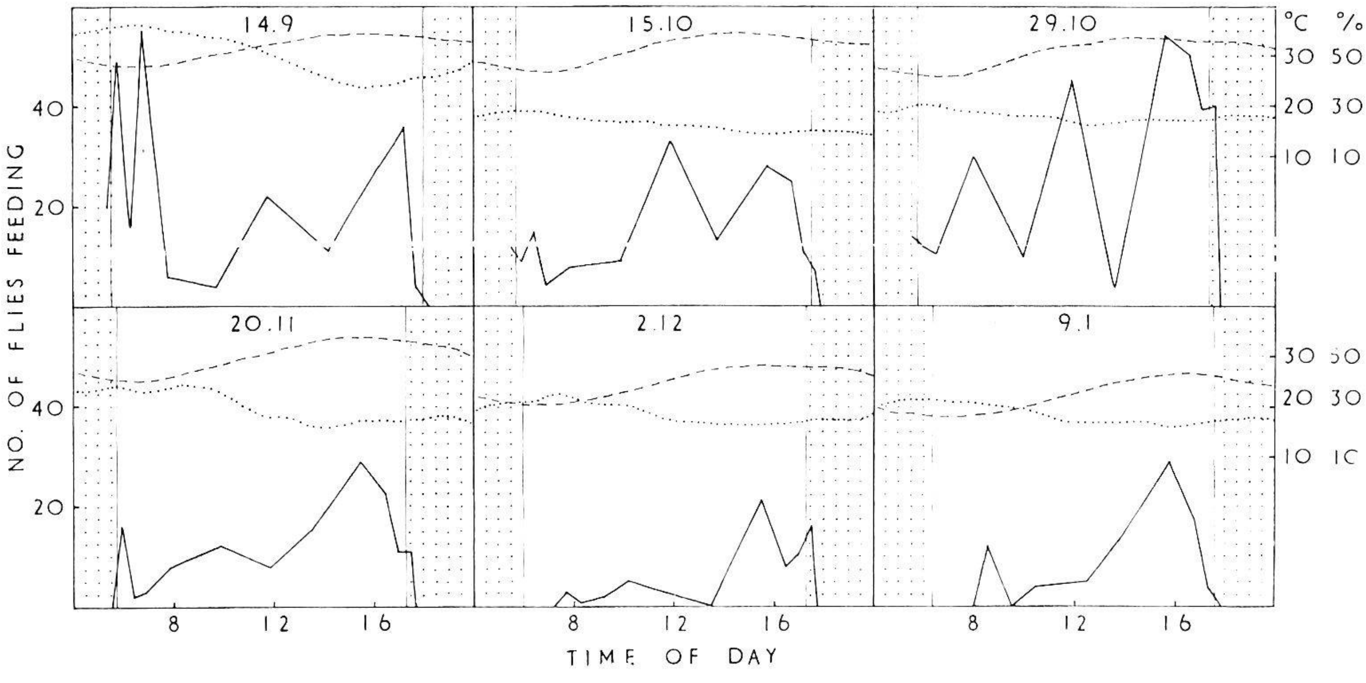

Fig. 5. Diurnal fluctuations in the number of *M. domestica* adults feeding on a supply of diluted milk, as indicated by direct observations. Conventions as before.

luted milk were made at 15-second intervals over the 10-minute periods immediately following the equivalent periods in which counts of movement in general were made.

The results are shown in Fig. 5, and will be seen to have followed no very consistent pattern. Thus, while there was a general tendency for feeding activity to be higher in the afternoon than in the morning, there was one case (14th Sept.) when this was not so, and on 29th October the lowest as well as the highest reading occurred during the afternoon. The variations in the results do not appear to have been correlated with the climatic differences recorded except in so far as feeding, like movement in general, started later on mornings when the minimum temperature was low than on warmer mornings.

Flies observed by dim light during the night were never on or in the food receptacle, and this, coupled with the absence of night-time movement recorded in the aktograph experiments (p. 100), indicates that feeding was virtually confined to the daytime.

Mating Reactions.

When flies of both sexes were present together, the males often attempted to mate with the females, and the frequency of such mating reactions was counted at intervals over the course of the day. The flies observed were again the ones used to obtain the results shown in Fig. 2, the number of attempted matings being counted during the 10-minute periods immediately preceding the

