

THE DIEL ACTIVITY RHYTHM OF
MICROTUS PENNSYLVANICUS PENNSYLVANICUS ORD

AN INVESTIGATION OF THE DIEL ACTIVITY RHYTHM
OF
MICROTUS PENNSYLVANICUS PENNSYLVANICUS ORD

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A Thesis
Submitted to the Faculty of Arts and Science
as a Requirement for the Degree
Master of Science

McMaster University

1955

The author of this thesis holds the following
degree:

Bachelor of Science with Honours,
School of Zoology,
University of Birmingham, 1952.

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PREFACE

The research presented in this thesis concerns the diel activity rhythm of the meadow vole, Microtus pennsylvanicus pennsylvanicus Ord, as shown under laboratory conditions. In the course of the investigations a general survey was made of rhythmic behaviour in the animal kingdom.

Part of this research has been made possible by a grant from the National Research Council under the administration of Dr. Kleerekoper and by a Studentship from the same organization.

I am indebted to Mr. D. Delzell for his help in trapping and identifying Microtus, to Mr. W. Brouwer for his technical assistance and to Dr. Herman Kleerekoper under whose guidance the research was carried out.

INTRODUCTION

The basic rhythmicity of a number of natural phenomena has been known though not understood for a long time; primitive man was aware that connected with seasonal, lunar and diel^{*} variations in climate, there were changes in animal behaviour such as migration, breeding and sleep. However, the approach if any to the reason why such periodicity occurred was either extremely teleological or mystical.

Aristotle recorded that some animals were active at night and others in the day time, and an early account of the rhythmic flashing of fireflies occurs in 1727 (Kaempfer); however, apart from such purely descriptive works, little was written on the subject before 1900. Since then there has been an increasing amount of attention given to the existence of rhythm in life processes and to the analysis of possible causative factors; the formation of an International Society for the Study of Biological Rhythms in 1935 which met twice before the war and twice since (Kalmus, 1953), shows the importance attached to the subject in recent years.

The author's problem is concerned with diel periodicity, however, it is considered that a brief review of related phenomena is called for; this is presented - together with a survey of

* For definition of terms, see Glossary.

diel rhythmicity - in two parts, the first, a short outline of the various rhythms and the second, a survey of relevant literature.

1. Cosmic rhythms

On a cosmic scale the suncycles, of which the magnetic thirty-five (Bruckner) and twenty-five year cycles and the eleven year sunspot cycle are the most clearly defined, are claimed to have a definite biotic significance (Allée, Emerson, Park, Park and Schaidt, 1949) particularly on population cycles (Mori, 1945; Rowan, 1954) but some doubts have been cast on the validity of the statistics involved (Cole, 1951).

On a smaller scale, seasonal, lunar and diel rhythms occur frequently in the animal kingdom; these would seem to be based purely on physical variations such as light intensity but experiments have shown that in some cases, particularly of diel activity, the rhythmic variation will persist for some time under constant conditions. This would suggest that the rhythm is endogenous but in phase with favorable external conditions.

2. Seasonal periodicity

Seasonal periodicity is expressed in the reproductive, hibernation and migratory cycles.

The breeding season of wild non-primate mammals is usually constant for the species, and its regular recurrence

is a good example of the balance between internal physiological rhythm and external physical stimulus. In the middle of the nineteenth century, the effect of the testes in promoting and maintaining secondary sexual characters was demonstrated, starting the work on hormones and their influence on animal behaviour (Berthold and Claude Bernard in Rolleston, 1936). Bird fanciers in ancient Japan knew that a gradual increase in daily light in November induced birds to sing in the winter (Mizaki, 1934), and in 1802 in Spain, that maintaining summer length days in winter would induce hens to continue egg laying; however, the first experiments on the effect of change in day length on sexual development were much more recent (Rowan, 1925).

Migration is "A more or less continuous and direct movement, under the control of the animal, coordinated with or controlled by periodic environmental influences, from one locality to another, in which there is a periodic return to the original locality" (Allee, Emerson, Park, Park and Schmidt, 1949).

Hibernation - the passage of an unfavorable (cold) season in a state of torpor involving considerably reduced metabolism - is a phenomenon found among representatives of a number of groups of animals, in particular those incapable of accurate temperature regulation, (poikilotherms) and some herbivorous mammals.

3. Lunar rhythms

As far as is known the lunar rhythms affect only marine and estuarine populations. Tidal variation radically affects the oxygen supply, reproduction and movement of the littoral fauna, some members of which are only covered at the highest tides, and others only uncovered at the lowest. In deeper waters, currents and eddies are set up the effect of which on animals is not fully understood. As might be expected, animal behaviour associated with the mathematically predictable moon and tides is likewise very regular.

4. Diel rhythms

With the exception of the truly social animals such as ants and man, and certain animals in arhythmic environments such as the cave crayfish, animals show a marked rhythm of activity associated with the diel change in light intensity (Welsh, 1938; Park, 1940; Park, Roberts and Harris, 1941). In some cases this appears to be endogenous as in members of the Crustacea, Insecta and the vertebrates, and in others exogenous; among mammals a completely functioning cerebral cortex seems to be necessary since decorticated dogs and cats are arrhythmic (Galhoun, 1946).

Also included under this heading is the pupation rhythm of some insects which continue to emerge at a certain hour for several generations under constant conditions (Kalmus, 1938).

The historical and experimental work on biological

rhythms is reviewed in the next chapter.

LITERATURE SURVEY

A comprehensive review of the vast literature on climatic seasonal and lunar cycles is not considered necessary in this context, the survey of these topics is intended solely to indicate the effect of certain physical factors on animal behaviour.

1. The effect of climate on animal populations

The importance of the green plant as an initial food source for all animals has only in recent years been fully appreciated, any physical factors affecting the flora or any section of the fauna is bound to change the food supply of other sections of the population. However, to what extent climatic change and possibly associated population fluctuation can be said to be rhythmic or cyclic in occurrence is open to discussion. The following is a brief review of relevant literature.

As early as 1727 the effect of the alteration of day length on plant growth was noted (Trew in Davenport, 1927); this was interpreted to be a result of a change in temperature (Linnaeus, 1739 in Smith, 1933). The effect of plant growth on insect populations was shown (Robertson, 1899), and later, it was reported that the relative length of day affected plant growth which in turn determined the abundance of herbivores and

their parasites and predators; thus a season favoring plant growth also favored the dependent fauna (Garner and Allard, 1920). Cyclic changes in the population of Canadian lynx (Elton, 1942) and rodents (Shelford, 1929) have been associated with climatic and sunspot cycles.

2. Seasonal periodicity

Animal behaviour associated with seasonal periodicity is shown in reproduction, migration and hibernation. Evidence points to change in length of day and an associated increase in activity as the prime physical factor involved in the first two instances, and to generally unfavorable conditions in the third, the survey of the literature is limited to a review of a few outstanding articles.

Breeding. If transferred from one hemisphere to the other so that the physical seasons are reversed, some animals, (sheep) become immediately adapted with respect to breeding season, others take longer and some, for example the budgerigar, continue to breed indefinitely in the same calendar month as before (Baker and Ranson, 1938; Marshall, 1936; 1942, and Rowan, 1938).

When subjected to gradually increasing artificial light in November, some birds - *Junco hyemalis* (Rowan, 1925; 1929; Bissonette, 1950; 1951), *Fasser domesticus* (Hirschbaum and Ringoan, 1956), ducks (Benoit, 1935; 1938; Benoit and Ott,

1944; and Parkman and Coban, 1935) - show precocious development of the testes. A similar occurrence was shown in the ferret and it was also demonstrated that a reduction in light led to regression in sexual activity (Bissonette, 1932; 1935). These results were repeated with Microtus agrestis (Paker and Ranson, 1932), and with Peromyscus leucopus noveboracensis (Whittaker, 1936).

The immediate stimulus for gland development in birds was thought to be increased activity resulting from the longer photo-period. This was tested by placing birds in a cage with a bar moving along the perch disturbing the birds at regular intervals; the light was just sufficient to make the bar visible. It was found that the testes of birds subjected to this enforced activity were as developed as those in increased light and larger than the controls (Rowan, 1931). In ducks and ferrets it was found that light alone seemed to be the causative factor (Bissonette, 1931; 1936). Breaking the photo-period into nine periods of one and a half hours each had the greatest effect, suggesting that the early part of the photo-period was the most effective (Farner, Mewalt and Irving, 1953).

Hibernation seems to be linked with physiologically inaccessible water, lack of fresh food and the onset of cooler weather (Johnson, 1931). This has been denied on the grounds that some animals start to prepare for hibernation before these factors become apparent (Morgan, 1939); work on arthropods and

other cryptozoa suggests however, that the primary stimulus for hibernation is the onset of unfavorable weather conditions (Holmquist, 1926; Park, 1930; Cole, 1946).

Migration in birds was attributed to a "longing for light" (Runeberg, 1874, in Allee, Emerson, Park, Park and Schmidt, 1949). Rather surprisingly a connection between sexual development and migration was discovered; crows made sexually active in December (by artificial illumination) and released, were found to fly north from their northern territory in the direction normally taken in the spring by birds flying north from their southern territory (Rowan, 1951). Certain birds show very little variation in the arrival date in the spring migration, always appearing within two or three days of the average date, but others are affected by temperature difference (Leopold and Jones, 1947). Migrating adult salmon swim upstream in the light during the breeding season, and the young fry swim downstream in the dark; since this may happen concurrently it appears that identical physical conditions have different effects on different developmental stages (Mleitman, 1949). The fall migration of deer is initiated by a heavy snowfall, the spring migration by the resumption of plant growth; migration may be prevented by a year round supply of food (Allee, Emerson, Park, Park and Schmidt, 1949).

3. Lunar periodicity

The phenomenon of lunar rhythms in animals, particularly those not in the littoral zone is one that has aroused a great deal of interest and speculation. Metabolic and behavioural rhythms associated with diel tidal variation in the littoral zone are comprehensible, but the factors involved in behaviour associated with fortnightly and monthly rhythms especially when in deeper waters, in the rigid fashion shown below in the nereids, is less easy to understand.

The swarming of the nereid Leodice fucata is associated with the third quarter of the June-July moon (Mayer, 1908); the Bermuda fireworm, another famous example, "swarm on the second, third and fourth nights after the full moon, they appear at the surface on these days, 55 minutes after sunset throughout the year, whether the sky is overcast or clear, whether winter or summer" (Harvey, 1940 after Mark).

The grunion, Leuresthes tenuis breeds at high water-mark on the second, third and fourth nights after the spring tide. The eggs therefore are not covered until the next high tide two weeks later which washes the eggs from the sand, after which they hatch (Thompson and Thompson, 1913).

Various activities of the littoral fauna are associated with the twelve and a half hour daily tidal rhythm. Special attention has been paid to these in the last three years. Uca pugnax was found to have metabolic cycles associated with both tidal and diel rhythms showing a peak where the two coincided;

the tidal rhythm showed a maximum oxygen consumption at low tide and the diel rhythm, between 6.00 am and 10.00 pm (Brown, Bennett and Webb, 1953).

A chromatophore contraction rhythm as shown in autotomised legs of crabs was found to be associated with the tidal rhythm of the place of capture (Hines, 1953). In the clam, Venus mercenaria diel and tidal activity rhythms were found which showed a peak where the two coincided. The rhythm was speeded up by reversed illumination (Bennett, 1954). Activity rhythms in Mytilus were maintained in constant darkness; the rhythm remained in phase with the tide in the place where the mussel was caught so that specimens from different areas had different rhythms. The rhythm could be changed by subjecting the animal to a different time of tide, i.e. by moving down the coast. Specimens never uncovered by the tide, for example, those on the under side of floats, even showed rhythmic activity (Rao, 1954). Similarly activity rhythms found in the oyster were associated with diel, tidal and spring tidal periodicities (Brown, 1954).

4. Diel periodicity

The information concerning diel rhythms in the animal kingdom is complex and varied, the literature is extensive and covers many examples which point to the influence of a number of different determining factors. The following survey has

been confined largely to rhythmic activity of the individual, but there is some reference to metabolic rhythms as an indication of internal physiological periodicity. With the exception of that referring to the plankton the literature is presented here grouped under phyla.

Plankton

Most plankton organisms migrate away from the surface of the water during the day and towards it during the night (Allee, Emerson, Park, Park and Schmidt, 1949). This diel migration of pelagic marine plankton has been called the "best example of a whole community showing rhythmic activity" (Russell, 1927).

When kept in cylinders under constant dark conditions the plankton maintained the rhythm of migration to the surface at night and the deeper water at dawn for two days before dying (Esterly, 1917); the experiment has not been repeated successfully (Welsh, 1933). A record of the Crustacea in Lake Lucerne shows that the population begins to descend at dawn reaching a maximal depth of five to six metres at noon, and at dusk moves slowly upwards (Northington, 1931). The control of migration in marine plankton has been attributed to changes in "submarine irradiation" (Clarke, 1933).

Coelenterata

Rhythmic activity in the coelenterates has been found in Actinozoa species which show a diel contraction rhythm

when parasitised by Zooxanthella; individuals not parasitised show random contraction throughout day and night (Mori, 1943A). The anthozoan Cavernularia chesa valenciennes shows a persistent activity rhythm under constant dark conditions; exposure to reversed illumination reverses the rhythm after a while. An eighteen hour day was easily established but not one of twelve hours (Mori, 1943B).

Nematoda

Little investigation has been done into rhythmic activity in this phylum. The records mentioned were made in the medical investigation of the worms. The filarial parasite Wuchereria bancrofti migrated to the peripheral blood stream at night (Manson, 1897). This was later confirmed in patients leading a normal life, but when active at night and at rest in the day the migration was found to occur in the day time (Carmichael, Low and Manson-Bahr, 1933).

Mollusca

A study of 400 periwinkles (Littorina littorea) showed that oxygen consumption was at a minimum between 2.00 and 3.00 am and at 2.00 pm and at a maximum between 8.00 and 9.00 pm and at 10.00 pm (Sandeens, Stephen and Brown, 1955).

Arthropoda

The investigation of rhythmic activity in four species of millipede showed that they were stimulated by fluctuations in temperature; light had little effect, but constant tempera-

ture had a depressing influence (Cloudsley-Thompson, 1951). The same author also investigated the activity of certain woodlice and the cockroach Periplaneta americana (1952; 1953).

Rhythmic migration of chromatophores has been demonstrated in the iris, retina and general body colour of several arthropods. Considerable work has been done on this, the evidence points to a hormonal control of the migration, but the factors controlling the actual rhythm are not fully understood.

