

Activity Patterns of the Common Vole, *Microtus arvalis* – Automatic Recording of Behaviour in an Enclosure

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Summary. The activity behaviour of the common vole, *Microtus arvalis* was studied in an enclosure during a one-year cycle. The number of voles varied between 2 and 25 specimens. Emergence from burrows, running through pathways and visits at a feeding site were automatically recorded by passage counters which we developed for use in the field. The results can be summarized as follows:

1. The voles were day-active throughout the year – no change of the activity phase was observed. A significant proportion of activity at daytime was due to foraging trips to the feeding site, but the voles were active in the pathway-system, too. At night only a few short visits to the feeding site were recorded and almost no activity in the pathways was detectable.

2. In addition to the day-activity recorded by the passage counters we observed other activities like burrowing and storage almost exclusively at daytime, especially at dawn and dusk.

3. During daylight hours the voles were active on the surface in a synchronized short-term activity rhythm of about two hours.

4. This clear-cut activity pattern was changed for two reasons only: by juveniles beginning to venture from their burrows and by wet and cold weather conditions.

5. The activity pattern of voles kept in a cage within the enclosure was in accordance with previous investigations – the caged voles exhibited a distinct short-term rhythm of feeding bouts during daylight hours and showed extensive wheel-running activity at night. Thus they had maximum locomotor activity at a time, during which the voles in the enclosure were only occasionally active on the surface. Including previous results we assume from our investigations that voles are primarily day-active organisms. Although the short-term rhythm is closely related to metabolic demands there is evidence that its basic function is not to forage but to emerge for regular control of the territory. The hypothesis is put forward that short-term activity on the surface, which is synchronized with the activity of the population, might be advantageous to maintain territories. In continuation it is suggested that specimen which defend their territories effectively are most likely to survive at high densities in population cycles. Therefore the complex temporal structure of the voles' activity pattern might be favoured by selection.

species (*Microtus agrestis* and *Microtus arvalis*) it has been demonstrated that the short-term activity is essentially a feeding rhythm (Daan and Slopsema 1978; Lehmann 1976a). It is superimposed by an endogenous circadian rhythm of wheel-running activity during the night (Lehmann 1976a). Furthermore, a phase-shift has been observed twice during the year, in spring and autumn, with the voles becoming day-active in the winter (Ostermann 1956; Erkinaro 1969).

The physiological mechanisms as well as the adaptive significance of this complex activity pattern of behaviour is yet scarcely understood. This holds true especially for the short-term rhythm which differs from the circa-rhythms in that it does not correspond with any known environmental periodicity. An interpretation of its adaptive value, however, can only be possible if there is evidence that the behaviour of the captive voles reflects their activity pattern in the field, too. This cannot be taken for granted for two reasons:

– wheel-running activity only occurs in captivity. Its natural correlates are unknown, but may be very complex (De Kock and Rohn 1971);

– there is evidence that the properties of the cage may markedly influence the activity pattern (Lehmann 1976a).

From the field, quantitative data are available only from trapping and are contradictory. Some authors observed prevalent vole activity during daylight hours with peaks at dawn and dusk (Brown 1956; Frank 1954; Hamilton 1937) whereas Daan and Slopsema (1978) trapped most voles during the night with a distinct fall-off during dusk and dawn. Their catches are good evidence, however, for the existence of the short-term rhythm in free-living populations. But it must be considered that catches represent the “trappability” only, and can thus be only expected to reflect a selective activity pattern. It must be concluded, therefore, that the natural activity pattern of voles is yet unknown. Thus it is necessary to first obtain reliable data from the field to achieve a synthesis with the laboratory investigations. The analysis of behaviour in the field, however, depends on adequate recording methods. So far, only Mossing (1975) has developed and tested an automatic recording device based on passage counters, but limited to the laboratory. We have fitted such passage counters for fieldwork and as a first step employed them in an enclosure with a colony of the field vole, *Microtus arvalis*. This paper presents the recording methods as well as the results we obtained during a one-year-cycle.

Introduction

The temporal structure of the activity behaviour of captive voles is basically ruled by a short-term rhythm with a period of circa 2 h. This short-term rhythm stands out most precisely during the daylight hours but is less pronounced during the night. In two

Methods and Material

1. *The Enclosure.* The enclosure measured 3 × 4 m and was surrounded by a wall on three sides. The free side (exposed to NE)

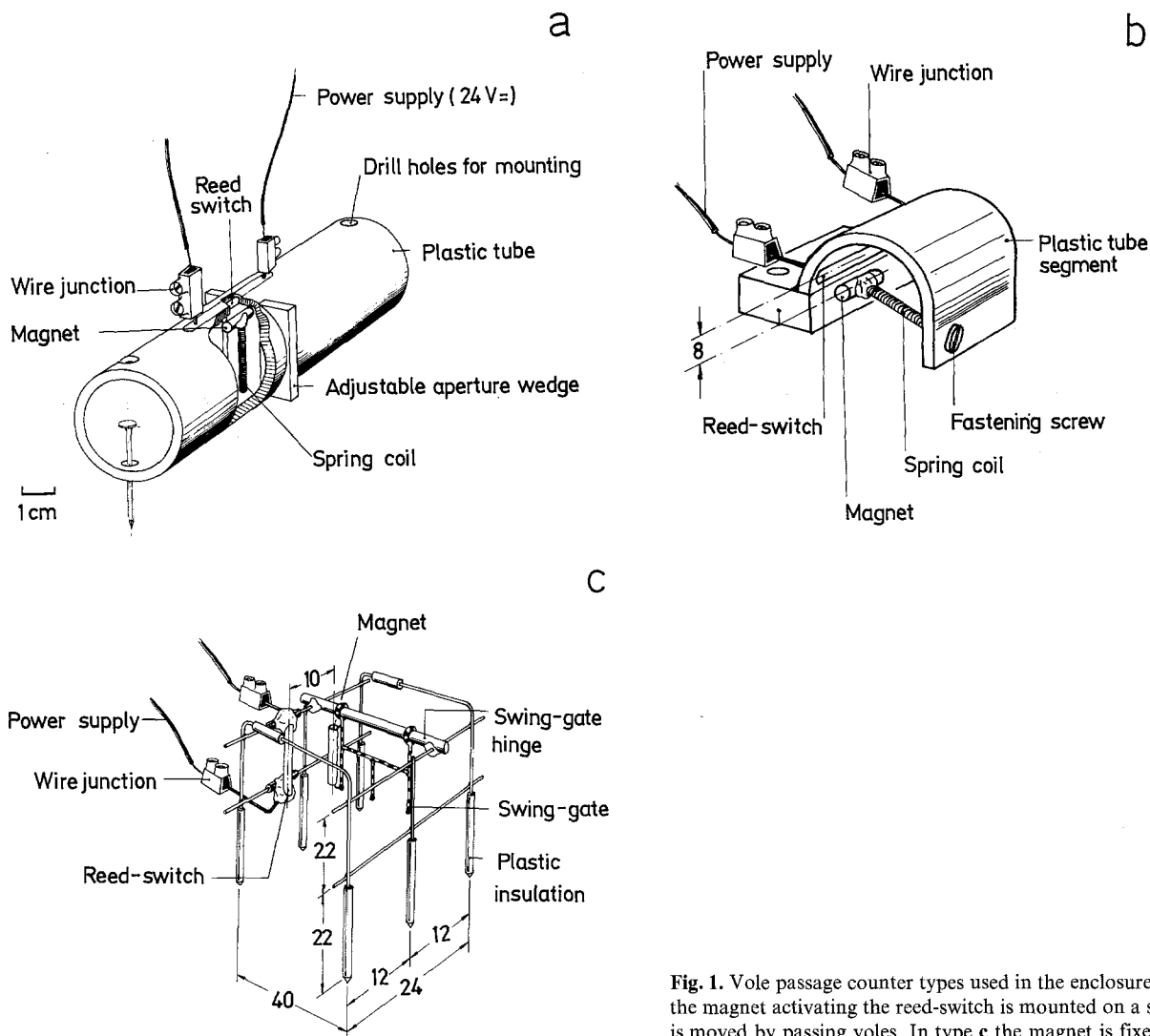


Fig. 1. Vole passage counter types used in the enclosure. In types a and b the magnet activating the reed-switch is mounted on a spring coil, which is moved by passing voles. In type c the magnet is fixed to a swing-gate