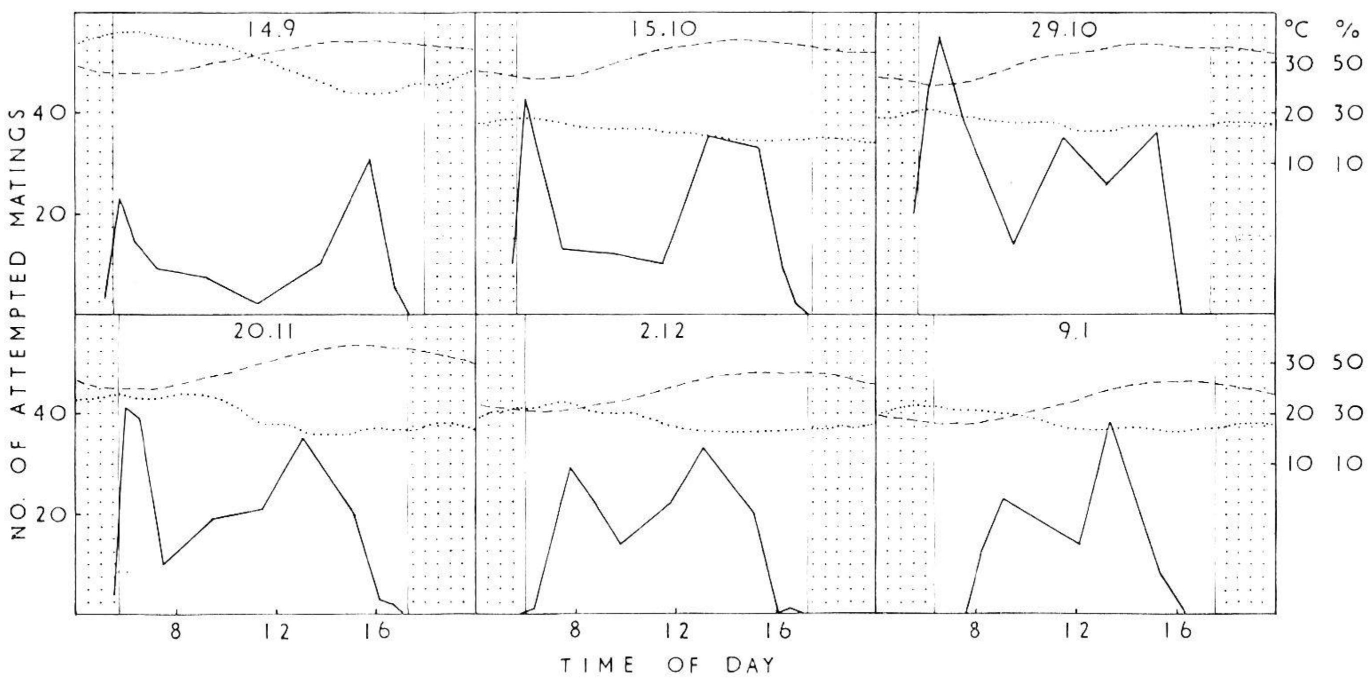

Fig. 6. Diurnal fluctuations in the number of *M. domestica* males attempting to mate, as indicated by direct observations. Conventions as before.

periods in which movement in general was assessed. Only definite attempts at mating in which the male actually seized the female, and at least momentarily brought the tip of his abdomen into contact with hers, were recorded. (It may be noted, however, that although the nature of these movements was obvious, only one out of the hundreds witnessed resulted in a successful copulation.)

The results are shown in Fig. 6, and can be seen to have resembled the movement in general of the males (Fig. 4) in that there was consistently both a morning and an afternoon activity peak, neither of which was invariably the higher. Similarly, the onset of activity was again delayed by low minimum temperatures. One well defined difference from the movement-in-general rhythm, however, was that mating activity always ceased before sunset—sometimes more than an hour before—whereas movement in some form always continued at least up to the time of sunset.

The results of the aktograph experiments (p. 100) indicate that no mating activity occurred during the night, for had it done so it would have been recorded as a form of movement.

Oviposition.

Approximately 100 wild-caught flies were confined in each of the mosquito-netting cages used to make observations on the time of oviposition. The milk-soaked cotton wool on which the eggs were laid in these cages was examined at intervals which equalled one sixth of the time between sunrise and sunset i.e. approximately every two hours; the first interval was so timed that sunrise oc-

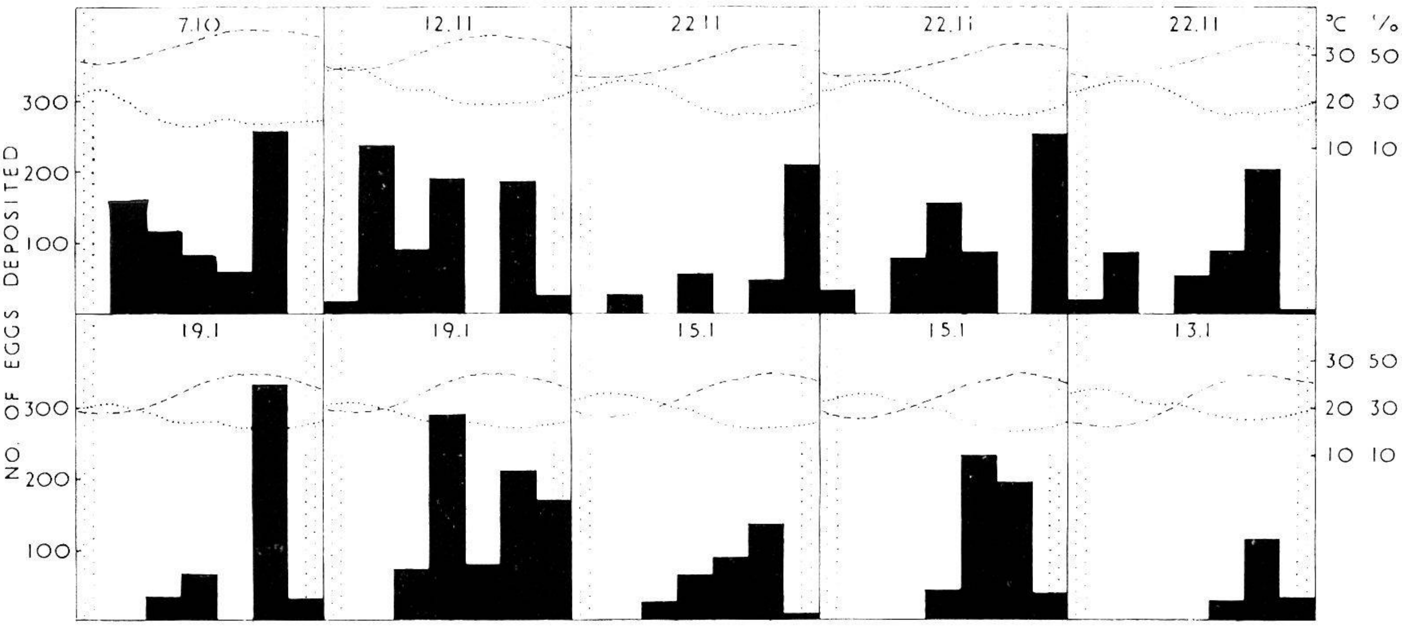

Fig. 7. Diurnal fluctuations in the number of eggs deposited by *M. domestica.* Conventions as before.

curred exactly half-way through it, and sunset similarly occurred exactly half-way through the last interval.

The results of observations carried out on six separate days, involving on each occasion the use of one to three cages, are shown in Fig. 7. There is little indication of any consistent pattern of egg-laying activity over the course of the day, for the time of maximum oviposition varied from the second to the last period, and the times of the lesser peaks also varied considerably. Except in so far as oviposition never occurred during the earlier part of the day when minimum temperatures were low, there does not seem to have been any relationship between these differences and the climatic differences recorded; indeed, there were sometimes marked divergences between the results obtained from different cages on the same day.