The first investigation of pigment migration in arthropods was made with the moth Plusia gamma, it was found that the rhythm of pigment movement in the iris would continue for several weeks in constant dark conditions (Kiesel, 1904). It was later suggested that although no nervous connections with the chromatophores could be seen, the general nerve tonus controlled the movement since narcosis and death caused maximum contraction (Demoll, 1911).

The hormonal control of chromatophores in Crustacea was demonstrated by two workers in 1923 (Perkins; Holler); later it was shown that injections of extracts of the eyestalk of various crustaceans into Palaeomonetes brought about the migration of pigment in the retina (Kleinholz, 1954; 1955). The control of the movement by a rhythmic secretion of hormone or a cycle of nervous and general metabolic activity was postulated (Welsh, 1936). The same author also found that in the retina of the crayfish the migration rhythm continued for five months

in constant dark conditions at 7°C; at 21°C, the rhythm disappeared after four months (Welsh, 1936).

General colour change in Hippolyte varians was observed and the animal found to assume a different colour at night to that of the day when under constant conditions (Gamble and Hebble, 1930). This was not confirmed later (Kleinholz and Welsh, 1937), however, a persistent diel colour change was observed in an isopod, Iodothea. The rhythmic change was found to persist for 60 days in the dark; reversal of diel light and dark caused reversal of the rhythm, which was then maintained in constant dark conditions (Hanke, 1911).

The removal of the eyes and eyestalks of crustaceans was found to prevent the periodic colour change (Megusar, 1912); this was explained to some extent by the work of Perkins and Koller (see above), but it was not until some time later that the gland that produced the hormone was discovered (Hanstrom, 1937). In the same year other workers made extracts from the eyestalks of Ligia baudiniana at various times of the day and injected them into specimens which had been kept in the dark. They found the chromatophore response to be the same for all injections suggesting that the eyestalk hormone production was not cyclic (Kleinholz, 1937). However, in Palaeonetes more chromatophore hormone was obtained from the light adapted animal than from one kept in the dark (Abramowitz in Welsh, 1938), this confirmed the earlier work of Kleinholz (see above). It

would seem therefore that in some species hormone production is cyclic in part at least, while in others, other factors are involved.

Drosophila species have been investigated by various people with regard to pupation rhythm; a rhythmicity in the emergence of Drosophila from its puparium was noted which was maintained in constant dark conditions (Premer, 1936). Later it was found that entirely dark conditions made emergence arrhythmic but that exposure to light for a period of two to four hours was sufficient to initiate the rhythm. Exposure to dark for such a short time had no effect, but a longer period was sufficient to determine the rhythm in otherwise constantly light conditions (Bunning, 1935). Reversed light and dark caused the rhythm to be out of phase by twelve hours (Bunning, 1935), evacuation to 15mm. for eight hours caused an eight hour delay in emergence (Malmus, 1935; 1936). Warmth speeded up the emergence, and cold delayed it (Bunning, 1935).

Similar work was done with Anastrepha indana (Darby, 1933) and the dung fly (Lewis and Bletcherley, 1945).

Drosophila species in Brazil showed a variation in diel activity in accordance with the weather conditions. On clear, warm, dry days they were active in the morning and just before sunset, in humid forests and on rainy days there were active throughout the day; apparently no species were active at night. The Brazilian species showed more plastic behaviour

than those in the south-eastern United States, particularly Drosophila pseudobscura (Dobzanski and Burla, 1950).

The beetle Ptinus tectus was found to be arrhythmic when reared under constant conditions but when raised under normal diel changes in illumination became active at night with a maximum at dusk and a small peak at dawn. Continuous light upset the rhythm and reversed lighting reversed it after three weeks. If raised in constant light but with the temperature varying in a rhythmic fashion the beetles became active in the falling phase (Pentley and Gunn, 1941). Species of Blatta were active only at night and were inhibited by illumination of six foot-candles or more. Darkening of the room during the day time did not cause emergence unless the night was illuminated (Mellanby, 1940).

Chordata

Most of the work on diel activity has been done with the vertebrates, and particularly, small mammals, the literature dealing with the latter is reviewed chronologically, in some detail; while being mainly concerned with the rhythmic activity of the whole animal, some mention has been made of internal diel rhythmicity as an indication of its existence.

Various fresh water fish, (Cyprinus carpio and Umbra limi) were found to be active at night, and others, (Epiplatys gibbosus and Sarassinus auratus) in the day. In both groups, feeding was followed by one to two hours intense activity, both

were affected by a change in light intensity (Spencer, 1939). Working with salmon and eels in an artificial tank, it was recorded that salmon swim in the day time against the stream, while eels swim with the stream at night (Davidson, 1949).

In the class Reptilia lizards were observed to be active at noon with, in general, a rise of temperature leading to a rise in activity (Marx and Kayser, 1949). The lizard Anolis carolinensis showed a rhythmic pigment migration from green in the day time to dark at night, which persisted under constant dark conditions but not in constant light nor when the hypophysis had been removed (Rosendale and Rahm, 1941).

It is commonly known that the majority of birds are active in the day, particularly at dawn, the following survey indicates however that migratory species show a variable distribution of activity at different seasons. The non-migratory English sparrow Passer domesticus was found to have a peak of activity when the light was turned on in the morning, however early, this was followed by a decline with a second peak of varying size in the evening. Extreme cold reduced the overall activity which was then spread fairly evenly throughout the day, very warm temperatures (52°C) led to a rest period at noon. There was no nocturnal activity; during a period of continuous light, most of the activity was confined to the normal solar day time, but there was no prolonged rest period.

The white crowned sparrow Zonotrichia leucophrys, a

migratory bird, had the major part of its activity including frequent singing, during the night; this was particularly marked during the spring and fall migratory seasons. In the white throated sparrow Z. albicollis activity was mostly in the day, with some nocturnal unrest possibly associated with the spring and fall migration; very high (31°C) and very low (15°C) temperatures led to a decrease in total activity. The slate-coloured junco had two peaks of activity, one when the light came on in the morning, and the other, just before it went off. Birds captured in April showed nocturnal unrest associated with spring migration. It was suggested that the amount of nocturnal activity was indicative of the migratory urge (Nycter, 1954).

The author could find no reference to work on mammalian activity prior to 1900, early work was done with the white rat which was observed to have an activity peak at night (Slonaker, 1907). It was not until some years later that the persistence of the rhythm under constant conditions of illumination, and the effect on it of pregnancy, castration and other physiological changes was investigated (Szymanski, 1918; Richter, 1927).

Experiments on the activity of the white rat indicated a one to two hour rhythmicity with feeding usually occurring at the height of the activity period (Richter, 1922). In man, a two hour contraction rhythm during a fast had been detected (Martin and Rogers, 1927), and it was suggested that the hunger pains so caused were the stimulus for activity, i.e. general

activity is dependent on rhythmic contraction of the stomach which is in its turn dependent on an internal physiological rhythm (Wada, 1922).

Investigation of the occurrence of rhythmicity in very young mammals showed that the new born rat was arrhythmic but that rhythm developed gradually up to 16 days of age. On the other hand the rabbit and kitten were rhythmically active on the first day suggesting that rhythmicity was innate but was not apparent before a certain developmental stage (Richter, 1927).

Work with female rats showed that activity increased fairly sharply at puberty (Wang, 1923), and developed a four-day cycle with a peak at oestrous; pregnancy caused an abrupt drop in activity that lasted until the litter was weaned, pseudo pregnancy a drop of 15 days. Removal of the ovaries caused a drop in activity that was reversed by injections of oestrogen (Wang, 1923; Slonaker, 1924; Richter, 1927).

Activity in the male rat did not show a four day rhythm and was not as great as the overall activity of the female; castration leads to a drop in activity. In either sex, the removal of both adrenals caused a drop (Richter, 1927).

Other rhythms detected in the rat were a two and a half hour thirst rhythm, a five hour defaecation and a two hour urination rhythm. Evidence was also given for five to eight day rhythms in spayed and castrated rats, a normal 29 day cycle and a 90-100 day cycle (Richter, 1927), however, the validity

of statistics related to longer cycles in general has been questioned (Cole, 1951).

The white footed and Canadian deer mice, were observed to be active from just after dusk until dawn, experiments run both in the laboratory and in a cage set in the woods showed that the rhythm was not affected by laboratory conditions. The rhythm was maintained for seven months in total darkness, though it gradually became out of step with solar day; young born under these conditions showed the parental rhythm. On reversing the light and dark periods the mice eventually reversed their rhythm, but attempts to establish a 16 hour day were unsuccessful (Johnson, 1926). The same author concluded that rhythmic activity was not dependent on light but was influenced by it. Later work again showed Peromyscus leucopus noveboracensis to be nocturnal but that it would be active in the day if there was snow in which to burrow or if it were starving (Belney, 1936). Work on the British field vole Microtus agrestis showed the vole more active at night than in the day with a distinct two to four hour feeding rhythm, the rhythm persisted for 24 days in the dark (Davis, 1933).

Investigation of some internal rhythms showed a diel rhythmicity in the deposition of enamel and dentine in the teeth of rats (Schour and Steadman, 1935), and in the metabolic rate as shown by oxygen consumption in rats and men; during a 36 hour fast there was an initial high level which dropped to a

maximum low at 16 hours rising again up to 24 hours after which there was considerable fluctuation (Werthesen, 1936). The mitosis rate in rats was found to be greatest at 8.30 pm and lowest at noon (Carlton, 1934), and a daily rhythm was recorded in the erythrocyte haemoglobin content (Johres, 1937). Geritzen (Kleitman, 1949), spent seventy-four hours in bed taking the same nourishment every hour and found urinary excretion to have a peak in the afternoon, the author concluded that the liver and kidney are rhythmic in function.

Variation in the ability to maintain an activity rhythm was demonstrated with two bats, Myotis species and Pipistrella species, it was found that Myotis maintained its rhythm of activity (for two or three hours after sunset) for the duration of the experiment (four days). Pipistrella on the other hand developed a rhythm related to the feeding time which was constant (Griffin, 1937).

A series of experiments on the effect of light and temperature on the white rat indicated that it was possible to reverse the activity rhythm by reversed light and dark and that in continuous dark, the rhythm shown at the outset, whether normal or reversed, was the one maintained; continuous light tended to make the oestrous period longer. Blinding by removal of the lenses, closure and severance of the optic nerve had no effect on the activity, nor did auditory and temperature stimuli, excess of vitamins or pituitary extract (Browman, 1937).

However, in a blinded rat, the rhythm was reversed by temperature change indicating that this has an effect which is normally masked (Browman, 1943). Later, the same author, using rats that had been closely inbred for twenty-five generations, succeeded in establishing a 16 hour rhythm by alternating eight hours light and warm environment with eight hours dark and cool; the rats showed activity peaks in the dark period that were not affected by feeding time, which was constant, nor by the solar day (Browman, 1952).

Records of trapping and experimental investigations of the activity of Microtus californicus showed the greatest activity at night (Hatfield, 1938), the same author records that Grinnell in 1908 claimed that the mice were more active in the day time and suggests that this may have been the result of very cold weather in the district at the time which would make the day more suitable. Later, working with Microtus pennsylvanicus pennsylvanicus and Peromyscus leucopus noveboracensis, a two hour food seeking rhythm was detected at temperatures between 9 and 28°C; above 30°C the mice were active all the time (Hatfield, 1940). Trapping records for Microtus p. pennsylvanicus show the greater number trapped and therefore presumably active, just after dawn and before dusk, it was suggested that the activity of predators had some part in determining this (Hamilton, 1937).

The effect of constant light of a moderate intensity

on Peromyscus species was to delay the activity period a little each night, continuous bright light disrupted the activity pattern completely; the presence of nesting material lessened the disruption appreciably (Johnson, 1939). The activity of Microtus ochragaster was found to be mostly between 6.00 pm and midnight, feeding was arrhythmic; in continuous dark the peak moved to between 9.00 pm and 1.00 am. The rhythm was broken after 20 days in continuous light but exposure to light and dark for one day was sufficient to restore it; attempts made to get a 48 hour rhythm were partly successful but the 24 hour rhythm predominated. High temperature and light intensity partially inhibited activity; the young of the species tended to be arrhythmic (Calhoun, 1945).

In Peromyscus, shortage of food lead to an increase in activity (Stinson, 1952). The same genus was called "typically nocturnal" since it has a pure rod retina adapted to night vision and since its activity was inhibited by bright moonlight. Heavy rains increased the number caught in traps, probably as a result of their taking shelter; activity was reduced by strong winds, and was less - though spread over a longer period - in the winter than in the warmer weather (Falls, 1953). The same author suggested that Microtus could be active at all times during the day because it burrowed and had covered runways.

Summary

The evidence presented in the literature points to the existence of two sets of factors controlling rhythmic activity in animals, which are present to different extents in different species. These factors are: the physical influences, of which the most important are light (whether expressed as intensity of illumination or length of day) and lunar phase, and the physiological influences, whether hormonal, nervous or metabolic.

The relative importance of these sets of factors varies from species to species, at the one extreme animals with an exogenous activity rhythm will be completely governed by physical stimuli, and at the other, those with an endogenous rhythm will be unaffected by all external variations. In most cases the balance lies somewhere in between.

In summarising the literature survey the relative importance of the physical and physiological factors involved is discussed.

Light

By far the most important physical stimulus to terrestrial and limnic populations is light. The activity rhythm of many animals is in time with solar day and although in most cases the rhythm will continue in a constantly dark environment (nocturnal and crepuscular animals) or in a constantly light

environment (diurnal animals), the physical stimulus of bright light, even moon light, or darkness, will frequently inhibit the activity of animals not normally active under those conditions. Furthermore, a reversal of diel light and dark will, after an initial disruption, cause a reversal of the activity pattern. However except in closely inbred strains it has been found possible to change the activity pattern only within the twenty-four hour rhythm, attempts to get a forty-eight or sixteen hour periodicity have failed. This suggests that there is a basic physiological or innate rhythmic tendency which can only be lost by inbreeding and which is capable of maintaining itself under constant physical conditions but which is kept "in time" by physical stimuli.

The effect of varying length in the illumination period is reflected in the work on migration and reproduction. Whether the factor affecting gonad development is increased light or the resulting increased activity has not been decided. In either case, the susceptibility of the rhythm to change varies from species to species and also according to the physical state of the animal. Complete lack of light has not been shown to inhibit sexual development entirely.

Lunar Phase

The effect of change in lunar phase and hence in tides and currents on the marine fauna is little understood. In the

littoral zone, activity and metabolic rhythms have been found in a variety of molluses and crustaceans; analysis shows that these rhythms will maintain themselves in still water but will change rapidly to coincide with a different time of tide.