we closed with corrugated polystyrene sheets 50 cm in height. To keep out cats and birds we sheltered the enclosure completely with wire netting. The ground was originally well turfed. During preliminary tests with different types of passage counters, however, we had to enter the enclosure so many times, that all the grass was trampled down. In the period under report, therefore, there were only poor remains. Thus we established a feeding site – an overturned transparent plastic box was provided with a top-hinged swing door which served as a passage counter. The passages were recorded on a separate channel of the event-recorder (see page 63). Food was given ad libitum – mouse feed pellets, carrots, lettuce, grass, bread, etc. On a low platform in the enclosure we placed a cage of the type described by Lehmann (1976a) for measuring captive vole activities.

2. *The Colony.* After several preliminary tests on June 17 (1978) we released two adult specimens of *Microtus arvalis* – a male and a female trapped in the vicinity. On August 22 their first offspring became active above the ground (2 males, 4 females). These eight specimens made up the colony until April 2 (1979), when the old female died. Further development was then evaluated as follows. April 25: 4 juveniles (3 males, 1 female) above ground, thus total voles between April 25 – May 15: 6 males, 5 females.

Between May 15–24: two new litters with 5 males, 9 females, total 25 voles in the enclosure. On May 27 we reduced this number, leaving 3 males and 4 females. From these, new litters appeared above ground on June 13 and June 22 – at the end of June there were 22 voles active above ground.

During the experiment some voles were marked by clipping their fur, they thus could be distinguished by observation over certain periods. The old male released at the beginning was clearly observed all year.

In the cage placed in the enclosure between July and December we tested 3 males for about 4 weeks each (see Fig. 9). Between the testing periods they were kept in natural light and temperature conditions.

3. *The Passage Counters.* Initially, we used passage counters similar to those described by Mossing (1975): PVC-tubes with a magnet mounted on a spring coil. If the coil is displaced by a passing animal, the magnet activates a reed-switch (Fig. 1, a). This simple device is very dependable and therefore well suited for use in the field. Unfortunately we frequently observed the voles avoiding the tubes placed in their pathways: they tended either to pass beneath them or to dig their way underneath. The latter was observed especially when the tubes were placed at the exits of

the burrows. Thus the voles' emergence could not be controlled precisely. Therefore, we developed two other types of passage counters, also based on the activation of reed-switches by displaced magnets (Fig. 1, b, c). Both types operated well in the field, even during the cold winter 1978/79 with frost and under a snow cover. The semi-tube type (Fig. 1, b) was found to be suited best – it is less sensitive to interference from blades of grass or other objects carried into it by the voles. Observations demonstrated that the voles did not avoid these passage counters, and they never tried to dig under them. We believe that this is because the voles are not forced to leave the natural soil. To control the exits of the burrows, however, we had to use the wire-mesh type (Fig. 1, c) – obviously the voles require an obstacle-free view when inspecting their environment for several minutes before emerging.

These passage counters were always placed in discernible pathways and as far as possible at all frequented exits. The number of passage counters employed, therefore, varied due to the changing pathway system and to the number of open exits, but was in the mean about 15. The passage counters operated an event-recorder (Esterline-Angus). Using different channels, we always recorded passages at the exits, in the pathway system and at the feeding site, but we frequently connected groups of counters at both exits and pathways, in order to facilitate the evaluation.

The records of the event-recorder were analyzed at intervals of 30 min. To evaluate the voles' pattern in the course of the year we transformed these counts at each half hour to percentages of the total counts per day. This was necessary to adjust several significant changes in the recording conditions. On the one hand, the number of voles varied from 2 to 25, on the other, neither the pathway system nor the number and location of exits was constant. Especially during the months of September and March the voles were burrowing very actively. Thus we had to rearrange the positions of the passage counters several times. This means too, that the proportion of recorded passages at exits and in pathways varied, leading to incorrect conclusions about the amount and the proportion of passages actually occurring at these sites. Therefore, we present these counts as a summation only.

Results

The main features of the daily activity pattern of the voles are deducible from Fig. 2. It reflects the activity above ground of a male and of a female as recorded during a ten-day period. The counts of 18 passage counters are presented in three groups: a) 4 counters at the exits, b) 13 counters in the pathway system, and c) 1 counter at the feeding site. In the final graph (d) the records of all 18 passage counters are summarized. This figure demonstrates three distinct features:

1. The voles are more active during daylight hours than at night. This holds true especially for activity in the pathways which at night are only used occasionally. But this also applies to the frequency of emergence and of visiting the feeding site.

2. The records of the three groups of passage counters, as well as the summation demonstrate a fairly regular short-term rhythm during daylight hours. Beginning with a prominent peak shortly after sunrise a sequence of distinct peaks can be discerned following each other with a mean period of about 2 h. It is only during the hours before sunset that this sequence becomes irregular. During the night no regularity can be observed.

3. The beginning and the end of the period of increased diurnal activity above ground is phase-locked to the light-dark cycle. We

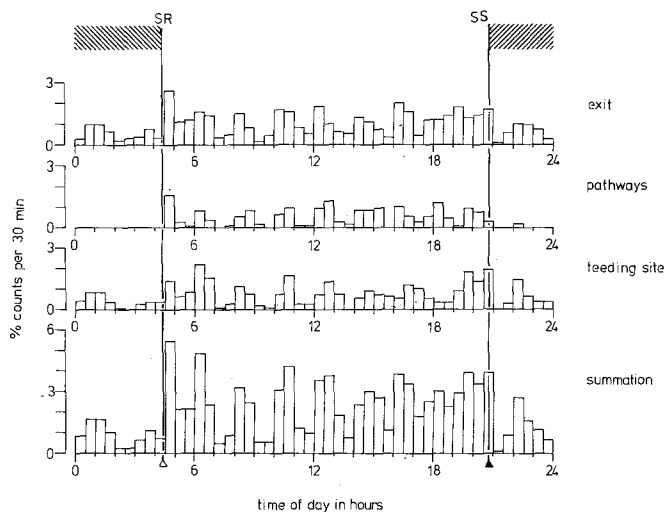


Fig. 2. Mean daily distribution of the activities of two adult *Microtus arvalis* at different sites in the enclosure within a ten-day period. Activity is expressed as a percentage of all counts recorded July 1–10 ($n=1,068$). SR sunrise; SS sunset. For details see text

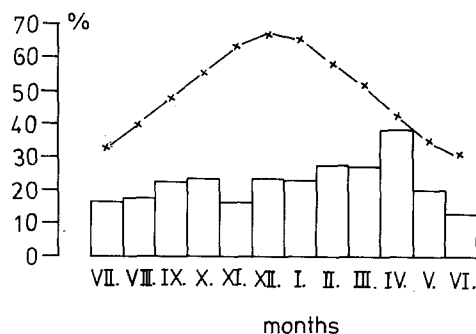


Fig. 3. Proportion of the vole activity at night over a one-year cycle (July 1978–June 1979). Columns: night-activity, expressed as percentage of the whole amount of activity recorded in each month. Curve: mean percentage of darkness during the 24-h-cycle in each month

measured a light intensity of circa 5 lx at the beginning as well as at the end of the diurnal activity phase.

This ten-day record of two voles during July is typical for the pattern we recorded all the year round in the enclosure. It was modified, however, in the course of the year by the photoperiod change, by weather conditions and by changes in the composition of the colony observed. In the following, these features and the influences of biological and environmental factors will be pointed out more in detail.