No eggs were ever found to have been deposited between the end of the last period in the afternoon and the beginning of the first period the following morning, so oviposition was evidently confined to the hours of daylight.

Emergence from the Pupa.

Glass rearing jars which contained pupae ready to emerge were examined at intervals equivalent to those described in the preceding section. The results of six sets of observations are illustrated in Fig. 8, which shows that emergence always rose to a single peak

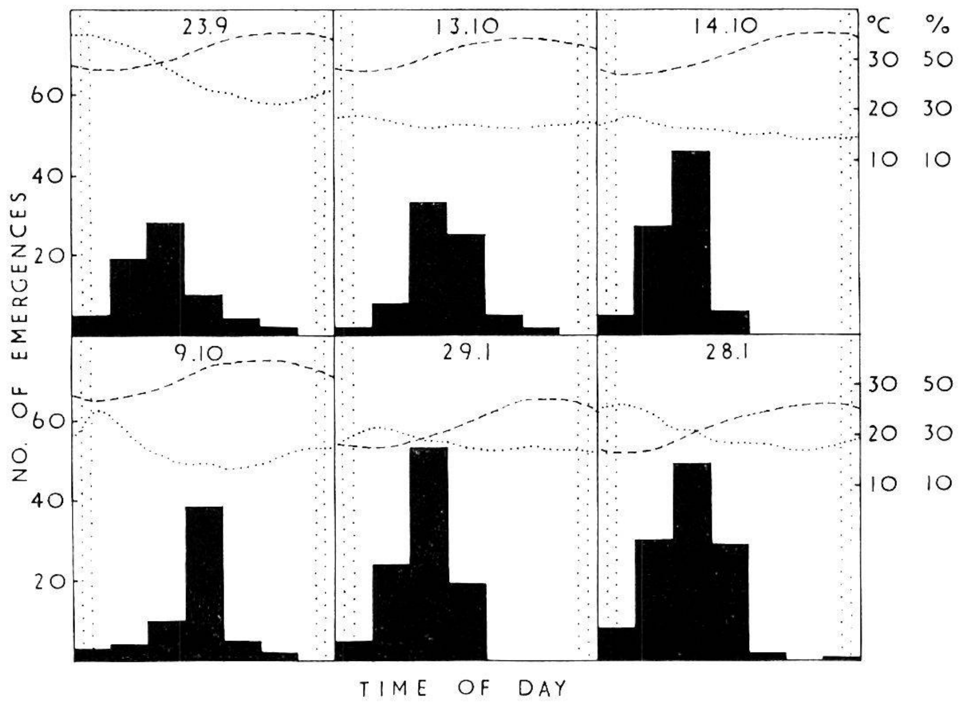

Fig. 8. Diurnal variations in the number of *M. domestica* adults emerging from pupae. Conventions as before.

during the course of the day. In one case (9th Oct.) the peak occurred at noon; in every other instance it occurred during the third period i.e. approximately two hours before noon. Unlike any of the other activities considered, emergence appeared to be unaffected by low minimum temperatures. This is evident from the results obtained on January 28th and 29th; the temperatures that occurred on these dates were certainly such as to have delayed the onset of movement in general by several hours (see Fig. 3), but they had no such effect on the time of emergence.

Like the other activities considered, emergence was virtually confined to the hours of daylight, although on two occasions one emergence took place between the end of the last period in the afternoon and the beginning of the first period the following morning.

Discussion.

In demonstrating the locomotory activity of the flies to be virtually confined to the hours of daylight, the results confirmed general experience and the customary description of *Musca domestica* as a diurnal insect. As regards fluctuations in activity occurring during the daytime, it is interesting to note a parallel to the present results in the suggestion of a double peak obtained by SHINODA and ANDO (1935); these authors report that in Japan, between May and September, flies of various species including *M. domestica* were most numerous at 9 a.m. and again at 3 p.m.

A double peak in the mating reactions of *M. domestica nebulo* is recorded by ILSE and MULHERKAR (1954), who, in India, observed the first peak to occur between 6.30 and 9.00 a.m., and the second between 11.30 a.m. and 3.30 p.m. Except in one case, when the two peaks were of the same height, the first was the higher, a result which does not conflict with those described here. Although these investigators do not provide any climatic data, there is also an indication that, as in the present investigation, the onset of activity was delayed by low temperatures. Thus, in November and December the morning peak occurred about two hours later than in June to September, and the former season is evidently the one in which lower minima normally occur.

No previous observations on fluctuations in the feeding activity of *M. domestica* seem to have been made, but HAMMER (1941) found that the numbers of *M. autumnalis* present on six cattle between sunrise and sunset rose fairly consistently to a peak in the early afternoon provided the weather was warm. That there is little similarity between this result and those presented here is not altogether surprising in view of the specific difference, coupled with the fact that HAMMER's observations were carried out in the field under the temperate climatic conditions of Denmark.

The oviposition time of *M. domestica nebulo* was found by DEORAS and RANADE (1957), working in India, to be mainly early morning or late evening, and this observation, as far as it goes, is not incompatible with those described here. The same authors' claim that emergence from the pupa usually occurred in the early morning appears to imply a somewhat earlier emergence peak than was recorded in the present investigation. The climatic conditions under which these observations were made are not recorded.

The various diurnal rhythms described in this paper, although differing in the degree to which they conformed to a consistent pattern and in the exact nature of that pattern, were all alike in that activity was virtually confined to the hours of daylight. The existence of this well-defined major rhythm immediately raised the question as to whether it would persist under constant conditions, i.e. whether it was primarily exogenous or endogenous. An investigation into this and related problems is reported in Part II.

II. Activity under Controlled Conditions.

In Part I diurnal fluctuations in various activities of *M. domestica* as displayed by wild-caught flies kept on a shaded verandah were studied. In the present part of the investigation, activity was studied under constant or artificially varied conditions in an attempt to determine the nature of the diurnal rhythm which previously received most attention, namely, that of 'movement in general' This form of activity, which included any movement resulting in a displacement of the position of the insect, was previously found to be confined to the hours of daylight, and to follow a double-peaked pattern when both sexes were present (Fig. 3).