Work on the reproductive rhythms of nereids has been confined to observations of the natural phenomenon of which as yet little is known.

Temperature

Daily temperature variation has been shown to be the controlling stimulus for activity rhythms in certain millepedes but otherwise seems to be of little importance under natural conditions. However, various workers have shown that in the absence of any change in illumination, a normal diel activity rhythm may be reversed by an appropriate temperature variation.

Humidity

A combination of warmth and high humidity on the one hand and coldness and low humidity on the other has been shown to affect the activity pattern of Drosophila species, but there is no evidence of other classes of animal being influenced.

Hormones

The possibility of the existence of an hormonal control of rhythmic activity has been investigated by several workers

in various animals. The most striking result was found in the female rat which has a distinct four-day activity rhythm associated with oestrous, the effect of oestrogen on the activity of male and spayed animals is to raise the general level; both factors point to oestrogen as a strong activity stimulant. Investigations of the hormonal control of chromatophore contraction in crustaceans have pointed to considerable variation between species, in Palaemonetes the hormonal production itself seemed to be rhythmic but in Ligia it appeared that other factors were involved. Work with other hormones has shown that pituitary extracts have no effect on rat activity, but that removal of both adrenals causes an abrupt drop in the general level.

Other Physiological Factors

The facts that in most cases a rhythm of activity will continue under constant conditions, that in young animals, rhythmicity appears either at birth or later according to the developmental stage and that inbreeding renders the rhythm more susceptible to change suggest an inherent physiological basis for such activity. Various metabolic rhythms have been detected, for example, in mitosis, blood sugar level and urinary excretion, however it is probable that these are secondary to the diel activity rhythm and dependent on the same basic factor.

Origin of rhythmicity

Where the rhythmic recurrence of a phase of activity or behaviour exists it is usually of an adaptive nature. Breeding seasons are such that the young are usually born at a favorable time of the year, migration would appear to be adapted to climatic change, and it has been suggested that diel activity rhythms are determined in part by predators. The adaptive theory receives further support from the fact that animals in arrhythmic environments do not show rhythmicity. Such secondary adaptations as colour vision in diurnal animals or a good sense of smell or emission and perception of high frequency signals in nocturnal animals would arise in the course of normal selection processes; similarly selection might favour a coordination between the general metabolic processes and behavioural rhythms. It is therefore suggested that the rhythmic activity pattern of an animal is innate and was formed during the processes of adaptation and selection in the course of the evolution of the species.

Conclusion

In conclusion, it may be said that rhythmicity appears to be widespread in the animal kingdom and is expressed in various ways. The evidence points to the existence of a basic physiological rhythm, present to different extents in different

animals, which is in phase with and to some extent, regulated by certain physical conditions but which cannot be entirely abolished by experimental procedures.

EXPERIMENTAL WORK

The experimental work presented in the following pages was concerned with the diel variations in activity of the field mouse Microtus pennsylvanicus pennsylvanicus Ord. The aspects investigated were:

- (1) Whether there was a rhythmic pattern of activity.
- (2) Whether the nocturnal and diurnal activity were significantly different.
- (3) Whether there was any marked correlation between activity peaks and time of day.

All the investigations were made with mice caught in the field and kept in an experimental cage in the laboratory.

Materials and methods

One of the chief difficulties which arose in the experimental work was catching and keeping the mice. Live traps of a modified Sherman type were set in runways in damp meadowland near the University, along the railway embankment running parallel to highway 102, and in fields along Sulphur Springs Road, Ancaster, all in Wentworth County, Ontario. Few mice were caught at any time and only rarely were any large specimens found; weights varied between 20 and 50 grams. The identity of the mice was confirmed by Mr. D. Belzell of McMaster University.

In the laboratory it was found that mice either died within a few days of capture or lived a long time; the longest survival period for any mouse was six months. On two occasions mice were kept in a large glass tank for observation and were noticed to be much healthier than those in the smaller cages. Initially the mice were fed on a diet recommended by Hatfield (1940) without the hemp seed which was unattainable, however a lot of the grain was left uneaten. The normal rat diet of rolled oats, codliver oil, wheat germ and salt supplemented by fresh grass, milk, corn and carrots was later found to be quite adequate for the purposes of this investigation. Three pregnant females were caught but the young did not survive, attempts at mating animals in the laboratory were unsuccessful.

Apparatus

Previous workers have used either an activity wheel (Richter, 1927) when recording daily variations in activity, or a cage suspended from springs or resting on tumbours with a pointer adjusted to write on a kymograph (Richter, 1927; Davis, 1933) when recording diel variations in activity. More elaborate cages designed to test other aspects of activity have also been used (Richter, 1927; Rayrs, 1954). The activity wheel is not suitable for measuring activity within the 24 hour period, the suspended cage is subject to lateral movement

and is necessarily rather small; it was therefore decided to design a new type of activity cage.

1. Activity cage

In designing a suitable activity cage the aim was to allow greater freedom of movement than in the average laboratory cage and at the same time to have a sensitive method for detecting the activity of the mouse.

The cage (Fig. 1 and 2 a) consisted of four walls and a separate floor; the cage was suspended over the floor so that there was a two millimetre gap (Z) between the two and free vibration of the floor was possible. The cage was three feet long by one and a half feet wide by nine inches deep. The walls were made of $\frac{1}{4}$ " plywood mounted on a strong frame and varnished. There was a cross beam in the centre supporting the activity recording unit (Figs. 1 and 2 b) and another at one end with the feeding unit (Figs. 1 and 2 c). The cage walls were supported by four metal shelf angles with stove bolts as feet (Figs. 1 and 2 a, F) so that the level of the cage could be adjusted.

The floor was made of thin rubber cot sheeting (Figs. 1 and 2 a, D) stretched between two wooden frames (E) the insides of which were covered with sandpaper to prevent the rubber slipping; the frames were held together by six bolts. The dimensions of the floor were six inches greater in each

direction than those of the cage, this prevented any loss of sensitivity round the walls of the cage. Resting on the rubber floor was a sheet of stainless steel mesh (J), the same dimensions as the cage, wire diameter 0.002", mesh 1/65 X 1/65, with a rim of brass one thousandth of an inch thick and three inches wide (H) bent up at right angles. The brass rim fitted loosely over the lower edge of the cage walls. The stainless steel prevented the mice chewing the rubber but did not lessen the sensitivity appreciably; the brass strip which was stapled to the steel mesh, prevented the mouse from pushing under the walls of the cage.

Vibrations from the rubber floor were transmitted up a light aluminium rod (Fig. 2 b, L) resting on the floor in the centre of the cage; the rod was protected from interference from the mouse by a glass tube (R) suspended from the cross beam by a rubber stopper (N). The upper end of the rod was bent twice so that a platinum electrode (M) at the end just cleared the surface of the mercury (O). The mercury cup was made of a piece of test tube with rubber hose attached to the base, the mercury level could be adjusted by a screw dip (P). Vibration of the floor transmitted through the rod caused the platinum electrode to make and break the circuit.

Food was provided in a tray (Fig. 2 c, Y) hung from a rod (X) at the top of which was a spring (U); the mouse had to climb on to the dish to eat, this compressed the spring and

closed the contacts (T and W). No record of drinking was made, water was supplied from an ordinary drip bottle attached to the wall at one end of the cage (not shown in diagram).

In the course of testing the cage it was found that the mice preferred running in a low space, i.e. in a tunnel. In accordance with this finding, metal strips (Fig. 1 and 2 a, C) were fastened to the wall for the length of the cage in such a fashion that there was just room for the mouse to run underneath but it was impossible to climb on top. Towards the end of the experiment several mice succeeded in escaping from the cage and frames covered with transparent plastic were used to prevent jumping.

2. Recording unit

Recording was done by a spark on electro-sensitive paper. The recording unit was separate from the activity cage. Two car ignition coils (Fig. 3, H and J, Fig. 4, H) were used in conjunction with a six volt car battery (F) to make sparks between electrodes (H) and (G) and an aluminium base plate mounted on a platform (A) (for details of circuit, see below). Electro sensitive paper (L) (Phipps and Bird teledeltos paper, 1½" wide) was used for the recording; it was drawn along the platform under the electrodes at the rate of ten inches an hour by a rubber covered wheel (D) on a gear shaft (C). The gears (Meccano parts) were driven by a turn table motor (N).

The electrodes were mounted so that (G) was just touching the paper $\frac{1}{2}$ " from one edge, and (H), $\frac{1}{4}$ " from the other, thus the black marks made on the paper by sparks from the electrodes were in two parallel lines.

3. Electrical circuits

The activity and feeding circuits were essentially identical, the only difference being in the copper (Fig. 2 c, T and W) and platinum-mercury (Fig. 2 b, M, O) electrodes. The activity circuit is described (Fig. 4).

The activity circuit consisted of a Heathkit D.C. Power supply (D) a solenoid (B) acting as a double throw switch, a condenser (E) and a second solenoid (C). Excessive sparking at the mercury surface (A) was prevented by a resistance divider as shown in the circuit diagram (Fig. 4). Solenoid C connected the main circuit with the recording circuit which was made up of a 6 v. car battery (F) and a car ignition coil (H). Electro-sensitive paper was pulled between the poles of the spark gap (G) (see above). In the resting system the condenser was in series with the power supply and became charged; when the mercury-platinum key (A) was closed, solenoid B changed the double throw switch putting the condenser in series with the second solenoid (C). The condenser discharged over the solenoid closing the recording circuit and causing a spark to be made through the electro-sensitive paper

at G.

Conditions for experiments

The first two runs were made with the cage in the open in the fish room at McMaster in January and February; the room was heated a little, temperatures were between 5°C and 15°C, sunrise and sunset times were taken from the Dominion Public Weather office in Toronto.

Mice were kept in small cages in the fish room for a week before being transferred to the activity cage. After a month in the open the activity cage was placed in a large insulated box so that the animals were not disturbed. The box was six feet long by three and a half feet wide by two feet deep, lined with one and a half inch thick glass fibre board. Lighting was provided by a single fluorescent tube wrapped in semi-transparent plastic hose which was fixed at one end to a cold water tap. A steady flow of water reduced the heat from the light and made the illumination more diffuse. The light was controlled by a Paragon Poultry Timer. Records of temperature fluctuation throughout the summer as shown on a thermograph indicated a maximum diel variation of 10°C.

Experimental procedure

The aim was to record as long a period of activity as was possible for each mouse, owing to occasional mechanical

difficulties and the occasional escape or death of a mouse, some discontinuities occurred. However, with the number of results available this was not considered important.

Recording was not started until at least six hours after closing the activity cage; food and water were changed every four or five days, otherwise the mouse was not disturbed. The recording paper moved at a steady rate of ten inches per hour. Spark marks made at the rate of one every five seconds could be clearly distinguished, above that level the marks tended to be indistinguishable and were estimated by comparing with the size of one mark. The absolute activity was known only for low levels of activity, whereas very intense activity could only be judged approximately. Since the problem was concerned with the distribution and duration of periods of low and high activity rather than the actual intensity, this did not matter. The time of day was marked on the recording paper three or four times a day. For plotting purposes each hourly period was divided into ten six minute intervals; the spark marks in each section were counted and plotted on a histogram. Histograms were also made for each day at thirty minute intervals and for the total activity of each mouse at hourly intervals.

Results

Activity histograms for all uninterrupted periods for

all mice together with histograms showing the average hourly activity of each mouse and for all mice over the whole experiment are presented at the end of this thesis. Plotting at half hourly intervals was chosen as giving an undistorted picture of the activity rhythm while presenting the results in a concise fashion. Histogram 1. was included to demonstrate the initial method of plotting at six minute intervals and should be compared with histogram 2 b, c, d, and histogram 5. Differences in intensity of activity are in part due to differences in weight of the animals and in the delicacy of adjustment of the mercury switch.

Mouse No. 1. ♀ weight 40 grams. Histograms 1. 2. 3. 10. Table 1.

The investigation was conducted in February and March 1954 in the fish room. Activity is shown to be slightly greater at night than in the day; peaks are found just before sunrise and after sunset with a third smaller peak around noon. Particularly noticeable in all histograms is the drop in activity at sunrise and a corresponding drop in the late afternoon. Table 1 is a record of feeding, it indicates greatest activity between 5.00 am and 7.00 am and between 6.00 pm and 7.00 pm remaining fairly high until midnight; there was some feeding between 11 am and 2.00 pm. These results seemed to be in parallel with the general activity pattern.

Mouse 25 ♀ weight 35 grams. Histograms 4. 5. 6. 7. 9. 10.

This record was made in June and July after the cage was transferred to the sound proof box. The overall pattern of activity is the same as for mouse 1; in all histograms except one there is a pronounced drop in activity when the light came on in the morning and in all cases a rise, often abrupt, when it went off. Histogram 9 c shows the effect of a very warm environment on activity; July 26th, 27th and 28th were extremely warm days, and even with the water cooling system, the temperature inside the insulated box rose to 32.5°C, and fell only to 23°C. On these days there was the usual drop in activity when the light went on followed by great activity until 2.00 pm (temp. 27.5°C); thereafter activity dropped to a low level, with only a slight peak when the light went off. Histogram 5 a and b shows a similar drop corresponding to temperatures of 28°C and 29°C at 6.00 pm. The results shown in histogram 9 b are incorporated in 10 b and account to some extent for the high peak at 9.00 am and for the smallness of the 7.00 pm peak.

Mouse 55 ♂ weight 30.5 grams. Histograms 7. 10.

A very poor record of activity was obtained from this mouse; owing to technical difficulties the record is complete for only two days out of four, the mouse died on the fifth day

in the cage. Histogram 10c shows the same overall activity pattern as for the other mice.

Mouse 68♂ weight 40 grams. Histograms 9. 11.

Histogram 9 a shows activity at a very low level particularly in the evening, this was probably due to very high temperatures that day, the lowest recorded was 25.5°C and the highest 31.5 C. Histogram 9 b shows a more normal activity pattern associated with a temperature fluctuation of 20°C - 26°C. Only two complete days record was obtained as the mouse kept escaping, but several partial records obtained are included in histogram 11 a which shows the usual pattern.

Discussion

In determining the natural activity pattern of a small mammal such as the mouse the sensitivity of the apparatus is of prime importance. The activity wheel, a standard recording method has the disadvantage that the only type of activity possible is extremely unnatural and there is a strong possibility that the animal will be excited and not behave in a normal fashion; furthermore activity expressed as gnawing and nesting is not recorded. The second common type of activity cage is the one suspended from springs or resting on tambours. The sensitivity of such an apparatus depends on the relative weights of mouse and cage, so that size is a limiting factor. Further-

more, oscillations set up in the spring which continue after activity has ceased and variation due to lateral swinging will cause further artefacts in the record.