Day-Night Activity

The activity pattern recorded in the enclosure suggests that the voles are day-active throughout the year. In the mean only about 20% of all counts of the passage counters occur during the night between sunset and sunrise. But this percentage is not constant. There is a fairly continuous increase from July to a maximum value of about 39% in April, followed by a decrease to the low percentage of 17–23% during the summer again (Fig. 3). The remarkably high night activity in April may be caused partially by an experimental manipulation (see page 72), but this would not alter the general annual trend. Thus it is evident, that there

is no correlation at all between the percentage of night activity and the length of the darkness – from July to December the length of darkness increases from circa 7 h to 16 h but activity varies only between 17 and 23%. This can be seen also in Figs. 4, 5 with the activity high during the daylight hours. That means that no indication of a phase-shift in autumn and in spring is detectable, as it has been observed in *Microtus arvalis* by Oster-

mann (1956). This point will be discussed later on in connection with the activity pattern of voles kept in a cage within the enclosure.

For counts recorded at night, the significant decrease of as much as 25%, as compared to daytime, is very surprising. All caged voles tested so far were night active with respect to locomotor activity (at least during summer) and the caged voles in our encl-

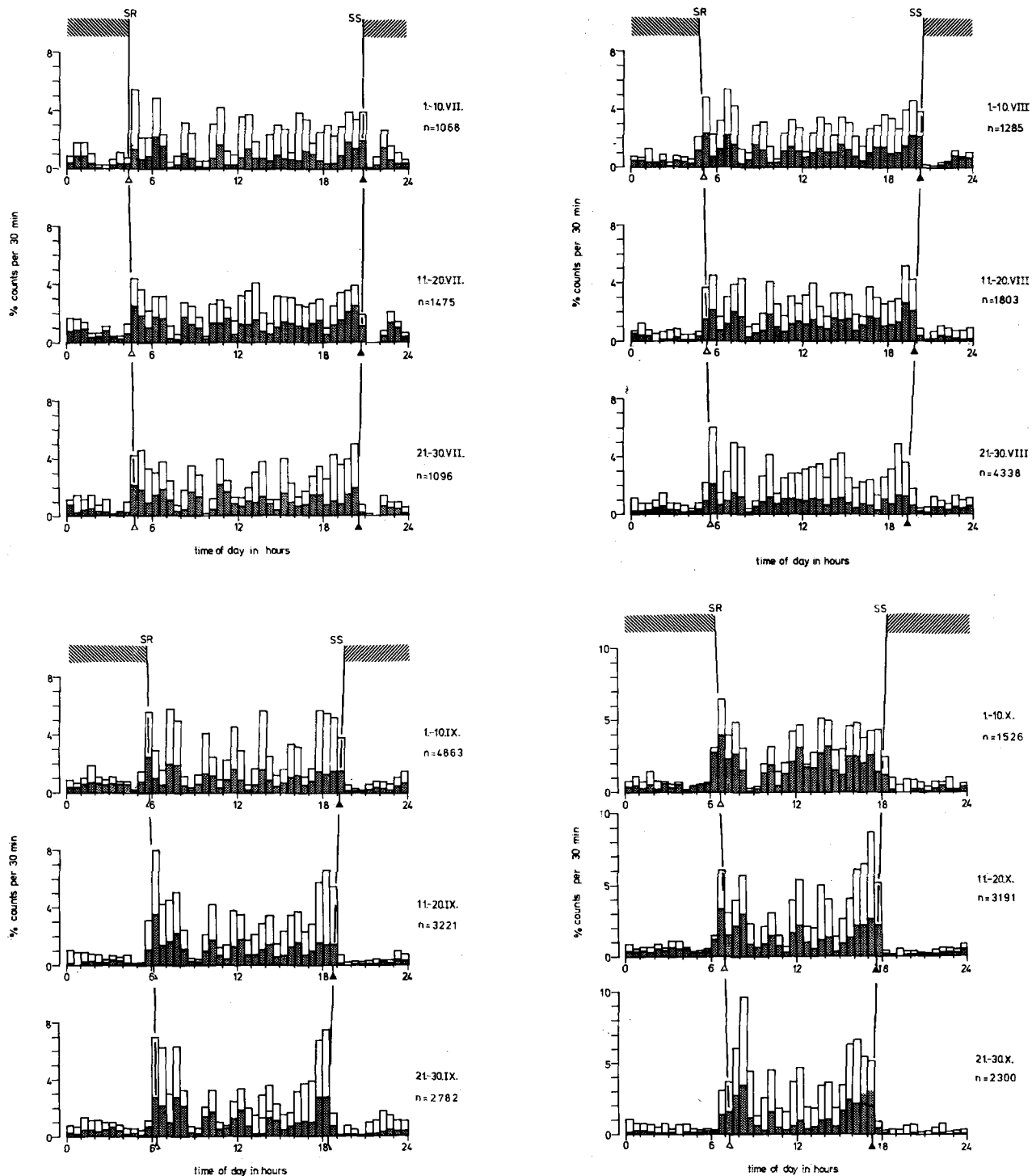
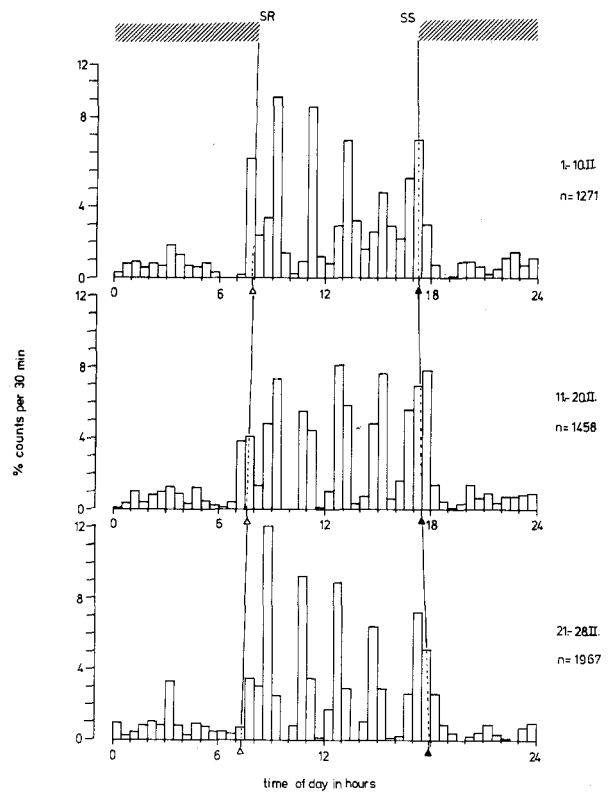
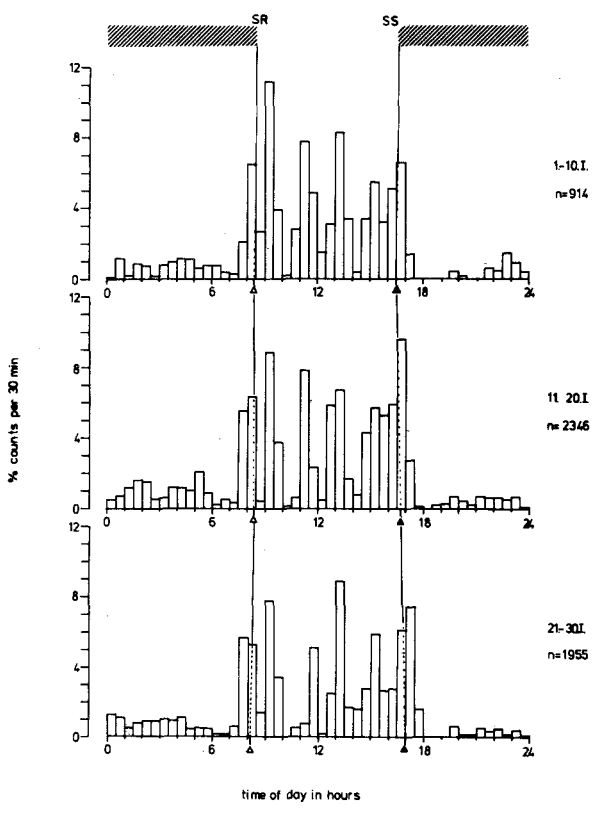
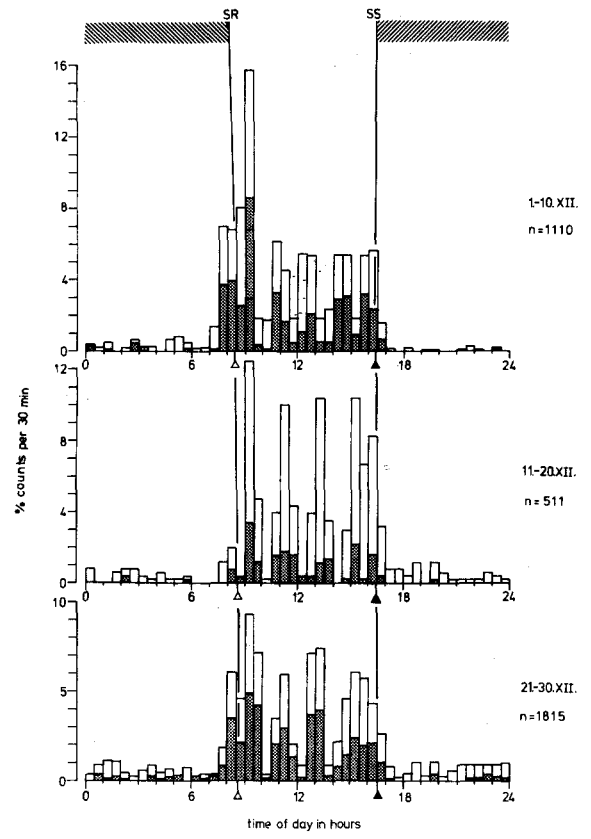
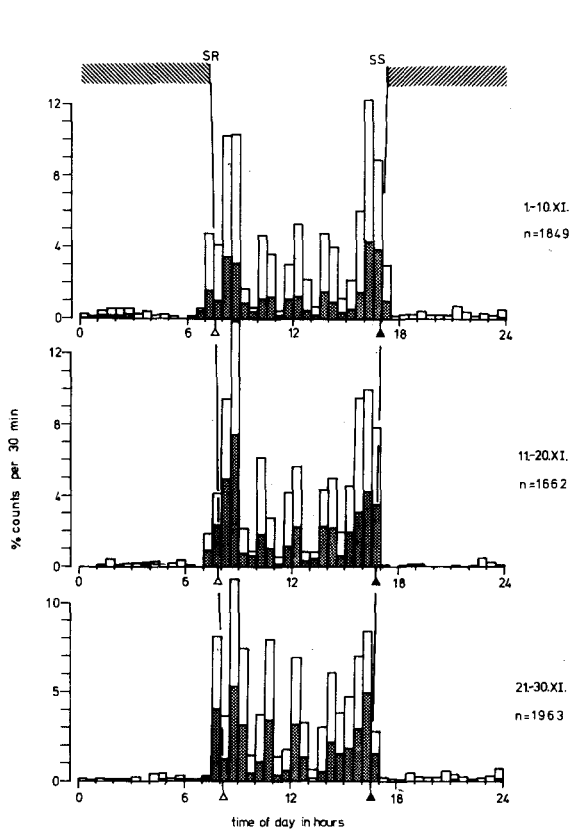
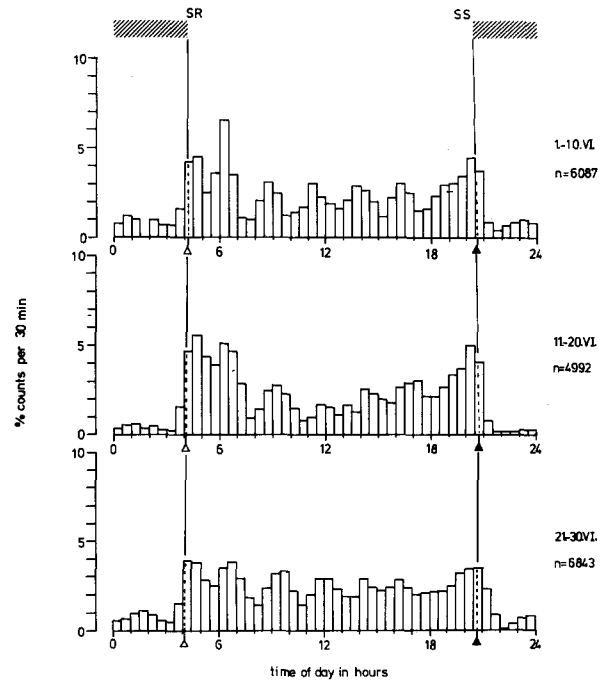
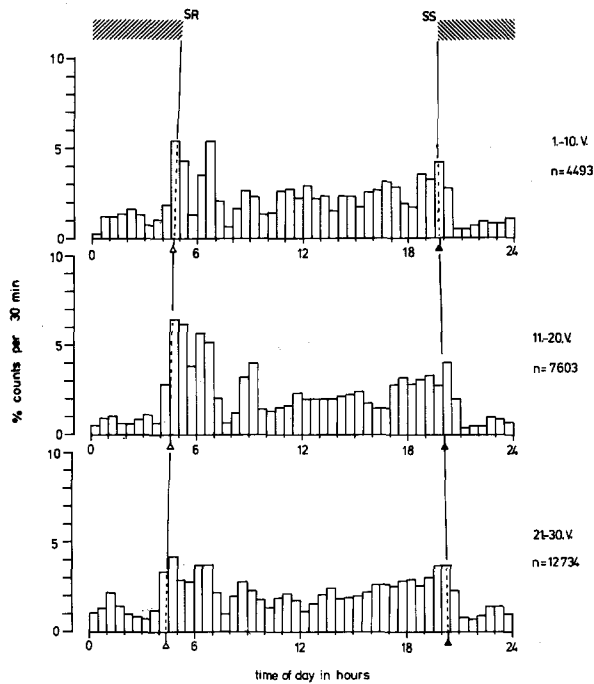
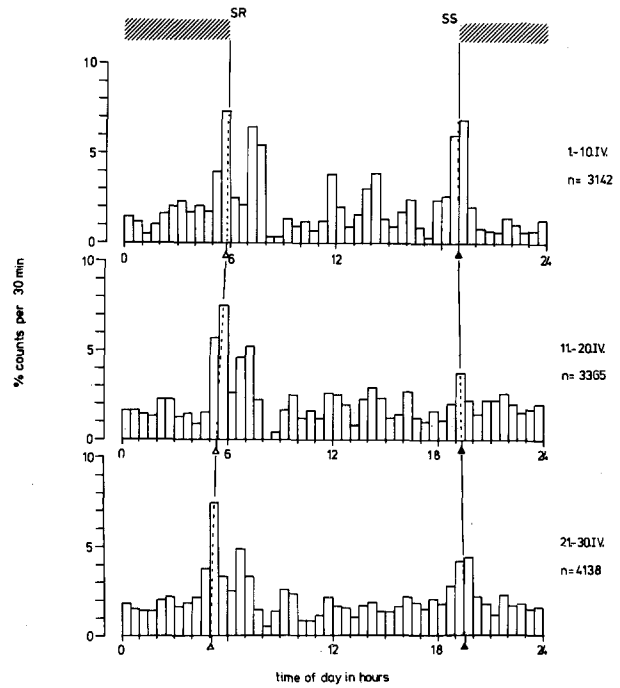
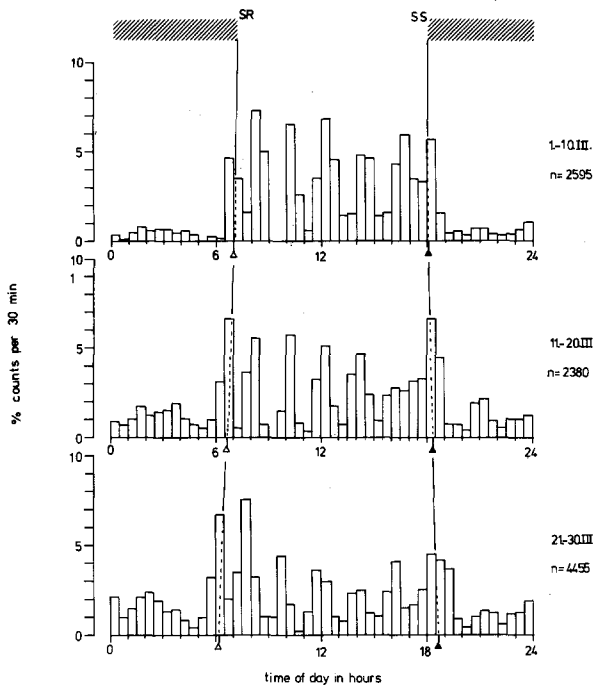