The only previous attempt to investigate the nature of the diurnal rhythms of *M. domestica* seems to have been that of ILSE and MULHERKAR (1954), who, in India, observed the mating rhythm of this species under reversed illumination, as well as under normal conditions.

Material and Methods.

The aktograph described in Part I was again used to record locomotory activity. Four flies (two males and two females) were captured in the wild state during the earlier part of the morning, and immediately after an identification check, placed inside the tube of the apparatus. As before, a small receptacle containing diluted fresh boiled milk was included in the latter; this food and water supply was not renewed during the course of an experiment, as to do so would have disturbed the flies and affected their activity rhythm.

As soon as the flies had been placed in the aktograph, this apparatus was placed in the same position on the verandah as it had occupied in the previous experiments, and left there until sunset of the same day. It was then removed to a light-proofed air-conditioned room, the temperature in which could be controlled to within ± ½°C over the range required. The subsequent procedure varied, and will be described in the succeeding sections.

Activity in constant dim light.

In these experiments the controlled room was continuously illuminated only by a shaded 15W bulb, the light provided by which was too dim to stimulate the flies to any visible form of activity. The temperature was 28.5°C; this was within the range to which the flies had been exposed on the verandah.

From Fig. 9, which shows the results of two experiments, it can be seen that on the first three days activity was very largely confined to the hours when it was daylight outside. On the first day activity was in both experiments low and did not cover the whole period of daylight, but on the second and third days it was higher and extended from the first or second period after sunrise to the

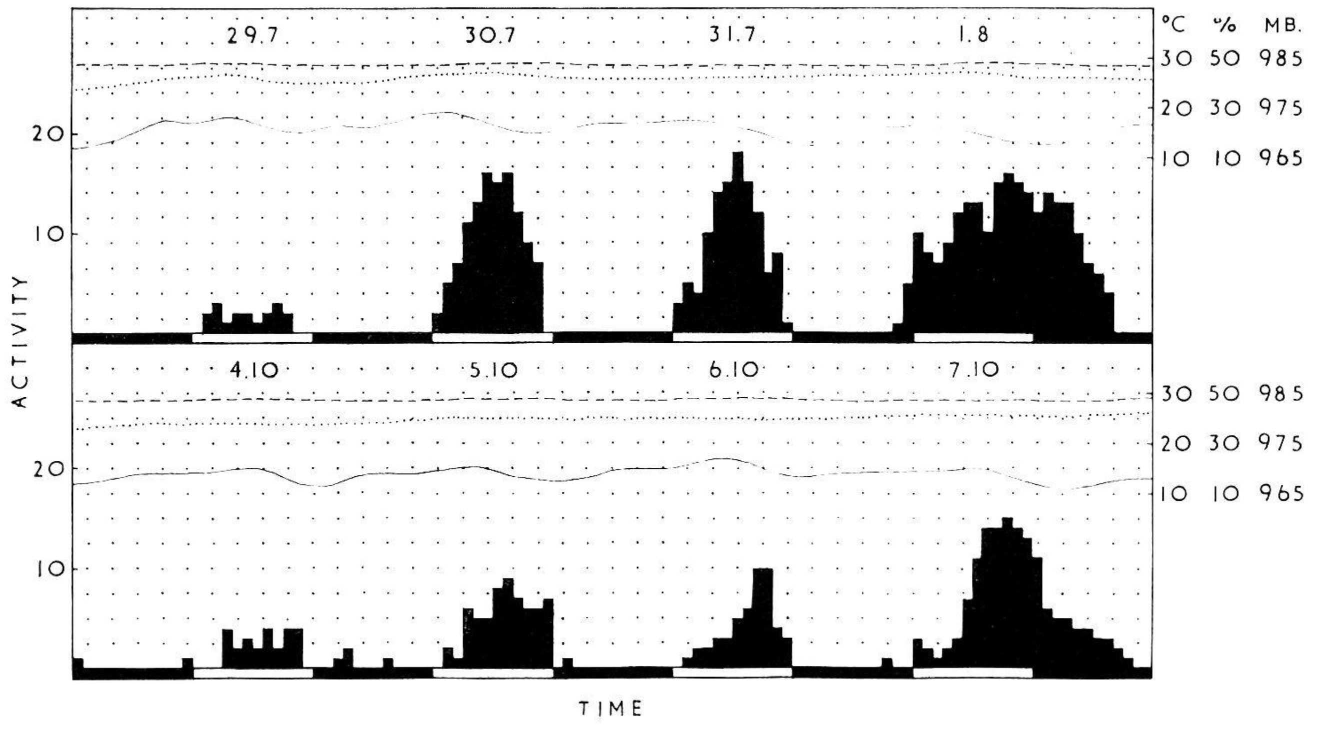

Fig. 9. The locomotory activity of *M. domestica* adults kept continuously in very dim light (two experiments). Broken lines: temperature; dotted lines: relative humidity; continuous lines: barometric pressure. Times of day and night (i.e. of sunrise and sunset) indicated on the bands at the bases of the figures.

first or second period before sunset. On the fourth day activity continued well into the following night, but since by the fifth day the supply of milk had dried up and all the flies had died, it may be presumed that this was an effect of food and water deprivation.

The active-by-day/inactive-by-night rhythm thus appears to have been largely endogenous, for the temperature in the controlled room was constant to within ½°C, and the relative humidity varied only within the ranges 37-44% and 36-42% with no consistent tendency towards a diurnal fluctuation. The barometric pressure, which varied from 967-974 and 966-972 millibars, did show some tendency to follow a diurnal cycle, but these fluctuations were too irregular conceivably to have been responsible for the consistent activity rhythm recorded.

A further feature of the results is that activity did not follow the usual daylight pattern of a small activity peak early in the morning and a second larger peak in the afternoon, thus indicating that some environmental condition not supplied in the experiment was necessary for this feature to be exhibited.

Activity under bright illumination during the daytime.