In an attempt to eliminate these defects a new type of activity cage was designed which had the following advantages; the sensitivity of the cage was not reduced by the larger size, with the introduction of a second activity recording unit the size could be made greater still, considerable freedom of movement was therefore obtained. Oscillations set up in the rubber were not recorded because of the brief lag necessary to recharge the condenser; recording was frictionless and so less susceptible to error, and it was possible to record feeding without changing the sensitivity of the cage. It was possible therefore to get an accurate recording of activity under conditions of greater freedom than is possible with other cages.

The results obtained for Microtus pennsylvanicus pennsylvanicus using the new activity cage showed that there was a regular pattern of activity present in all the specimens examined. The mice were active to some extent all the time but the average activity for each mouse was greater at night than during the day; further analysis of the activity pattern reveals that the greatest activity occurred for two hours before sunrise and after sunset; this confirms the work of Hamilton (1937). In all the results obtained the most striking

feature is the occurrence of a clearly defined drop in the level of activity at sunrise and sunset and with the turning on and off of the artificial light. The drop, which lasted about two hours emphasised the dawn and dusk peaks and also the midday increase. The fact that there was a drop in activity in the evening in both natural and artificial conditions of illumination suggests that the decrease is not dependent on a gradual reduction in light intensity but rather on some innate factor.

The results obtained from mice 1 and 25 are very consistent over a period of several weeks and may be regarded as a true representation of the activity pattern. Results from mice 55 and 68 are not in themselves sufficient for any conclusions to be formed but they show a great similarity to the earlier results. The effect of heat on activity was not tested specifically but results obtained with mouse 25 at temperatures of 30°C. and 31°C. suggest that activity is depressed in very warm conditions. Histograms 5 a and 9 c show activity to be greater than in other records between 7.00 am and noon, followed by a depression as the temperature rose higher; the evening peak in activity was greater than usual.

Significance of the diel variation in activity

Using the results plotted in histograms 10 and 11 a statistical analysis of diel activity was made. The means for

nocturnal and diurnal activity were compared according to the following equation (Fisher, 1946).

$$\bar{x} = \frac{1}{n'} \sum S(x), \quad \bar{x}' = \frac{1}{n''} \sum S(x')$$

$$S^2 = \frac{1}{n'} \sum (x - \bar{x})^2 = \frac{1}{n''} \sum (x' - \bar{x}')^2$$

$$t = \frac{\bar{x} - \bar{x}'}{S} \sqrt{\frac{(n' - 1)(n'' - 1)}{n' + n'' - 2}}$$

$$n \quad n' \quad n''$$

A probability of 0.05 or less is regarded as being significant, i.e. as showing a significant difference between nocturnal and diurnal activity.

The calculations, presented in the appendix, show the following results.

Mouse	Probability	Difference between nocturnal and diurnal activity.
Mouse 1	0.02 - 0.01	Significant
Mouse 25 a	0.2 - 0.1	Not significant
Mouse 25 b, omitting results obtained in hot weather	0.02 - 0.01	Significant
Mouse 55	0.04 - 0.03	Not significant
Mouse 68	0.04 - 0.05	Not significant
Total results	less than 0.01	Significant

Summary

1. A new type of activity cage was designed which allowed greater freedom for spontaneous running activity than is found in the standard activity cages. The cage had the further advantages that artefacts resulting from unnatural oscillation and lateral swinging were not recorded.
2. Records of activity for four mice, two male and two female, were obtained over a period of six months.
3. Grouping of the results in six minute and thirty minute intervals and averaging for each mouse and for all mice reveals a constant pattern of activity.
4. Activity for mice 1 and 25 is significantly greater at night than in the daytime. The average activity for all mice is also significantly greater at night, mice 55 and 68, for which there is only an incomplete record, do not show this difference.
5. Unusually warm conditions, 28°C to 32°C causes a reduction in activity. It is suggested that temperatures between 25°C and 28°C might cause an increase in activity.
6. Under all conditions there was a drop in activity at sunrise or when the light came on and at sunset or when the light went off.
7. The average activity for all mice is greatest two hours before dawn and for two hours after dusk.
8. Feeding activity as shown with Mouse 1 follows the general pattern of activity but is greater between 7.00 pm and midnight than between midnight and 7.00 am.

APPENDIX

$$\bar{X} = \frac{1}{n' + 1} S(X),$$

$$\bar{X}' = \frac{1}{n'' + 1} S(X')$$

$$S^2 = \frac{1}{n' + n''} \left\{ S(X - \bar{X})^2 + S(X' - \bar{X}')^2 \right\}$$

$$t = \frac{\bar{X} - \bar{X}'}{S} \sqrt{\frac{(n' + 1)(n'' + 1)}{n' + n'' + 2}}$$

$$n = n' + n''$$

\bar{X} = average activity for any one hour of the night for one mouse or for all mice.

\bar{X}' = average activity for any one hour of the day for one mouse or for all mice.

$n' + 1 = N$ = number of hours of darkness.

$n'' + 1 = N'$ = number of hours of light.

SX = total of average activity at night.

\bar{X} = mean of activity at night.

House 1.

Nocturnal activity			Diurnal activity		
x	$x - \bar{x}$	$(x - \bar{x})^2$	x'	$x' - \bar{x}'$	$(x' - \bar{x}')^2$
32	-14	196	10	-22	474
58	- 8	64	19	-13	169
38	- 8	64	21	-11	121
39	- 7	49	25	- 7	49
39	- 7	49	29	- 3	9
42	- 4	16	30	- 2	4
42	- 4	16	32	0	0
48	2	4	32	0	0
55	9	81	36	4	16
56	10	100	36	4	16
57	11	121	40	8	64
<u>70</u>	24	<u>576</u>	<u>68</u>	56	<u>1296</u>
556		1336	378		2218

$$\bar{x} = \frac{556}{12} = 46.4$$

$$\bar{x}' = \frac{378}{13} = 29.08$$

$$s^2 = \frac{1336 + 2218}{22} = 161.7$$

$$s = 12.7$$

$$t = \frac{14}{12.7} \times 2.45$$

$$= 2.71$$

$$P = 0.02 - 0.01$$

Mouse 25 (1).

Nocturnal activity			Diurnal activity		
X	$X - \bar{X}$	$(X - \bar{X})^2$	X'	$X' - \bar{X}'$	$(X' - \bar{X}')^2$
14	-13	169	10	-12	144
19	-8	64	12	-10	100
19	-8	64	13	-9	81
20	-2	4	17	-5	25
23	-2	4	20	-2	4
26	-1	1	20	-2	4
28	1	1	22	0	0
30	3	9	25	3	9
32	5	25	27	5	25
35	8	64	27	5	25
36	9	81	31	9	81
<u>37</u>	10	<u>100</u>	<u>44</u>	22	<u>484</u>
326		586	268		982

$$\bar{X} = \frac{326}{12} = 27.0$$

$$\bar{X}' = \frac{268}{12} = 22.3$$

$$s^2 = \frac{543 + 982}{22} = 74$$

$$s = 8.6$$

$$t = \frac{5}{8.6} \times 2.45$$

$$= 1.43$$

$$p = 0.2-0.1$$

Mouse 25 No. 2. Without the results in histogram 9 c

Nocturnal activity			Diurnal activity		
X	X-X̄	(X-X̄) ²	X'	X'-X̄'	(X'-X̄') ²
16	-12	144	8	-12	144
21	- 7	49	10	-10	100
23	- 5	25	11	- 9	81
25	- 3	9	13	- 7	49
26	- 2	4	17	- 3	9
29	1	1	17	- 3	9
30	2	4	21	1	1
30	2	4	21	1	1
33	5	25	26	6	36
34	6	36	29	9	81
35	7	49	29	6	36
<u>37</u>	9	81	<u>36</u>	16	<u>256</u>
339		431	238		848

$$\bar{X} = \frac{339}{12} = 28.25$$

$$\bar{X}' = \frac{238}{12} = 19.83$$

$$s^2 = \frac{431 - \frac{848}{12}}{11} = 58.2$$

$$s = 7.61$$

$$t = \frac{8}{7.6} \times 2.45 = 2.58$$

$$P = 0.02-0.01$$

Mouse 55

Nocturnal activity			Diurnal activity		
X	$X - \bar{X}$	$(X - \bar{X})^2$	X'	$X' - \bar{X}'$	$(X' - \bar{X}')^2$
3	-15	225	1	-13	169
7	-11	121	2	-12	144
10	- 8	64	4	-10	100
14	- 4	16	5	- 9	81
15	- 3	9	8	- 6	36
18	0	0	10	- 4	16
21	3	9	12	- 2	4
21	3	9	15	1	1
24	6	36	20	6	36
26	8	64	24	10	100
28	10	108	25	11	121
<u>29</u>	11	<u>121</u>	<u>42</u>	28	<u>748</u>
216		774	168		1592

$$\bar{X} = \frac{216}{12} = 18$$

$$\bar{X}' = \frac{168}{12} = 14$$

$$S^2 = \frac{774 + 1592}{22} = 107.5$$

$$S = 10.7$$

$$t = \frac{4}{10.7} \times 2.45 = 0.915$$

$$P = 0.4-0.3$$

Mouse 68

Nocturnal activity			Diurnal activity		
X	$X - \bar{X}$	$(X - \bar{X})^2$	X'	$X' - \bar{X}'$	$(X' - \bar{X}')^2$
7	-5	25	5	-6	36
7	-5	25	7	-4	16
7	-5	25	7	-4	16
8	-4	16	8	-3	9
10	-2	4	10	-1	1
10	-2	4	11	0	0
10	-2	4	11	0	0
13	1	1	11	0	0
14	2	4	12	1	1
16	4	16	14	3	9
18	6	36	14	3	9
<u>22</u>	10	<u>100</u>	<u>16</u>	5	<u>25</u>
142		260	126		122

$$\bar{X} = \frac{142}{12} = 12$$

$$\bar{X}' = \frac{126}{12} = 11$$

$$S^2 = \frac{260 + 122}{22} = 17.4$$

$$S = 4.17$$

$$t = \frac{1}{4.17} \times 2.45$$

$$= 0.59$$

$$P = 0.5-0.6$$

Total activity

Nocturnal activity			Diurnal activity		
X	$X - \bar{X}$	$(X - \bar{X})^2$	X'	$X' - \bar{X}'$	$(X' - \bar{X}')^2$
16	-8	64	9	-9	81
19	-5	25	13	-5	25
20	-4	16	14	-4	16
20	-4	16	17	-1	1
23	-1	1	18	0	0
23	-1	1	18	0	0
24	0	0	19	1	1
25	1	1	20	2	4
25	1	1	20	2	4
30	6	36	21	3	9
30	6	36	21	3	9
<u>34</u>	10	<u>100</u>	<u>25</u>	7	<u>49</u>
289		297	215		199

$$\bar{X} = \frac{289}{12} = 24$$

$$\bar{X}' = \frac{215}{13} = 16$$

$$S^2 = \frac{297 + 199}{22} = 22.6$$

$$S = 4.75$$

$$t = \frac{6}{4.75} \times 2.45 = 3.095$$

$$P < 0.01$$

GLOSSARY

Seasonal : Pertaining to climatic seasons, spring summer autumn and winter in temperate lands and wet and dry seasons in tropical regions.

Lunar : Associated with daily rise and set of the moon, twelve and a half hour with full and new moons, with the quarters and with the spring and autumn equinoxes (Allee, Emerson, Park, Park and Schmidt).

Diel Activity : Activity in the 24 hour period of a day and a night

Diurnal " : Activity between sunrise and sunset

Nocturnal " : Activity between sunset and sunrise.

Auroral " : Activity at dawn

Vesperal " : Activity at dusk

Crepuscular : Activity at dusk and dawn

Normally, diurnal includes activity at dawn, and nocturnal, activity at dusk (Carpenter, 1954).

Exogenous Activity: Due entirely to external physical factors

Endogenous " : Due to an internal physiological rhythm. (Park, 1937).