Fig. 4. Mean daily pattern of the colony of *Microtus arvalis* in the enclosure during a one-year cycle (July 1978–June 1979). Counts per 30 min over ten-day periods, each summarized and expressed as a percentage of this summation. *n* total counts per ten-day period. From July to December 1978, the proportion of counts recorded at the feeding site is indicated by the shaded area of the columns. SR sunrise, SS sunset





sure were wheel-running at night, too. These obvious discrepancies require accurate consideration of the reasons and of a possible methodological background.

The amount and the proportions of the different activities recorded can be seen from Table 1. Without any doubt the voles visit the feeding site less frequently at night than in the daytime. The reduction is about 80%. This must not necessarily indicate, however, that the time the voles spent feeding was reduced, too. It could be argued that under cover of night the duration of each visit was prolonged and in this way during few visits at night the voles could feed as extensively as during frequent visits in daylight hours. This hypothesis can be rejected.

Each foraging trip causes at least 4 spikes of the event-recorder – two spikes indicating emergence from and return to the burrow, and two spikes in between which indicate passing in and out of the feeding box entrance. Although the temporal sequence of single foraging trips cannot be read with certainty from charts, the overall impression suggests no actual differences between the sequences at night and in the daytime. This is confirmed, too, by several visual observations at night.

There is further evidence that only few foraging excursions, but with normal duration, occurred at night. The amount of food disappearing from the feeding site was significantly lower at night than in the daytime. We did not measure the proportions quantita-

tively (which would have caused regular disturbances) but based on reliable estimates it can be said that only about 20% or less food was taken away at night as compared to daytime. These estimates correspond well to the recorded proportions of visits at the feeding site (Table 1).

Coincident with the reduced number of visits at the feeding site at night is a reduction in the number of voles emerging from the burrows, too (Fig. 2, Table 1). This clearly results from the interrelation between emergence and visits at the feeding site discussed above. With respect to the increased locomotor activity of the caged voles at night, however, emergence of voles not connected with foraging trips is of special interest. Unfortunately this proportion cannot be discerned directly but must be concluded from other observations. On the one hand, there is very close agreement

between the patterns recorded at the exits and at the feeding site. This suggests that for the most part, emergence at night is due to foraging trips. On the other hand emergence not due to foraging trips is likely to be for excursions to other parts of the enclosure. This should be detectable by passage counters in the pathway-system.

As is documented in Fig. 2, however, there were only occasionally a few counts in the pathways at night. This is a typical feature which was recorded all the year. There are two alternatives of how this feature comes about – either the voles are not active on the surface at night, except for a few foraging trips, or they are probably active but do not use the pathway-system and therefore do not activate the passage counters. This is a crucial question. An attempt was therefore carried out to ascertain the voles' behav-

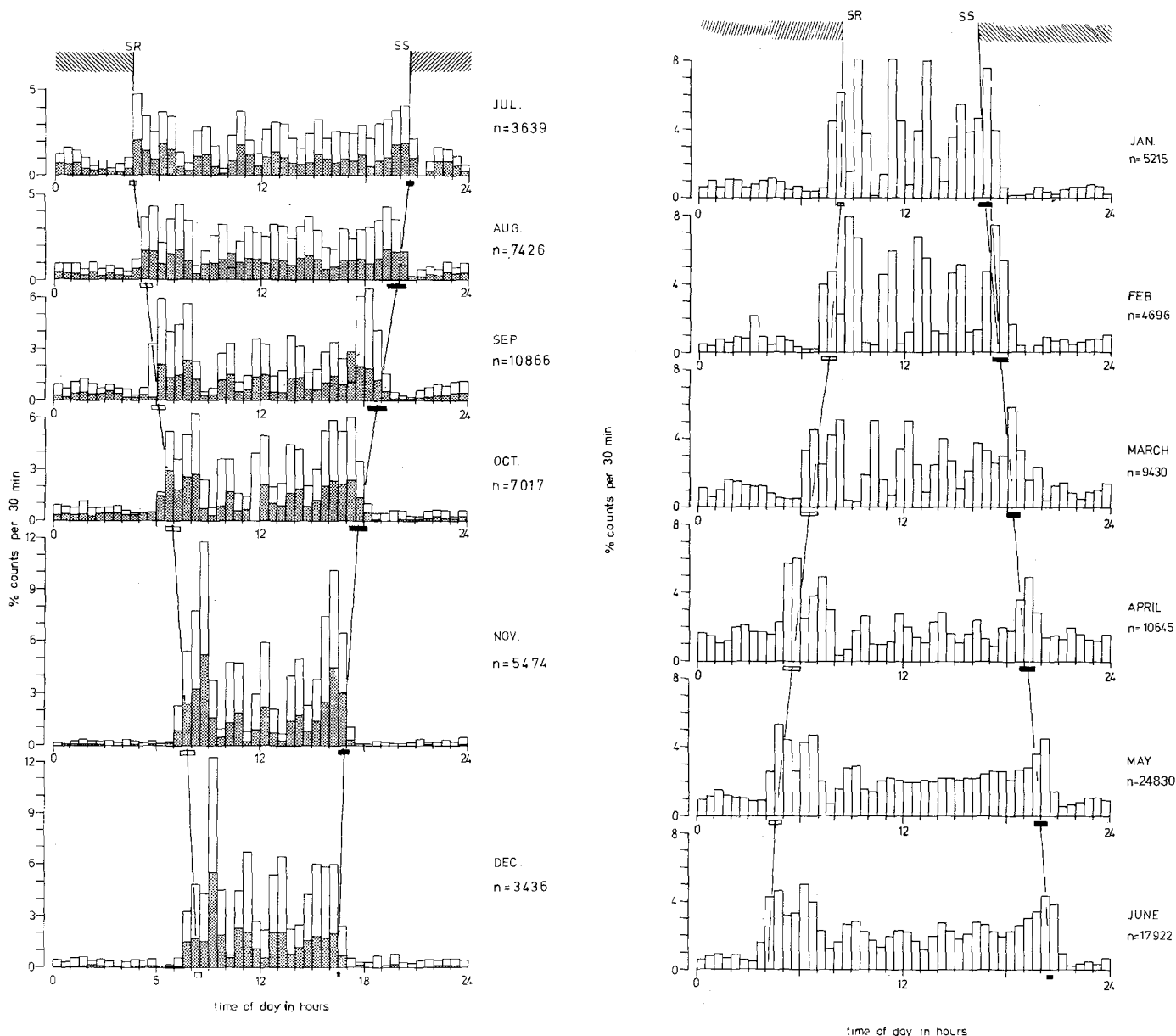


Fig. 5. Activity pattern of the colony of *Microtus arvalis* in the enclosure over a one-year cycle (July 1978–June 1979). Activity is expressed as a percentage of all counts recorded during each month. From July to December 1978, the proportion of counts at the feeding site is indicated by the shaded areas of the columns. *n* total counts in each month. *SR* sunrise, *SS* sunset

ior at night. Repeated visual inspections consistently revealed no obvious vole activity except at the feeding site or in the immediate vicinity of the exits. Thus it may be reasonably assumed that in our enclosure the voles markedly reduced activity above ground at night, whereas they were quite active during daylight hours.