Experiments were now carried out in which the flies were kept in very dim light during the night and in bright though constant illumination during the day. The latter was supplied by a 100 W bulb suspended above the aktograph, but separated from it by a screen of white poplin which diffused the light. The resultant light intensity to which the flies were exposed, as measured by exposure-meter readings taken in the same way as previously on the verandah, was within the range recorded at mid-day in the latter situation. As before, the temperature was 28.5°C.

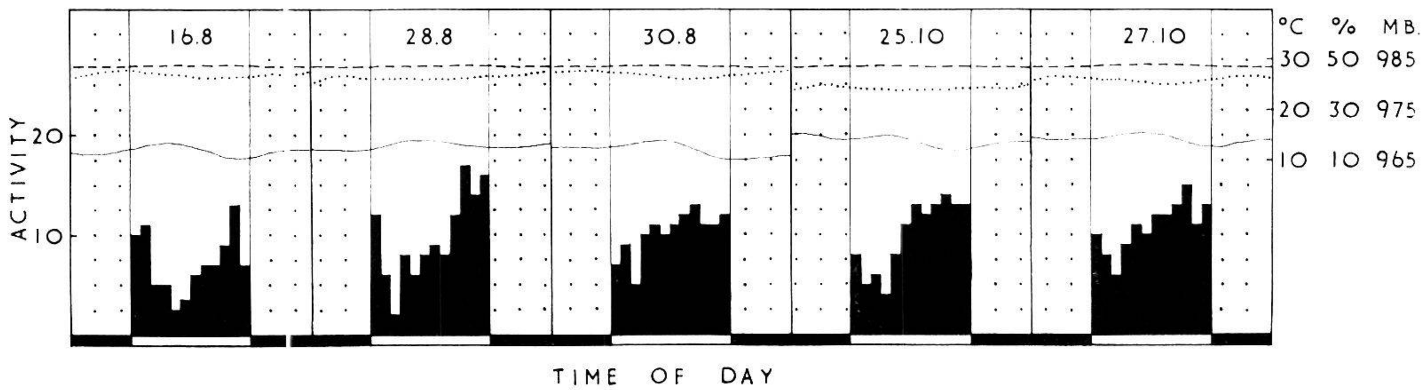

Fig. 10. The locomotory activity of *M. domestica* adults kept in very dim light during the night, and in constant bright light from sunrise to sunset (five experiments). Stippled areas: very dim light; clear areas: bright light. Conventions otherwise as in the previous figure.

The fluctuations in activity during the period of illumination (i.e. between sunrise and sunset) are shown in Fig. 10, from which it is apparent that activity tended to follow a pattern similar to that shown in natural daylight in so far as there was a small peak in the early morning, then a drop followed by a larger peak in the afternoon. This indicates that the activity of the flies was markedly affected by strong illumination, and that an activity pattern similar to that exhibited in natural daylight could be produced even when the light intensity during the daytime was constant.

As before, climatic fluctuations in the controlled room were apparently too small and irregular to have been responsible for determining the nature of the activity patterns.

Activity under reversed illumination.

The degree to which the entire day/night activity rhythm could be altered by reversing the light conditions was now tested by placing the flies in very dim light in the controlled room at sunset on the day of capture, and switching on the bright light 24 hours later. As will be seen from Fig. 11 (upper section), the higher illumination immediately induced high activity which continued at a generally diminishing level throughout the night. When, at sunrise the following morning, the bright light was switched off, activity ceased, immediately to restart when bright illumination was again supplied at sunset on the same day. On this second night of artificially induced activity, a double-peaked pattern bearing some resemblance to normal daytime patterns except in so far as the first peak was the higher, was displayed. The following sunrise the bright light was again switched off and left off permanently. In spite of this, activity recommenced soon after the next sunset and continued until two to three hours after sunrise. Activity started about the same time the next night, but did not continue all night, presumably owing to the death of the flies, none of which were alive the following morning. A reversed rhythm had thus, to a considerable degree, been established.

A further experiment was now carried out to determine how rapidly the reversal of the activity rhythm could be effected. In this case the bright light was switched on as soon as the flies were placed in the controlled room at sunset on the day of capture, and the following sunrise the bright light was switched off and left off for the remainder of the experiment. It can be seen from Fig. 11 (lower section) that although the flies had presumably been following their usual daylight activity pattern before they were placed in the controlled room, the bright light to which they were