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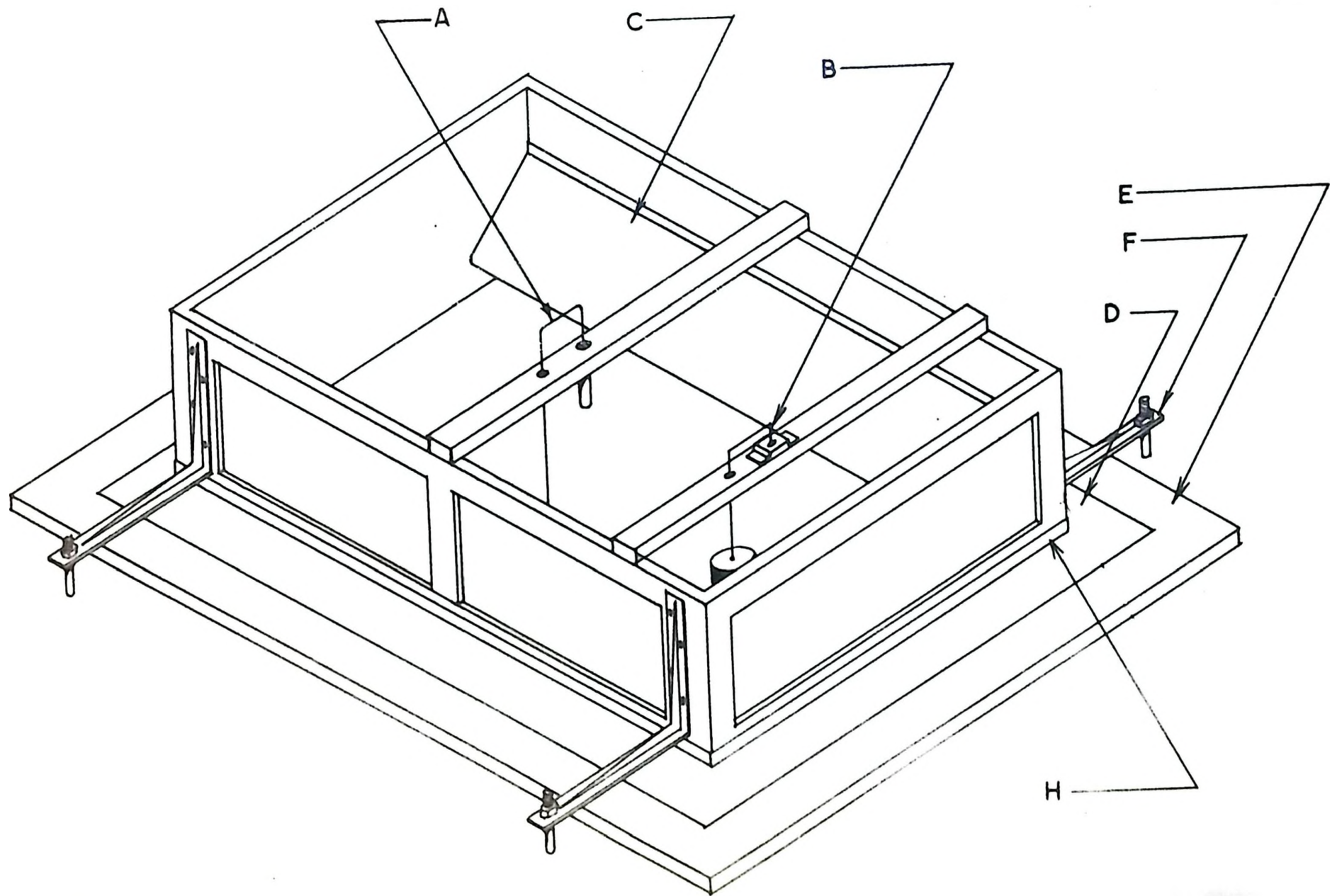
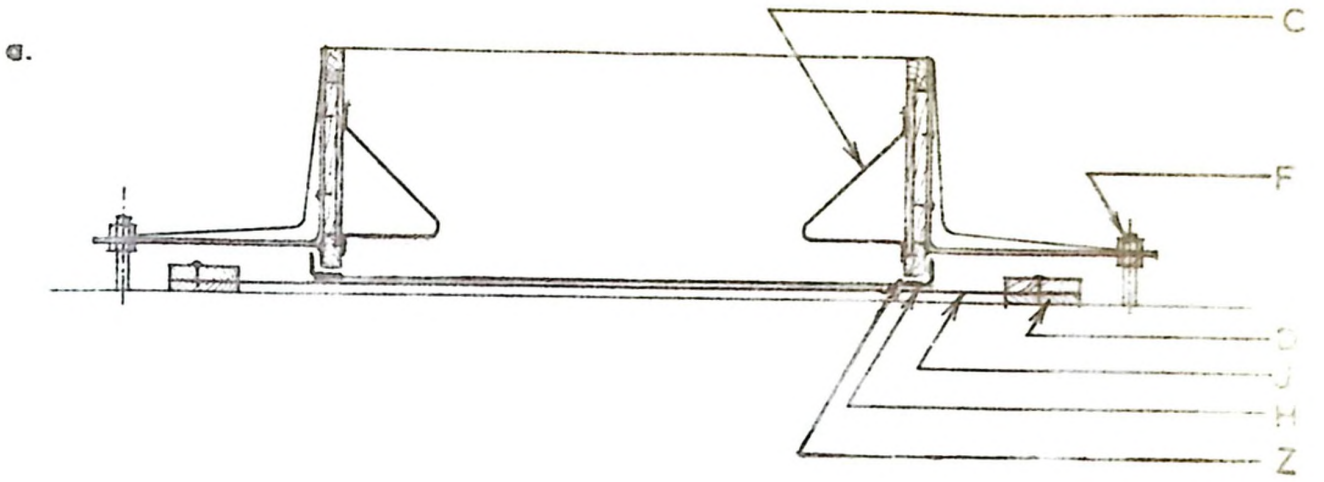


Figure 1. Activity cage.



CROSS SECTION OF CAGE

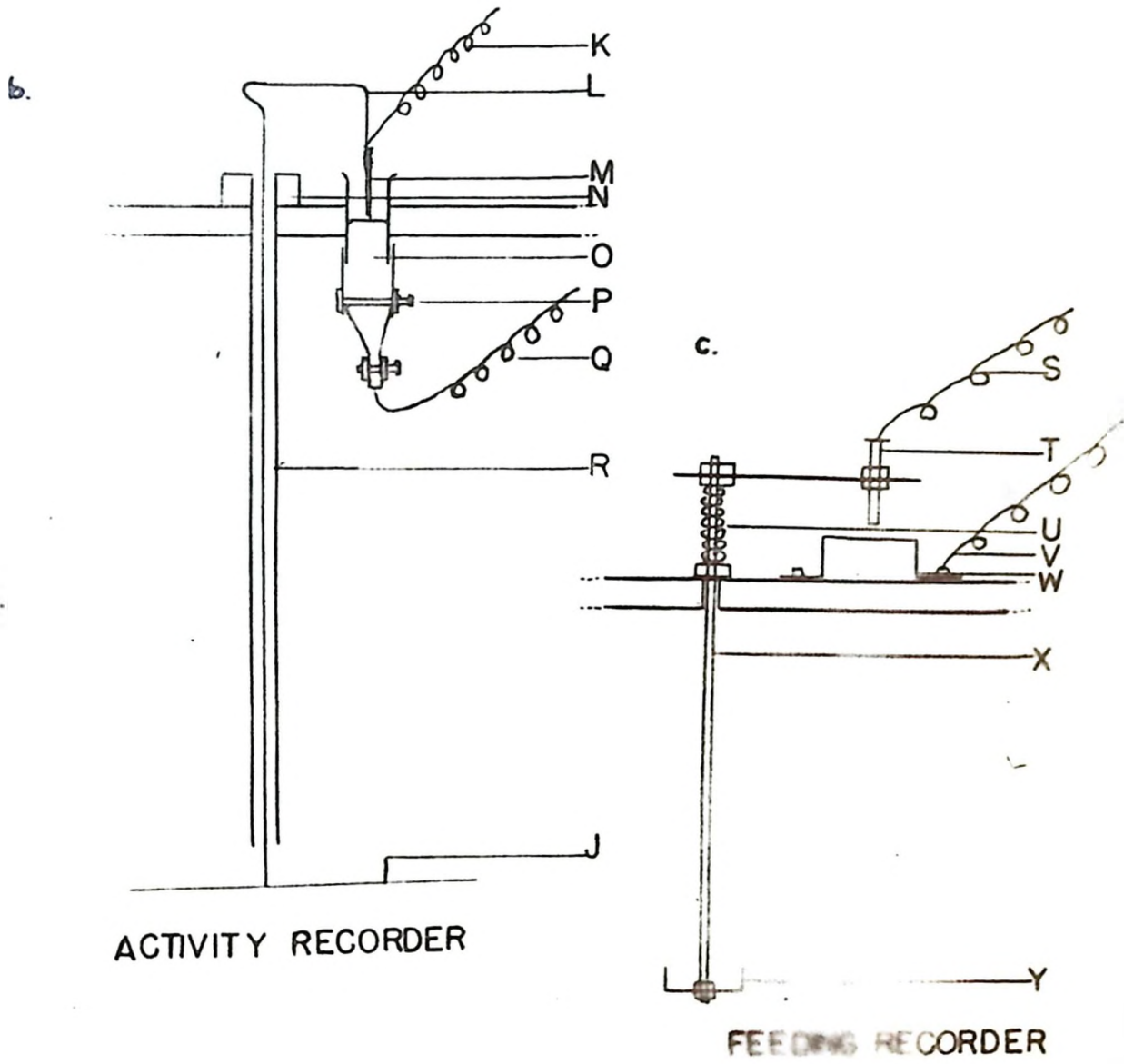


Figure 2. Detail of activity cage.

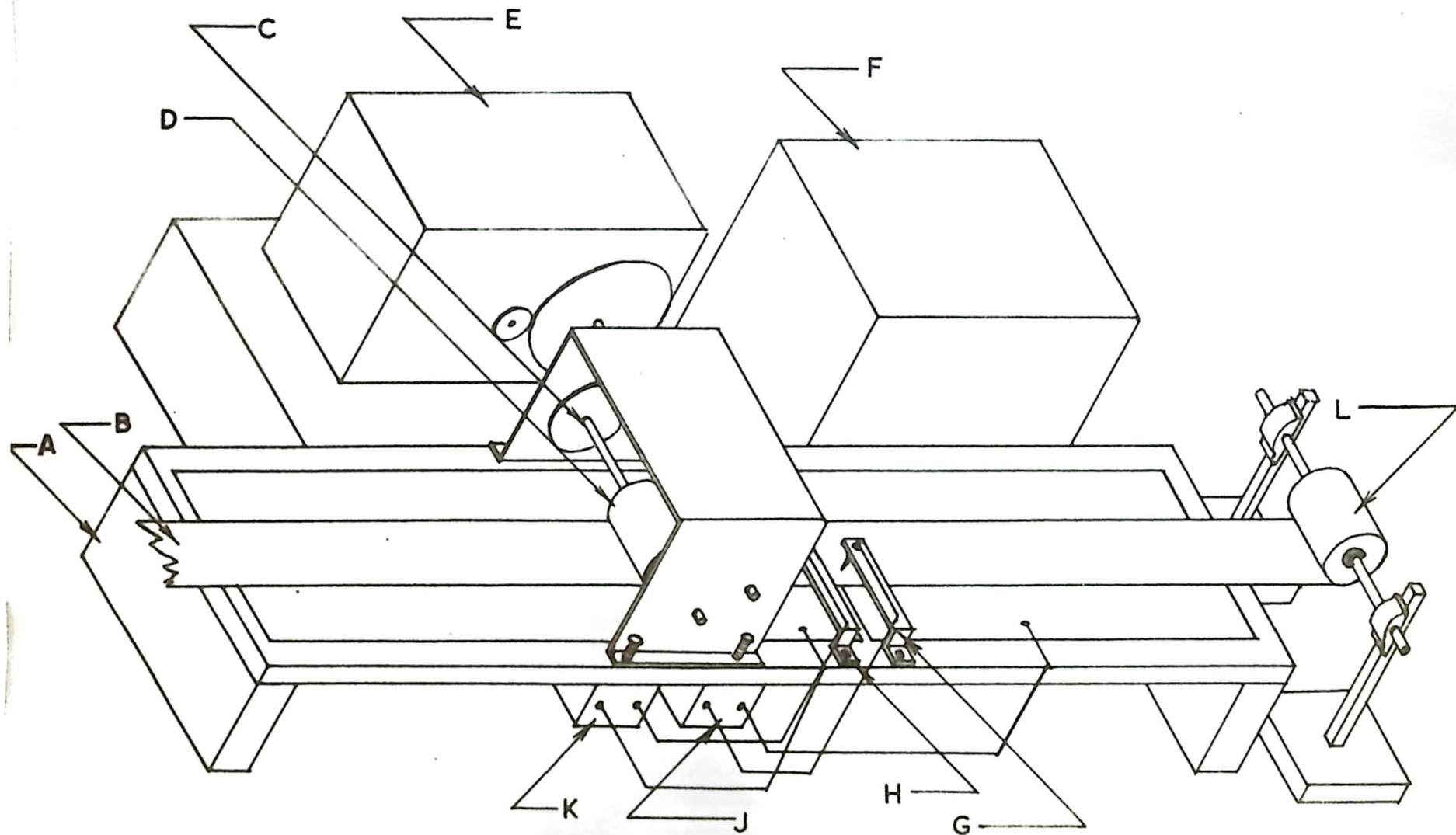


Figure 3. Recording unit.