As to the proportion of the different types of activity (i.e. emergence, running along the pathways and visiting the feeding site) in the course of the year, no definite conclusions can be drawn. This is due to the varying number of voles and of passage counters (see page 63). During a half-year cycle only, we therefore distinguished between records from "exits+pathways" and from the feeding site (Figs. 4, 5).

For the same reason the absolute amount of activity over the year cannot be deduced from our records. An exception is the months between September to March when the number of voles (3 males, 5 females) and the number of passage counters (16) as well as the arrangement of frequently used exits and pathways was fairly constant. In general, a markedly reduced activity above ground is indicated during the period without sexual activity. This holds true, even if extraordinary weather conditions during winter months are taken into account (see Fig. 8). The sudden increase in activity from February to March was due to the very intensive burrowing activity of the voles in March. They brought up a great quantity of earth out of the burrows and opened several new exits. The first juvenile specimens were then observed at the end of April.

The Short-Term Rhythm

The short-term rhythm stands out distinctly throughout the year (Figs. 4, 5). This pattern is caused primarily by the voles' feeding activity and is therefore in accordance with the behaviour recorded in captive voles. Beyond this there are several points of interest:

1. Feeding activity is most intensive during daylight hours although the voles stored food and consequently could feed in the burrows, too. But only during periods of unsuitable weather did they fail to visit the feeding site and therefore must have made use of their stored food (Fig. 8). This indicates that excursions to forage above ground make up quite normal behaviour during daylight hours. It is not only enforced in cage conditions which prevent storage. In natural conditions without a well stocked feeding site, these excursions may demand even more time and thus lead the voles to extended activity above ground.

2. The short-term rhythm stands out clearly, irrespective of the number of voles in the enclosure (2–25 specimens, see page 62). This is also in spite of the fact that most of the patterns presented are the result of ten-day records. A prior condition is that all voles have synchronized activity bouts. Especially during the period September–March, the voles' rhythm synchronization is obviated by an amazingly clear-cut periodicity. As there are no environmental time cues for the short-term periodicity this indicates an effective social synchronization. This supports the conclusions drawn by Daan and Slopeema (1978) from their trapping series.

3. A second precondition for the persistence of the short-term periodicity over ten-day periods is a precise phase-setting each day. Otherwise even small phase-shifts from day to day would obscure periodicity after summation. This phase-setting is realised each morning, as can be concluded from the correlation between the onset of both activity and sunrise (Fig. 4). In almost all records the morning peak is very prominent and clearly distinct from following peaks. In a similar way an activity peak coincides each day with sunset. But within 2–3 h before sunset, expected peaks are often not discernible. This suggests that the "free-running" short-term rhythm is again entrained by the light-dark cycle at the end of day. The entrainment is achieved either by shortening the preceding period (Fig. 4, December) or by splitting up a broad peak (Fig. 4, January).

4. Light intensity at the beginning as well as at the end of activity was measured in random tests at 5 lx approximately all the year round. But because a distinct threshold for both the beginning and end of activity for each day is difficult to determine, this value gives a rough estimation only. In the course of the year a distinct phase-shift can be seen – during the summer months activity starts at sunrise and ends at sunset whereas during the winter months activity is extended for at least 30 min each way. This change in phase-relationship suggests that the phase-setting of the short-term rhythm is not simply controlled by the light-dark regime but that a circadian mechanism may be involved.

Special Conditions

Changes in the voles' daily activity cycle came about for two reasons only – through juveniles beginning to venture from their burrows and through unsuitable weather conditions. The modifications of the pattern influenced by juveniles, as recorded during August to September, can be seen in Fig. 4. The female was not

Table 1. Activity pattern of *Microtus arvalis* in the enclosure as measured by passage counters. Values are given for the number of voles in each month, for the total of all counts recorded, the proportion of counts related to the day-night-cycle and the proportion of counts from "pathways+exits" to counts from the feeding site

Month	No of voles	Total counts	Daytime (counts in %)			Night (counts in %)		
			total	exits + pathway	feeding site	total	exits + pathway	feeding site
July	2	3,639	83,2	49,4	33,8	16,8	8,9	7,9
August	2/8	7,426	82,5	51,0	31,5	17,5	12,6	4,9
September	8	10,866	77,2	46,3	30,9	22,8	16,6	8,2
October	8	7,017	76,5	44,8	31,7	23,5	13,0	10,5
November	8	5,474	83,6	51,3	32,3	16,4	11,3	5,1
December	8	3,436	76,2	47,7	28,5	23,8	17,6	6,2
Mean		6,309	79,9	48,4	31,4	20,1	13,3	6,8

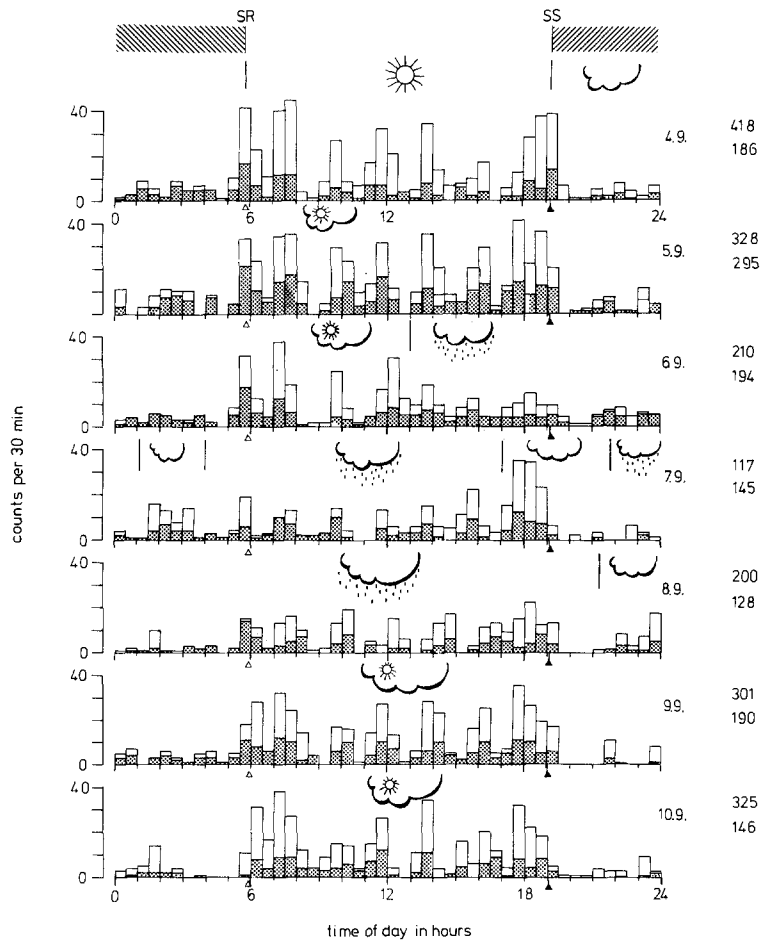


Fig. 6. Influence of wet weather on vole activity in the enclosure. The numbers on the right indicate all counts recorded at the exits and pathways (*above*) and all counts at the feeding site (*below*). For details see text. *SR* sunrise, *SS* sunset