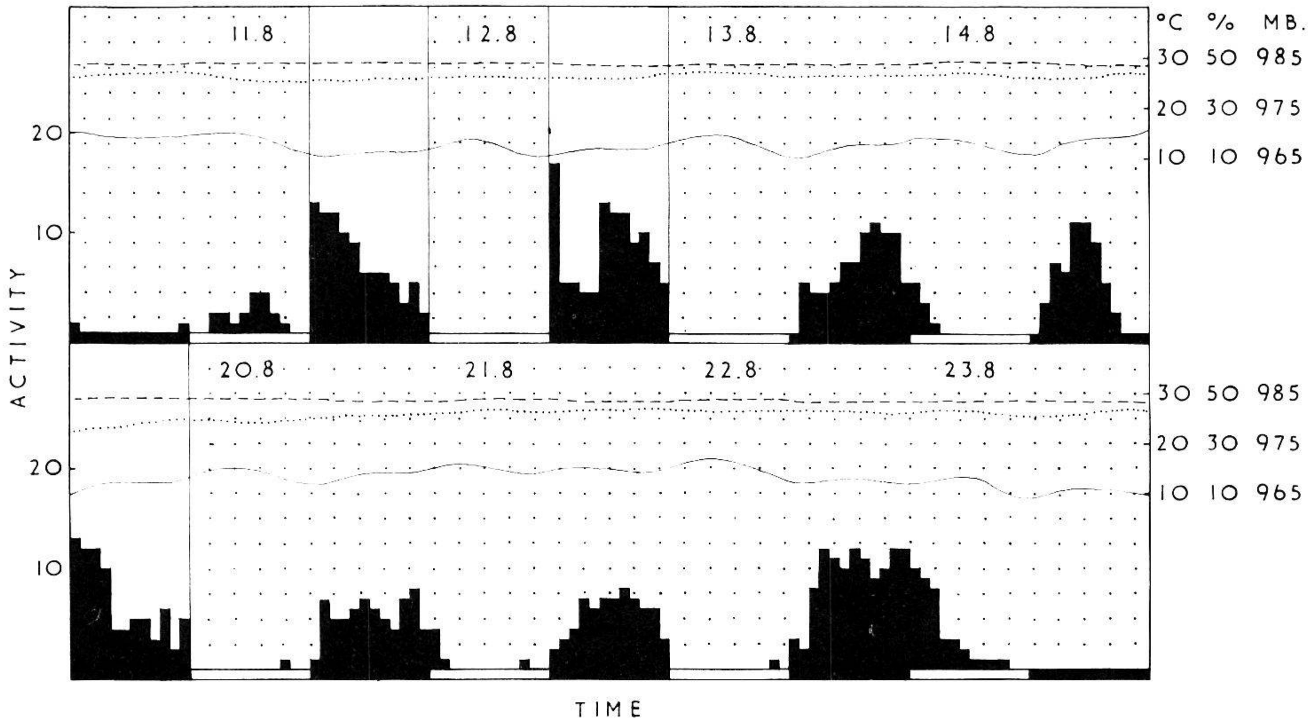

Fig. 11. The locomotory activity of *M. domestica* adults exposed to reversed illumination. Upper section: very dim light for 24 hours, then bright light for two successive nights, followed by continuous very dim light. Lower section: bright light for one night only, followed by continuous very dim light. Conventions as before.

then exposed stimulated them to activity throughout the night. There was virtually no activity the following day, but the following night it restarted, to continue until shortly after sunrise the following morning. The following night activity was even more precisely confined to the period between sunset and sunrise; the next night results began to be influenced by the hunger or water shortage of the flies, which led to their death the following day. In this experiment, the reversed rhythm was thus established by only 12 hours of night-time illumination following a day when normal daylight conditions were experienced.

Sudden changes in illumination halfway through the day or night similarly had immediate and pronounced effects on activity. Thus, when inactive flies that had been in darkness up to midnight were suddenly illuminated they immediately became very active. Similarly, when flies that had been in daylight up to noontime were suddenly plunged into darkness, their activity was greatly reduced, though it did not altogether cease.

Activity in continuous bright light.

Although all experiments so far described had shown that high activity was stimulated by a change from very dim to bright illu-

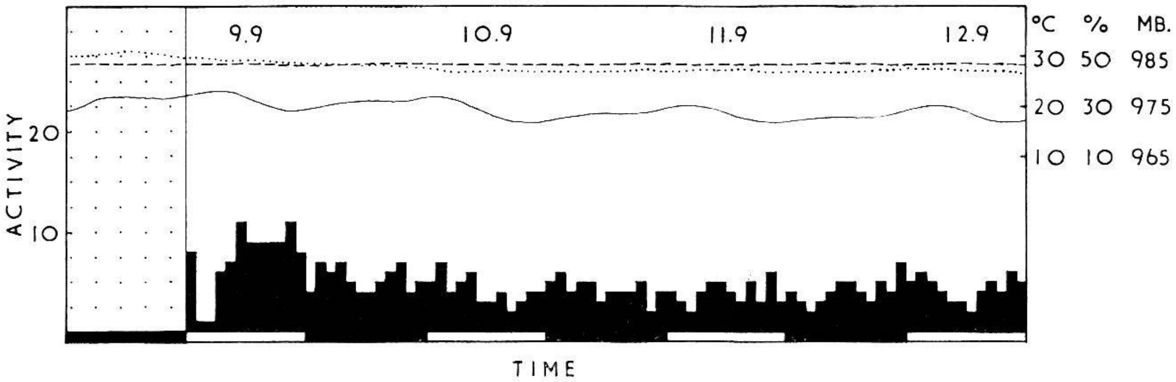

Fig. 12. The locomotory activity of *M. domestica* adults exposed to very dim light for one night, and then to continuous bright light. Conventions as before.

mination, it seemed possible that when the flies were exposed to continuous bright light they would display an endogenous day/night activity rhythm in the same way as they did in continuous dim light. To test this possibility, flies were left in very dim light for their first night in the controlled room, then the bright light was switched on and left on for the remainder of the experiment. As Fig. 12 shows, activity followed the expected two-peaked pattern the first day, but continued at a moderate level throughout the following night and the whole of the remainder of the experiment; during this period activity was no higher by day than by night, and such fluctuations as occurred were small and irregular. Continuous bright illumination thus suppressed expression of the endogenous rhythm.

Activity at low temperatures.

It was shown in Part I that the onset of activity in the morning was delayed by low minimum temperatures. There seemed no question of these temperatures having been too low for activity to be possible, for the temperatures recorded at the time that activity started varied considerably. To test the effect of a moderately low temperature on the endogenous activity rhythm, flies were kept in continuous dim light at a temperature of 20.0°C; activity had previously been found to be delayed by about two hours at this temperature (Fig. 3).

The results of two experiments are shown in Fig. 13, from which it is evident that activity was almost entirely confined to the daytime, that it was low, started late and finished early. The endogenous rhythm, though still present, thus appears to have been inhibited by the low temperature. Supplementary observations showed, however, that higher activity could still be induced during either daytime or night by switching on a bright light.