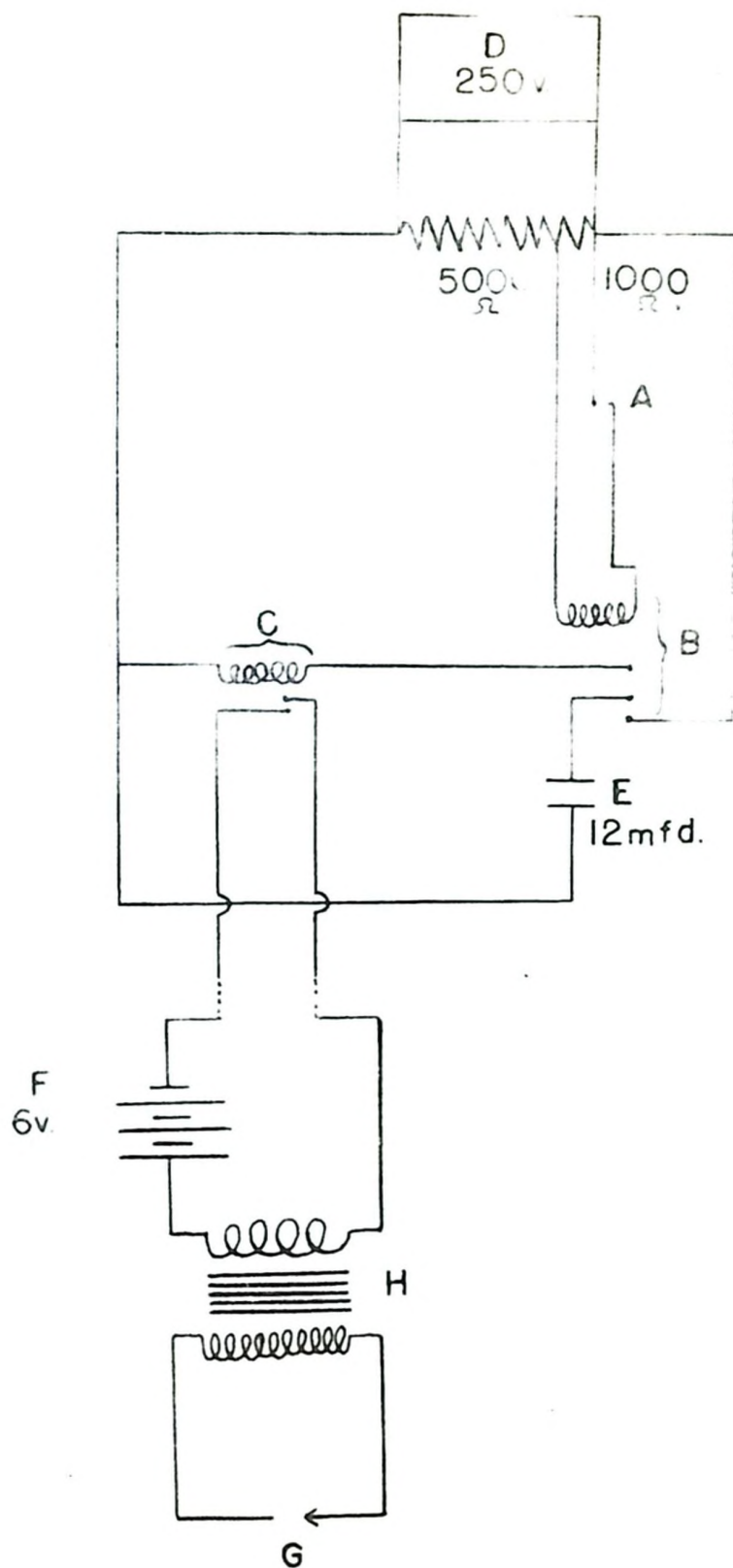


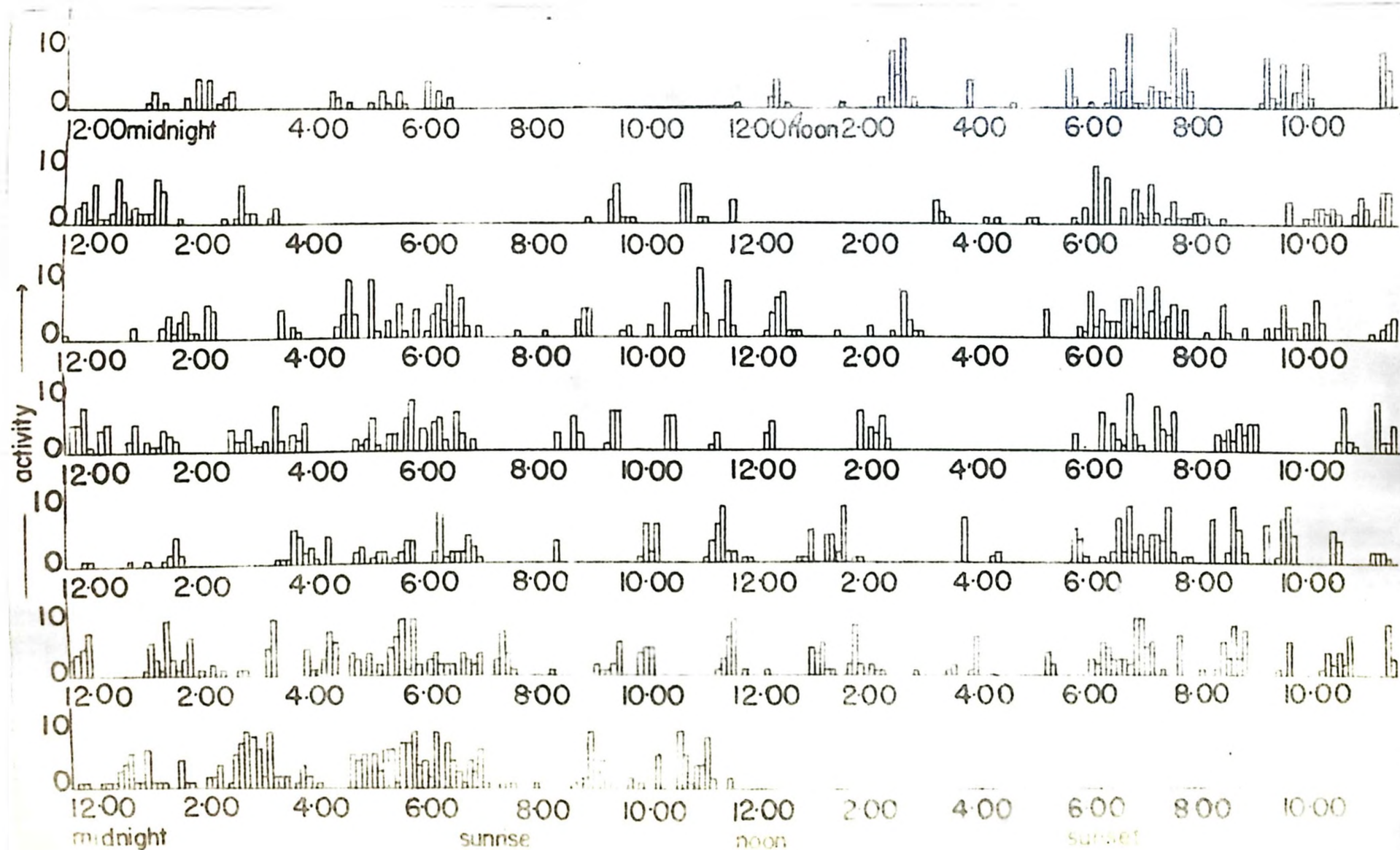
Fig. 4. Circuit Diagram.

FEEDING RECORD

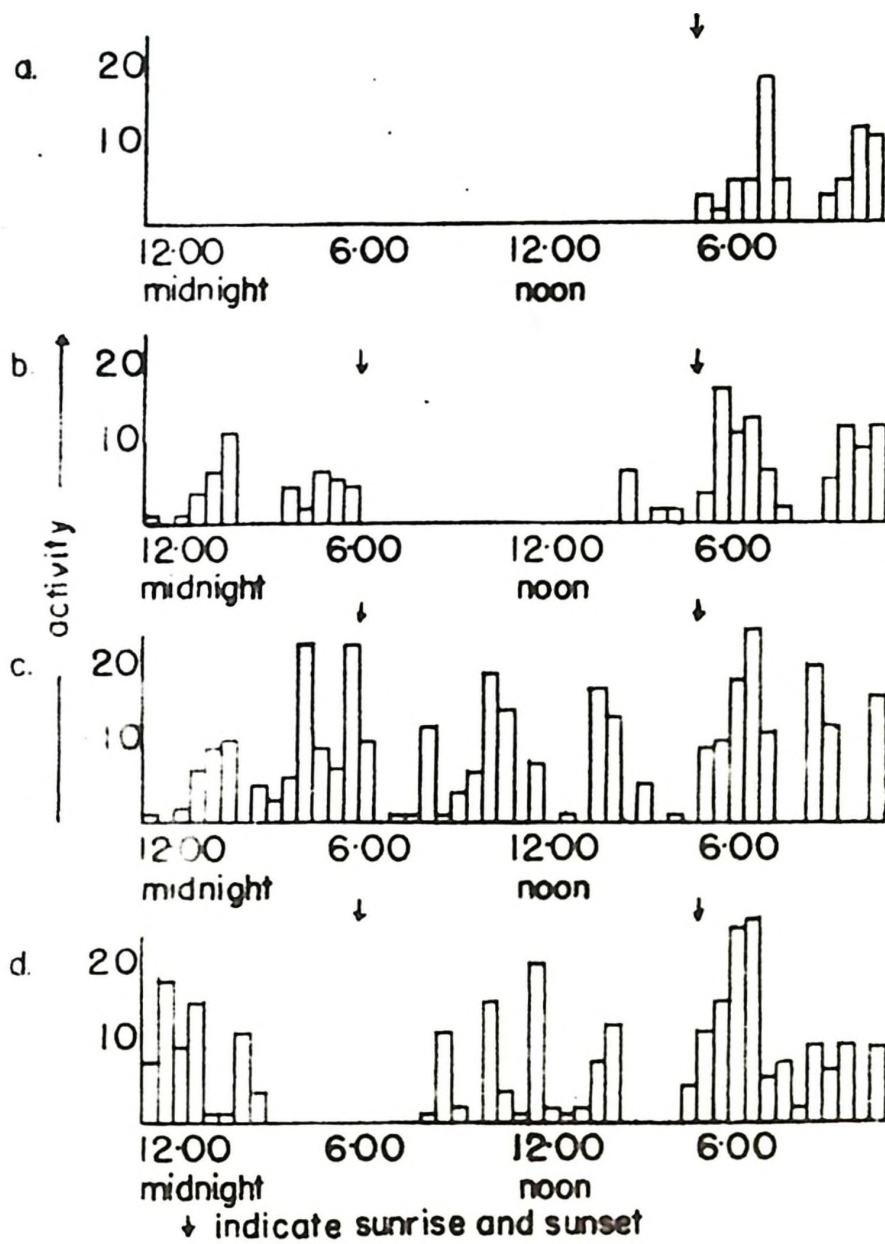
Mouse no. 1						
Noon Sunday				↑	o o o	o o o
Midnight	o	o	o	o o	↑	
Noon	o			o	o o o	o o o
Midnight	o o	o o			↑	o o
Noon		o		o	o o	o o o
Midnight	o o	o	o o	o o	↑	o o
Noon				o	o o o o o	o o o
Midnight	o	o o	o o	o o	↑	o o
Noon	o	o		o	o o	o o o
Midnight		o		o o	↑	o o
Noon				o	o o o o o o	o
Midnight	o	o	o o	o o	↑	o o
Noon	o			o	o o o o o	o o o
Midnight	o		o	o o o	↑	o
Noon	o	o		o	o o	o o o
Midnight	o	o	o	o o	↑	o

12:00 2:00 4:00 6:00 8:00 10:00
 ↑ indicate sunrise and sunset

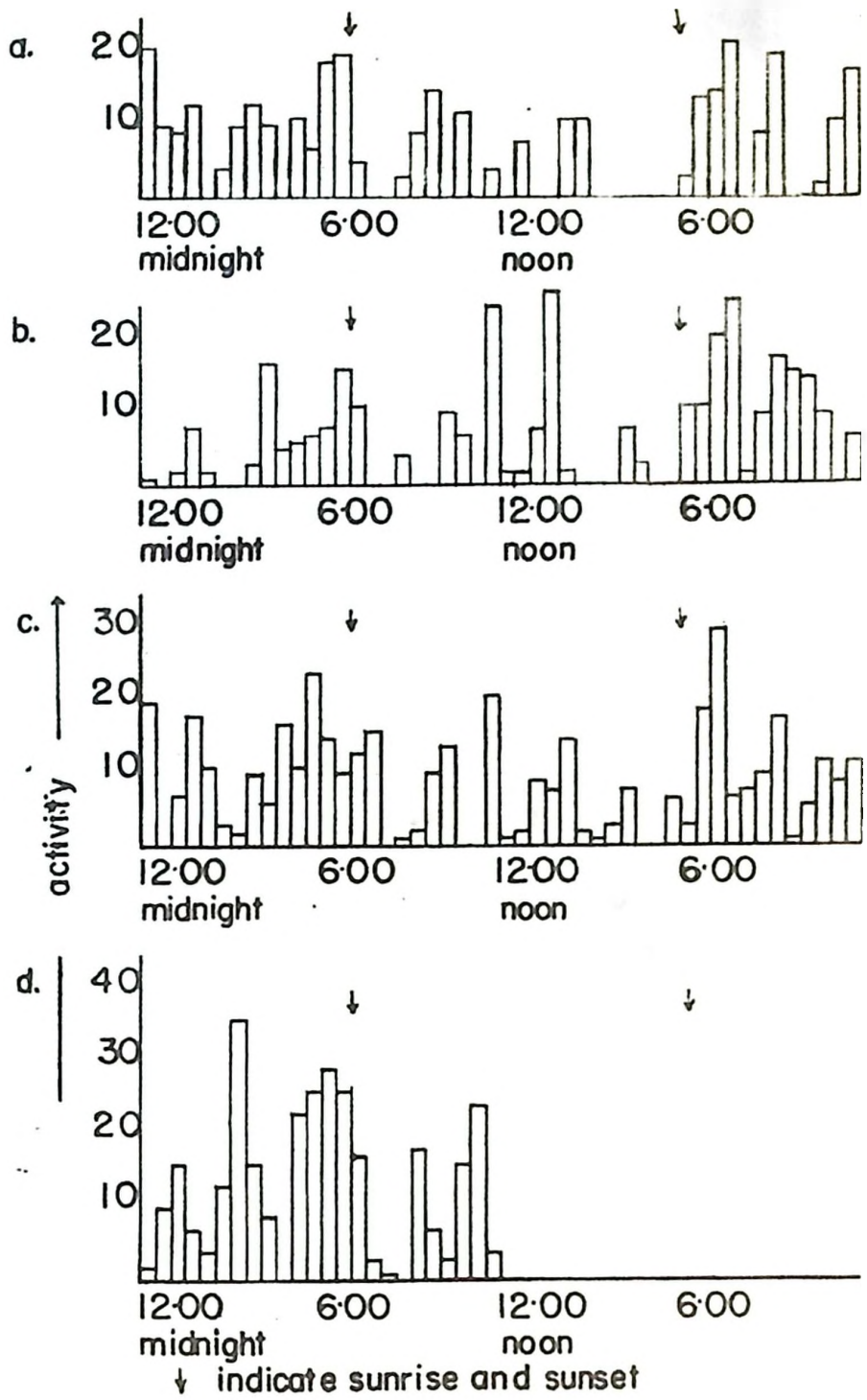
Table 1.



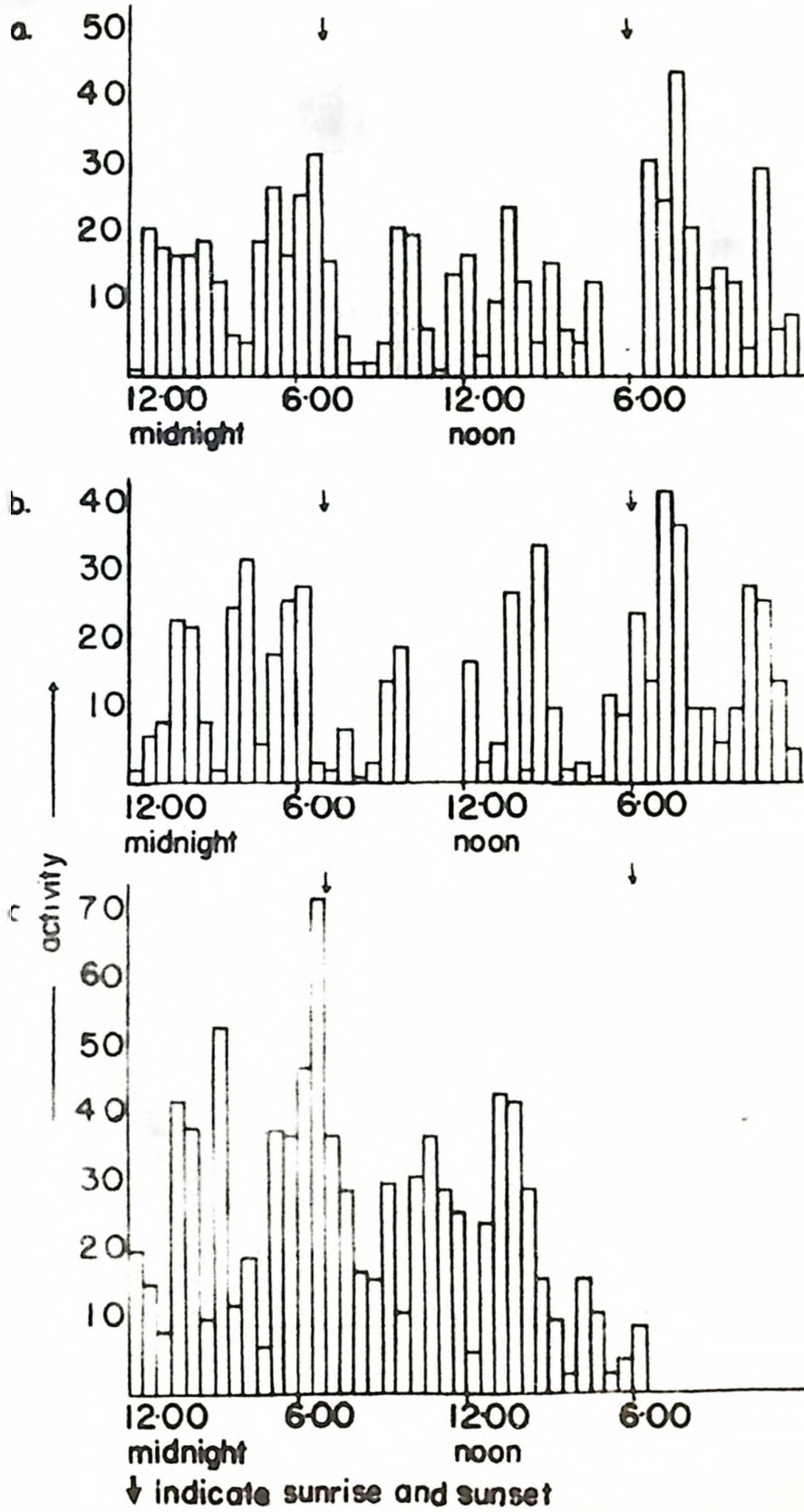
Histogram 1. Mouse 1.