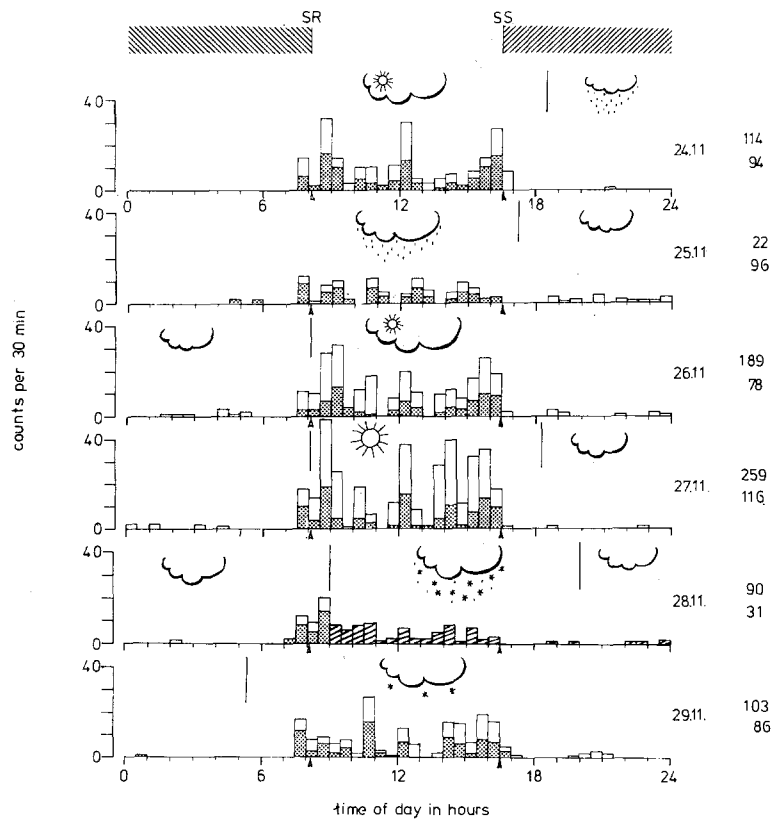


Fig. 7. Influence of different weather conditions on vole activity in the enclosure. The numbers on the right indicate all counts recorded at the exits and pathways (*above*) and all counts at the feeding site (*below*). The hatched columns only indicate counts at the exits (November 28). *SR* sunrise, *SS* sunset

detectable in the enclosure from the end of July until August 10. During this time the male hoarded to a significantly higher extent than before – especially during dawn and dusk he took pellets and pieces of carrots from the feeding site. The female reappeared at August 11 and the extensive hoarding was then continued by both male and female until August 22. On this day we observed 6 juveniles above ground for the first time. Up to August 20 the short-term rhythm is well expressed, there are eight clearly discernible peaks. In the last ten-day period of August, however, with the young voles active above ground, this sequence becomes irregular. Peaks only stand out clearly in the morning and evening hours. We observed the juveniles being very active at times when the adults were underground. Some days later the activity periods of all 8 voles were obviously synchronized (Fig. 4, September 1–10). The increase in readings from the passage counters from about 1,500 counts/10 days (August 1–20) to about 4,500 counts/10 days (August 21–September 10) corresponds well to the increase in the number of voles.

Later on we repeatedly observed that for several days after their first emergence the young voles were not synchronized with the short-term pattern of the adults. Whether, therefore, the non-rhythmic pattern recorded depends on an arrhythmic behaviour of the juveniles, or whether they have rhythmic activity bouts but

are not synchronized, or whether their short-term periods initially have another (higher) frequency than later, cannot be decided.

The amount of activity and the daily pattern of *Microtus arvalis* may be markedly influenced by certain weather conditions, too. Frank (1954) reports that, above all on cold and wet days, voles only rarely emerge. Our records confirm these observations and allow a quantitative estimation of the influences of climatic factors.

From Fig. 6 the voles' behaviour during wet weather over a period of seven days with moderate temperatures can be analysed. In the first few days the sky was clear or only partially clouded over. The pattern recorded is quite constant, prominent peaks of about equal height are repeated regularly up to the afternoon of September 6. With the onset of rainfall activity decreases markedly, but nevertheless small peaks are recorded in the intervals expected. Short breaks in the rainfall immediately cause vole activity bouts. (e.g. September 7 between 01.00–04.00 and 17.00–19.00 h., resp.). Rain finally stopped in the night of September 8 and now activity increases again, the pattern closely resembling that of the previous dry days. During the rainfall the counts recorded were reduced by an average of 33%. A closer analysis reveals that the counts from the feeding site decreased less, only about 23%, whereas readings from the other passage counters decreased

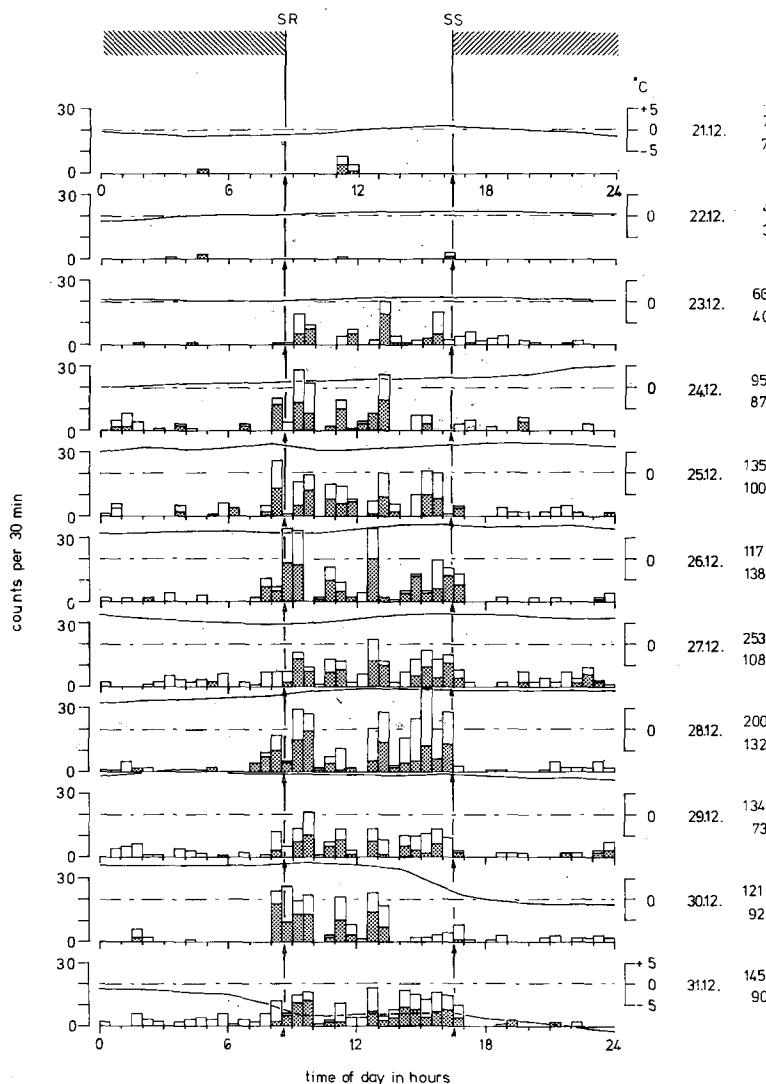


Fig. 8. Activity pattern of the colony of *Microtus arvalis* as influenced by different precipitation types (rain, sleet, snow) and under varying temperatures. The numbers on the right indicate all counts recorded at the exits and pathways (above) and all counts at the feeding site (below). SR sunrise, SS sunset. For details see text