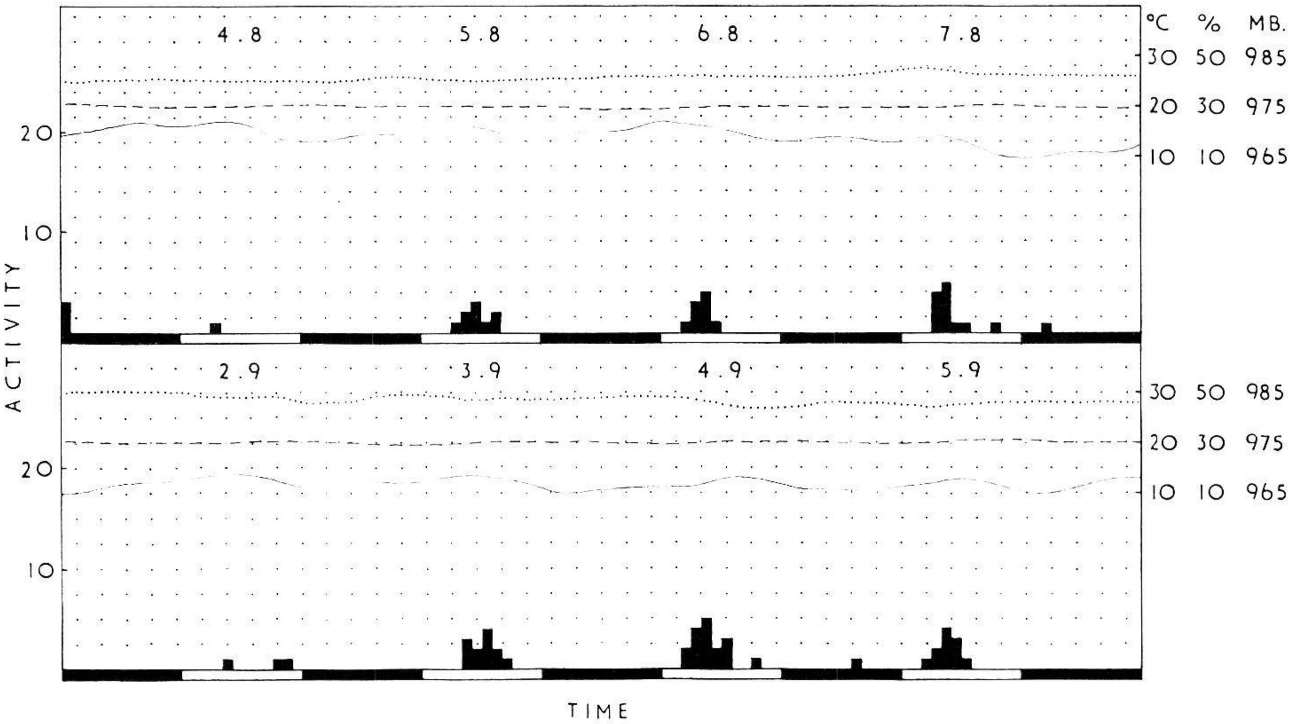

Fig. 13. The locomotory activity of *M. domestica* adults kept continuously in very dim light at a temperature of 20.0°C (two experiments). Conventions as before.

Discussion.

HARKER (1958) defines an endogenous rhythm as one which persists when an environmental condition is held constant, and it is known that this condition can, when fluctuating, affect or determine the form of the rhythm. These characteristics clearly apply to the diurnal rhythm which normally confines the locomotory activity of *Musca domestica* to the hours of daylight, the relevant environmental condition being, of course, light intensity. Similar endogenous rhythms of either diurnal or nocturnal activity have been demonstrated in a variety of other insects (e.g. LUTZ, 1932, *Gryllus;* KALMUS, 1938, on *Dixippus;* GUNN, 1940, on *Blatta;* CLOUDSLEY-THOMPSON, 1960, on *Blaberus*); indeed, such rhythms are considered by BRUCE & PITTENDRIGH (1957) to be the rule rather than the exception in living organisms.

The reversal of the rhythm under conditions of reversed illumination is also a familiar phenomenon, though it is evident that a reversed and persistent rhythm often cannot be established as rapidly as in the present experiments (HARKER, 1958). In this connection it may be noted that ILSE & MULHERKAR (1954) found that the mating activity of *M. domestica* adults which had been kept in darkness during the day and were illuminated at night was confined to the latter period.

The rapid disappearance of the diurnal rhythm in continuous bright light observed in the present investigation also appears to be in conformity with a general tendency, for HARKER (1958), in speaking of diurnal rhythms in general, points out that the rhythm commonly breaks down more rapidly in light than in darkness, and BRUCE & PITTENDRIGH (1957) draw attention to a similar tendency in insects in particular. As with the reversal of the rhythm in reversed light, however, it is evident that the disappearance of the rhythm in constant light often takes place less rapidly than in the present experiments (GUNN, 1940; BENTLEY, GUNN & EWER, 1941; CLOUDSLEY-THOMPSON, 1960).

Yet another feature that appears to be common to diurnal rhythms in general is their essential independence of temperature (BRUCE & PITTENDRIGH, 1957; WEBB & BROWN, 1959; HARKER, 1958, 1961). The present finding that the endogenous rhythm of houseflies was partially suppressed at 20.0°C does not imply any exception to this generalization, for the time of maximum activity was unaltered, and recurred at approximately 24-hour intervals as before.

Regarding the application of the latter results to the earlier finding that, under normal daylight conditions, the onset of activity was delayed by low minimum temperatures, it seems reasonable to suppose that the inhibition of endogenous activity that occurred at low temperatures reduced the responsiveness of the flies to a slight increase in the light intensity. This would explain why they were unresponsive to the first light of dawn, and did not become active until the light was much stronger, though the rising temperature doubtless also helped to initiate activity. That activity did not also cease earlier than usual on cool days is quite understandable because, by late afternoon, temperatures had always risen high enough to be outside the range found to have an inhibitory effect.

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Zusammenfassung.

Es wurde der Einfluß der Tageszeiten auf verschiedene Aktivitäten von wild gefangenen *Musca domestica,* die in Khartum, Sudan, auf einer schattigen Veranda gehalten wurden, untersucht.

Die Bewegung im allgemeinen, die durch direkte Beobachtung und mit Hilfe eines Aktographen verfolgt wurde, beschränkte sich im wesentlichen auf die Tagesstunden. Wurden beide Geschlechter zusammen gehalten, so konnte ein kleiner Höhepunkt der Bewegungsaktivität am Morgen festgestellt werden. Nach einer deutlichen Abnahme erfolgte dann im Laufe des Nachmittags eine zweite, länger andauernde Periode gesteigerter Aktivität. Das Einsetzen der Bewegungsaktivität am Morgen wurde durch niedrige Morgentemperaturen verzögert. Allein gehaltene Männchen zeigten einen ähnlichen Aktivitätsrhythmus, mit der Ausnahme, daß der zweite Höhepunkt mittags nicht unbedingt ausgeprägter war. Die Bewegungsaktivität der allein gehaltenen Weibchen setzte am Morgen später ein und stieg graduell zu einem Maximum im Laufe des Nachmittags.