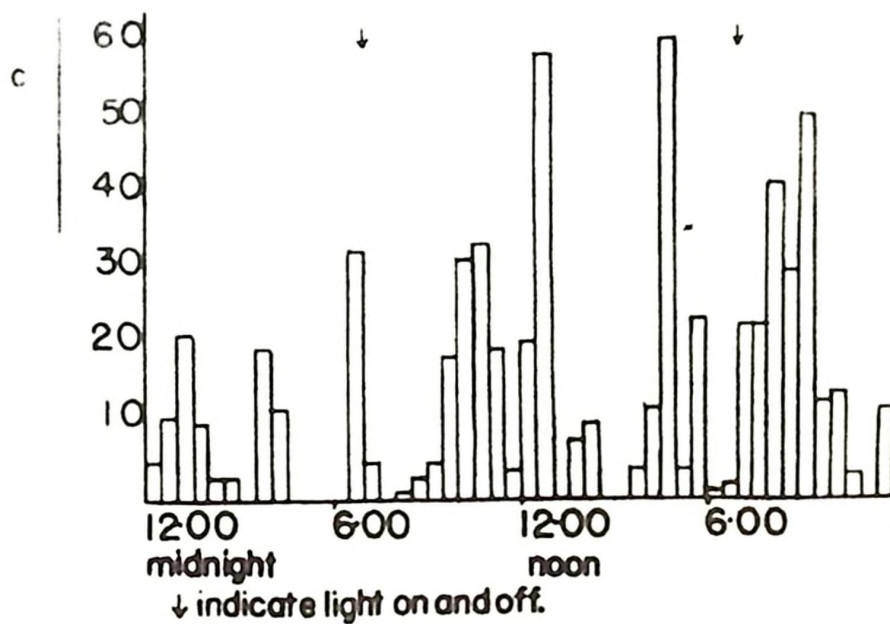
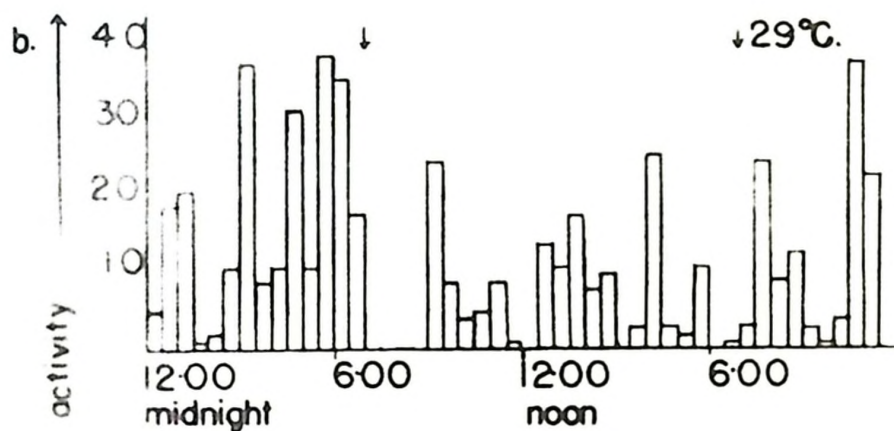
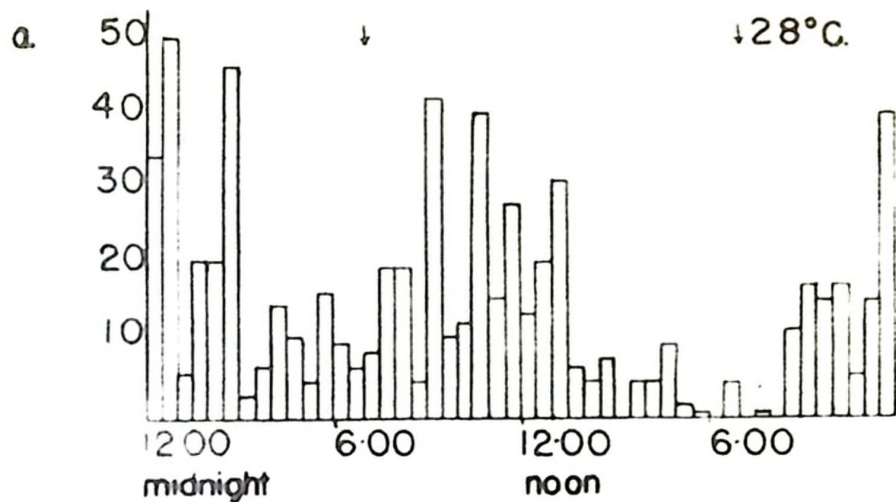
Histogram 2. Mouse 1.



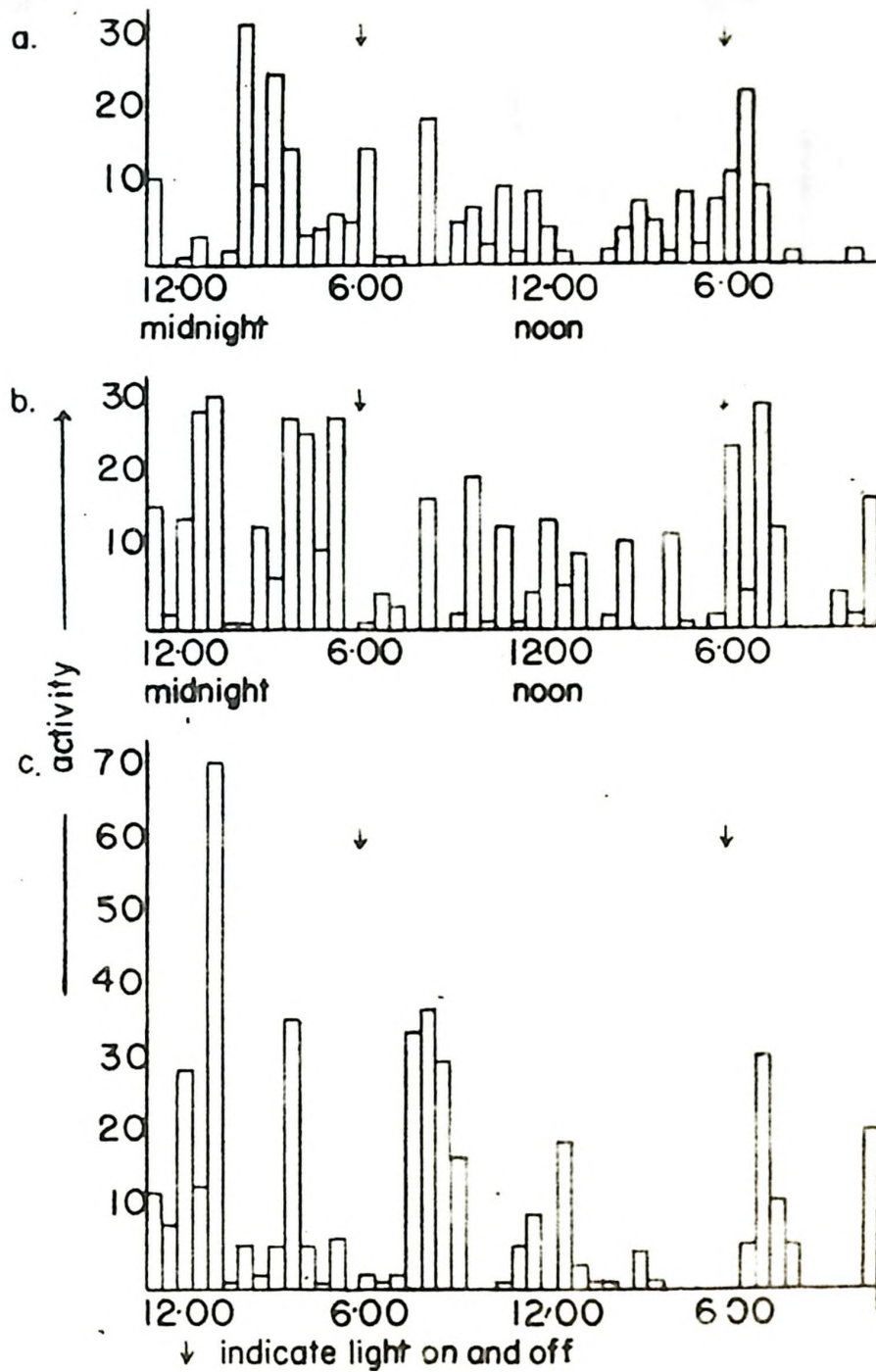
Histogram 5. mouse 1.



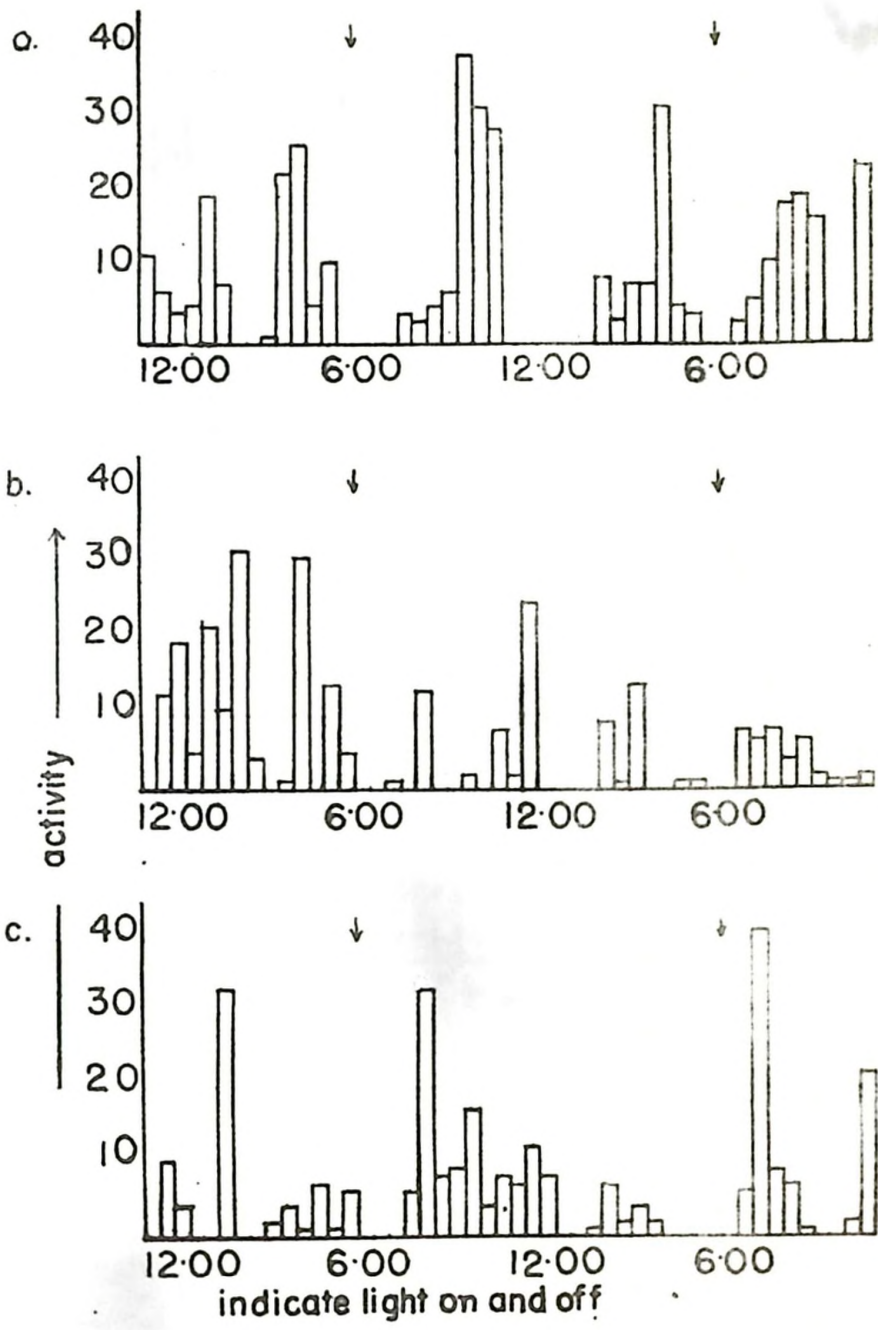
Histogram 4. House 1.



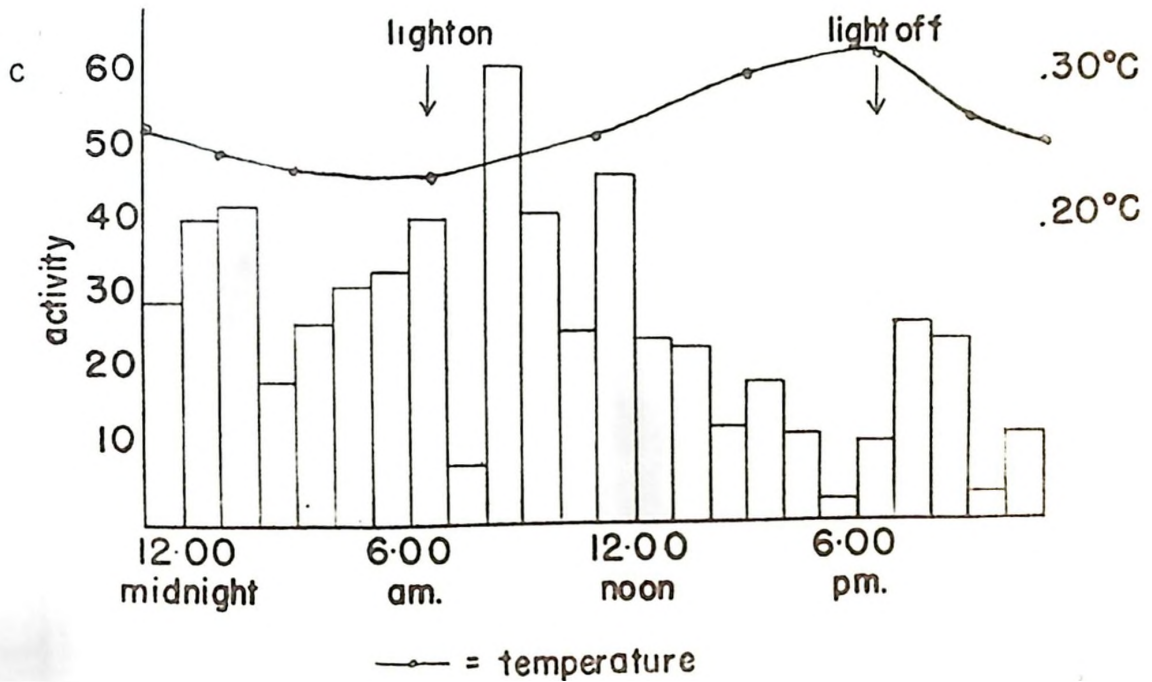
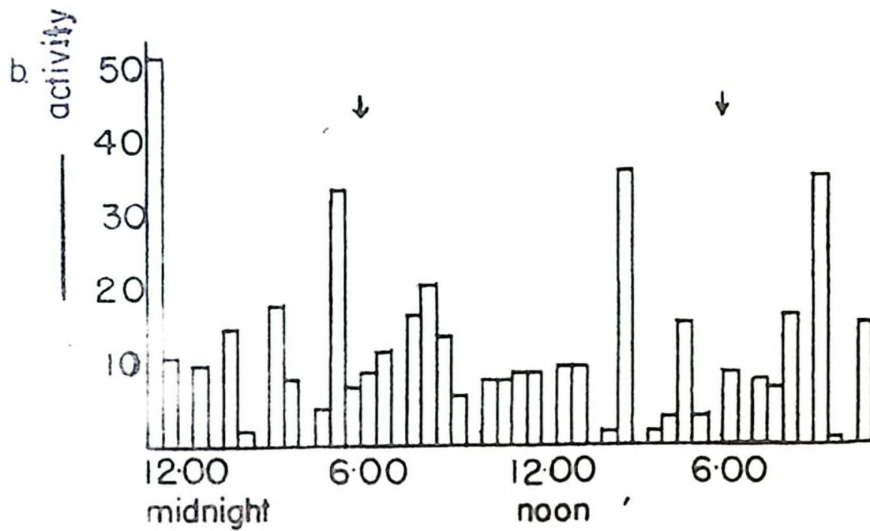
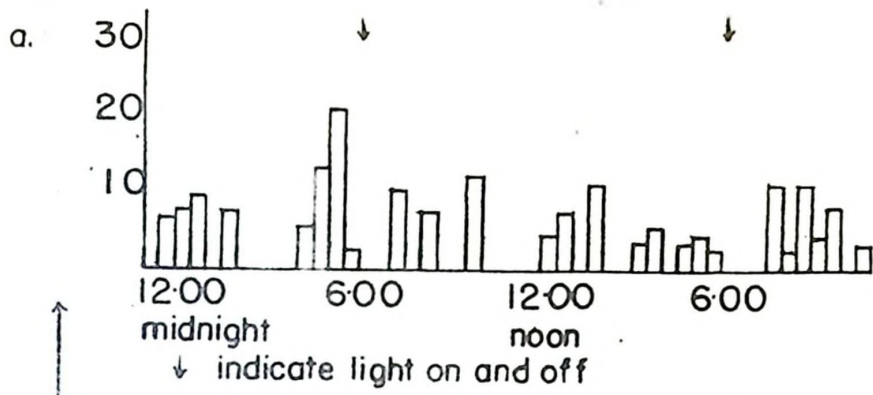
Histogram 5. Mouse 25.



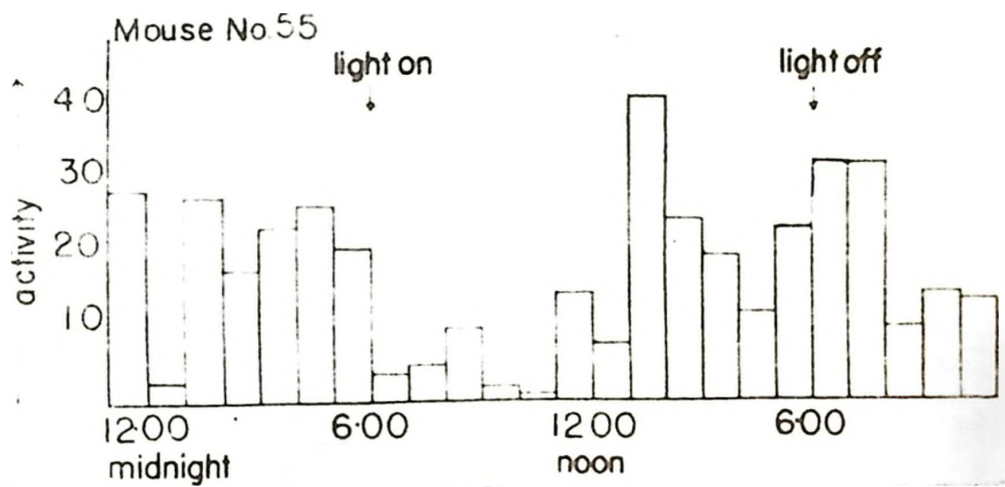
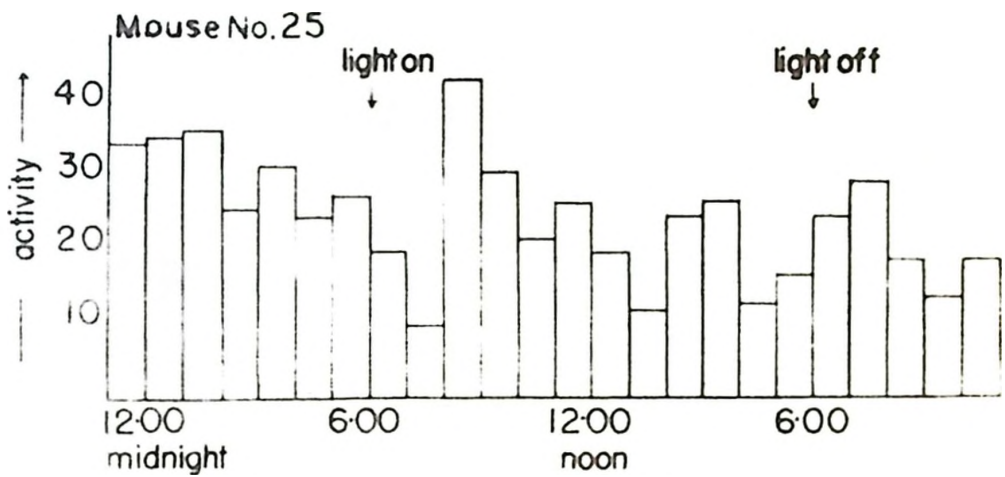
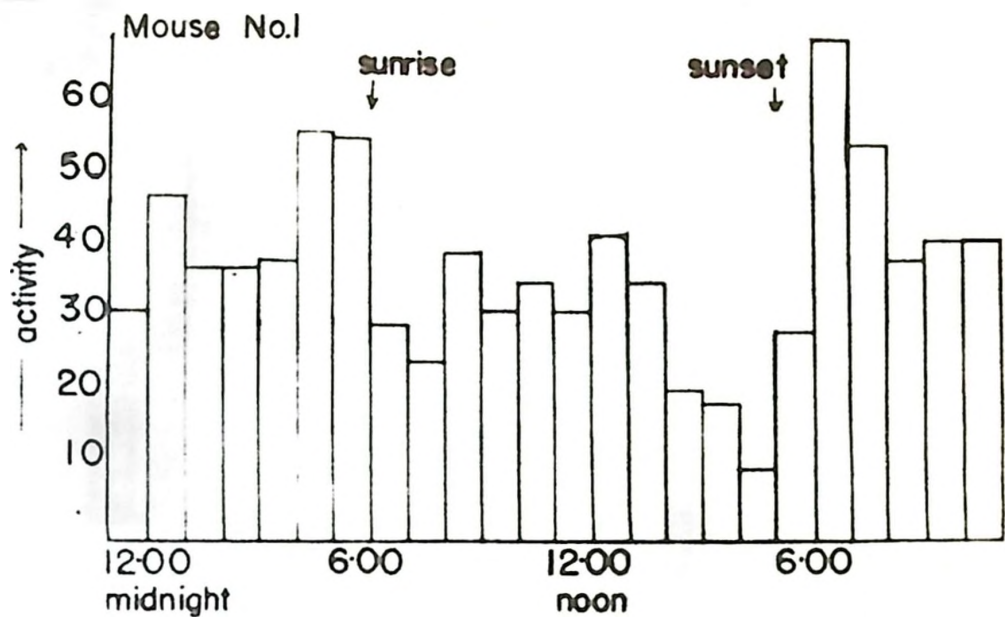
Histogram 6. House 25.



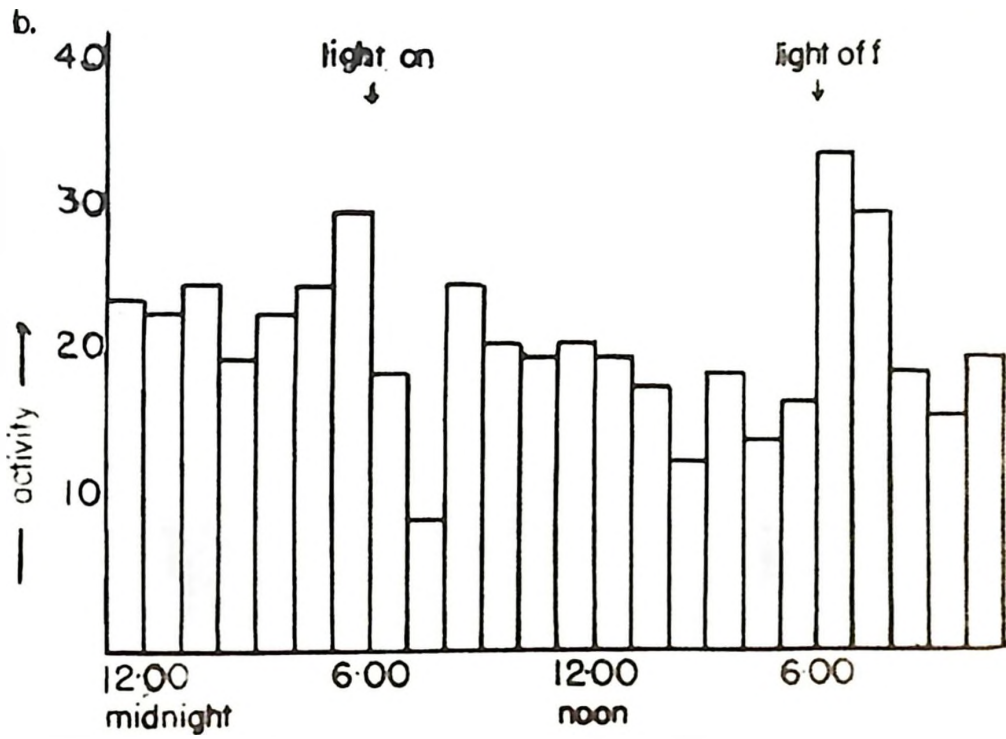
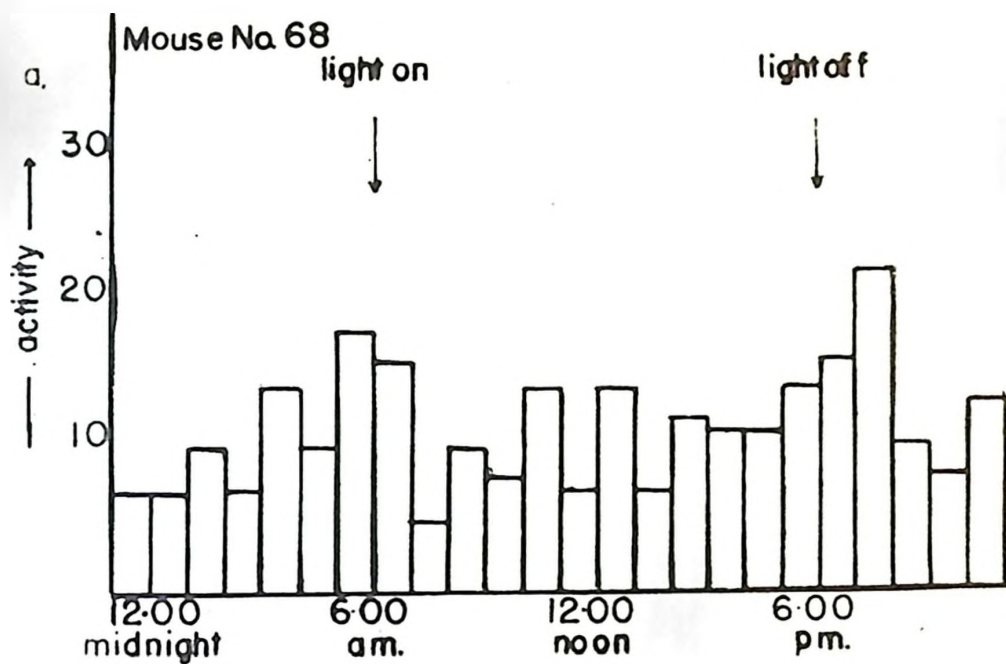
Histogram 7. House 25.



Histogram 9. a, b, Mouse 68. c, Mouse 25.



Histogram 10. Average activity for mice 1, 25, 55.



Histogram 11. a, average activity for Mouse 68.
 b, average activity for all mice.