Wasser- und Nahrungsentzug (verdünnte Milch) verlängerte die Bewegungsaktivität in die Nachtstunden hinein. War Milch ununterbrochen vorhanden, so beschränkte sich die Nahrungsaufnahme ausschließlich auf die Tagesstunden, variierte jedoch während dieser Periode unregelmäßig. Wie die Bewegung im allgemeinen, so wurde auch der Beginn der Nahrungsaufnahme durch niedrige Morgentemperaturen hinausgeschoben.

Die Zahl der Begattungsversuche folgte einem Muster, das dem allgemeinen Bewegungsrhythmus der Männchen sehr ähnlich war, hörte aber immer früher auf als alle andern registrierten Aktivitäten.

Die zeitliche Verteilung der Eiablage war unregelmäßig, doch war sie wie alle andern Tätigkeiten ausschließlich auf die Tagesstunden beschränkt und erfolgte nie am frühen Morgen, wenn die Temperatur tief war.

Das Schlüpfen aus Puppen, die im Freien aus Eiern von wild gefangenen

Fliegen gezüchtet worden waren, war ebenfalls auf die Tagesstunden beschränkt und erreichte einen einzigen Höhepunkt meist kurz vor mittags. Dieser Rhythmus wurde durch niedrige Temperaturen nicht beeinflußt.

Im 2. Teil untersucht der Autor die Aktivitäten der *Musca domestica* unter künstlich kontrollierten Bedingungen. Adulte Fliegen zeigten einen endogenen Rhythmus der Bewegungsaktivität, wenn sie dauernd in einem schwachen dämmrigen Licht bei einer Temperatur von 28,5° C gehalten wurden. Das Muster des Bewegungsrhythmus während der aktiven Phase (Tagesstunden) unterschied sich von demjenigen bei natürlichem Tageslicht darin, daß keine Tendenz zu zwei Höhepunkten gesteigerter Aktivität festgestellt werden konnte. Wurde jedoch während des Tages dauernd helles künstliches Licht verwendet, so folgte die Tätigkeit einem ähnlichen Rhythmus, wie es beim natürlich schwankenden Tageslicht zu beobachten war.

Durch sehr helles künstliches Licht während einer einzigen Nacht und sehr schwaches Licht während des folgenden Tages konnte der Tagesrhythmus umgekehrt werden, und dieser reversierte Rhythmus dauerte bei konstantem schwachem Licht mehrere Tage an.

Bei andauernd heller Beleuchtung zeigten die Fliegen einen dauernd mäßigen Grad von Aktivität, und der tageszeitliche Rhythmus verschwand.

Bei einer Temperatur von 20,0° C wurde der endogene Rhythmus teilweise unterdrückt, aber das Maximum der Tätigkeit erfolgte regelmäßig ungefähr um dieselbe Tageszeit wie bei höheren Temperaturen.

Die Resultate werden diskutiert und mit andern wesentlichen Beobachtungen an *M. domestica* und verwandten Arten verglichen.

Résumé.

On a observé, à divers moments de la journée, les activités de *Musca domestica* capturées en plein air et maintenues sur une véranda ombragée à Khartoum (Soudan).

Le mouvement en général, suivi de visu et au moyen d'un actographe, se limitait principalement aux heures de la journée. Lorsque les deux sexes étaient mélangés, on pouvait constater une petite hausse de l'activité motrice le matin. Puis, après une nette diminution, suivait, dans le courant de l'après-midi, une seconde période d'activité motrice plus élevée et plus longue. De basses températures matinales retardaient le début de la période active. Des mâles seuls avaient un rythme d'activité semblable, excepté que la hausse d'activité de l'après-midi n'était pas forcément plus élevée que celle du matin. L'activité des femelles seules se manifestait plus tardivement le matin et augmentait graduellement jusqu'à un maximum au cours de l'après-midi.

Lorsqu'on supprimait l'eau et la nourriture (lait délayé), l'activité motrice se prolongeait jusqu'en pleine nuit. Lorsque le lait était continuellement disponible, l'activité nutritive se limitait aux heures du jour tout en variant d'intensité. Ainsi que le mouvement en général, la nutrition était aussi retardée par des températures matinales basses.

Le nombre des accouplements variait généralement dans la même mesure que le rythme d'activité motrice des mâles, mais cessait toutefois plus tôt que toutes les autres activités déjà enregistrées.

La ponte des œufs se produisait irrégulièrement, cependant exclusivement de jour et jamais tôt le matin, lorsque la température était basse.

C'est aussi de jour qu'avait lieu l'éclosion des pupes provenant d'œufs de mouches capturées dans la nature. L'éclosion n'atteignait qu'un seul point culminant, en général peu avant midi. Ce rythme n'était pas influencé par de basses températures.

Dans la deuxième partie, on observe les activités de *Musca domestica* adultes, soumises à des conditions artificielles. Maintenues dans une faible lumière à une température de 28,5° C., les mouches adultes montraient une activité motrice endogène. Le rythme d'activité, observé dans les conditions décrites plus haut, pendant la phase active (de jour), différait de celui constaté à la lumière naturelle en ceci, qu'il ne se produisait pas les deux hausses sensibles de l'activité pendant la journée. Pourtant, si l'on maintenait une forte lumière artificielle pendant toute la journée, l'activité des mouches suivait le même rythme que celui soumis aux fluctuations naturelles de la lumière du jour.

En maintenant la forte lumière artificielle durant une seule nuit et une très faible lumière le jour suivant, on a pu renverser le rythme diurne et conserver ce même rythme plusieurs jours dans une lumière faible constante.

Un fort éclairage continu provoquait un abaissement de l'activité des mouches à un degré qui restait constant ainsi que la disparition du rythme diurne.

Le rythme endogène était en partie supprimé à une température de 20° C., mais l'activité atteignait régulièrement son maximum environ aux mêmes heures qu'à une température plus élevée.

Les résultats obtenus font l'objet d'une discussion et d'une comparaison avec d'autres observations sur *M. domestica* et sur des espèces voisines.