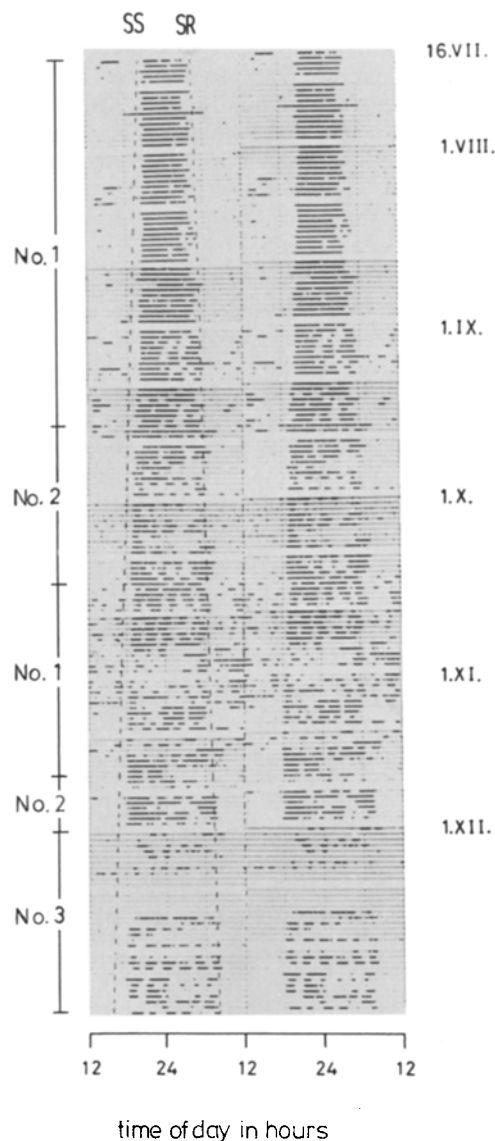


Fig. 9. Wheel-running activity of three adult males of *Microtus arvalis* as recorded in the cage within the enclosure. Testing periods of the males are indicated on the left. *SR* sunrise, *SS* sunset

as much as 40%. These remaining counts occurred mainly at the exits – that means the voles largely reduced excursions along the pathways, but visits to the feeding site were reduced to a lesser degree. Thus rainy weather with moderate temperatures reduces some types of vole activity but does not cease the pattern of emerging and feeding. This may happen, however, if it is rainy and cold at the same time, as demonstrated in Fig. 7. During the rainy day November 25, activity is about one half of the activity recorded the preceding dry day, resembling the features shown in Fig. 6. After two sunny days temperature decreased and the weather deteriorated to heavy sleet. Under these conditions the voles immediately ceased all excursions along the pathways as well as to the feeding site. The few counts recorded were caused by voles looking out of the exits and occasionally coming out for a very short distance to excrete. On the next day the temperature dropped further and a thin snow cover formed. The voles again became active above ground. They visited the feeding site and used the pathways, running on the surface or through tunnels

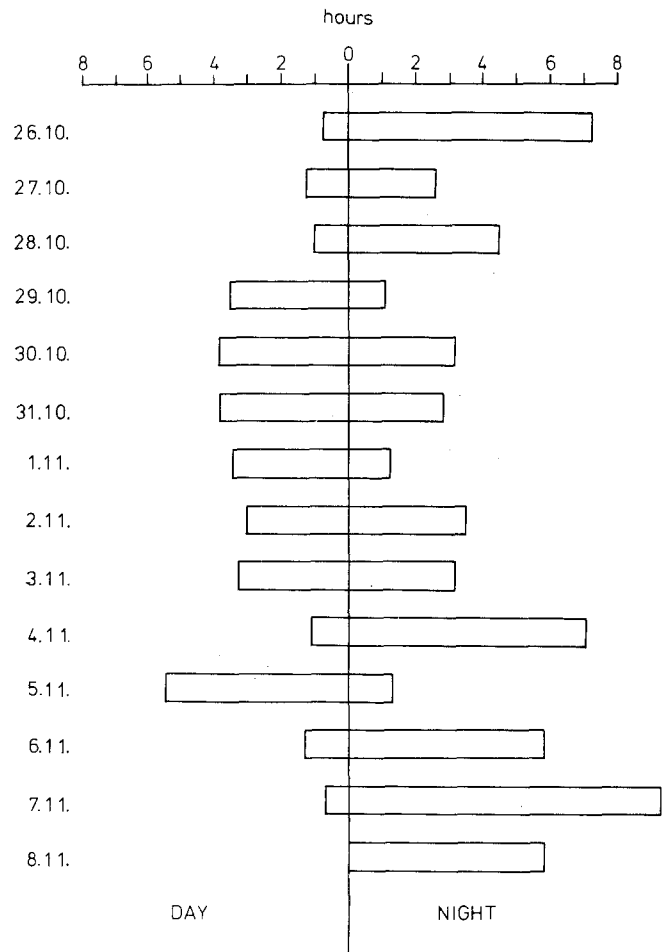


Fig. 10. Phase change of wheel-running activity of vole Nr. 1. during a two-week period in October/November 1978 (see Fig. 9). The columns indicate the duration of wheel-running activity each day (daytime on left, night on right)

in the snow. This demonstrates that it is the coincidence of wet and cold which the voles avoid as much as possible. It can be assumed that the loss of heat through wet fur is too extensive, whereas with dry fur cold is no problem to them.

Convincing evidence for this interrelation derives from Fig. 8. During three days (December 21–23) – with moist weather, temperatures about zero and the ground in the enclosure muddy – the voles only occasionally emerged. With increasing temperatures and the ground drying up they became very active. They opened exits which they had kept closed before and brought up a great amount of earth. They also gathered straw deposited in the enclosure and extensively stored all the food they could obtain. All these activities occurred almost exclusively during daylight hours. Beginning at 12.00 on December 30, within 24 h temperatures decreased suddenly from about +8° C to –10° C. This was accompanied by heavy precipitation – it fell for several hours as sleet and then as dry snow. On the next day the enclosure was covered with snow as high as 30 cm approx. It can be seen well in Fig. 8, that during sleetfall the voles stopped all activity. We recorded a certain amount of contacts at the exits only, caused by voles looking out without emerging. Later on, however, they became very active underneath the snow cover. Controls revealed that they used their normal pathway system. Passage counters from all parts of the enclosure were activated.

The Pattern of Cage Voles

During a half-year period (July–December) we compared the activity patterns of *Microtus arvalis* in the enclosure and in a cage. The cage was placed within the enclosure to ensure identical environmental conditions. We recorded the time the cage vole spent in the nest, its wheel-running activity, and its feeding and drinking (methods see Lehmann 1976a).

The pattern of all voles tested in the cage was in full accordance with those described for *Microtus agrestis* under natural light-dark conditions (Lehmann 1976a) – during daylight hours a distinct short-term rhythm of feeding and drinking was observed, at night a circadian rhythm of wheel-running activity. Thus the behaviour of the voles in the cage and in the enclosure was similar in that the short-term activity during daylight hours was essentially a feeding rhythm. However, the activity periods of the cage voles did not start at the same time as those of the voles in the enclosure, therefore the activity bouts did not coincide. At night when only small activity was recorded in the enclosure, the caged voles ran during daylight hours. But both before and after this ten-day period they spent only 10% of the time in the running-wheel in daylight hours (Figs. 10, 11).

As can be seen from Fig. 9, the cage voles are night active during the whole period July–December. A tendency to shift the phase towards day-activity was observed only for some days in September/October when a considerable amount of activity occurred during daylight hours. But both before and after this ten-day period they spent only 10% of the time in the running-wheel in daylight hours (Figs. 10, 11).

From Fig. 11 it is also evident that the time spent by the voles in the running-wheel remains fairly constant throughout the half-year period of investigation: irrespective of the length of darkness they run on the wheel about 360 min. This means

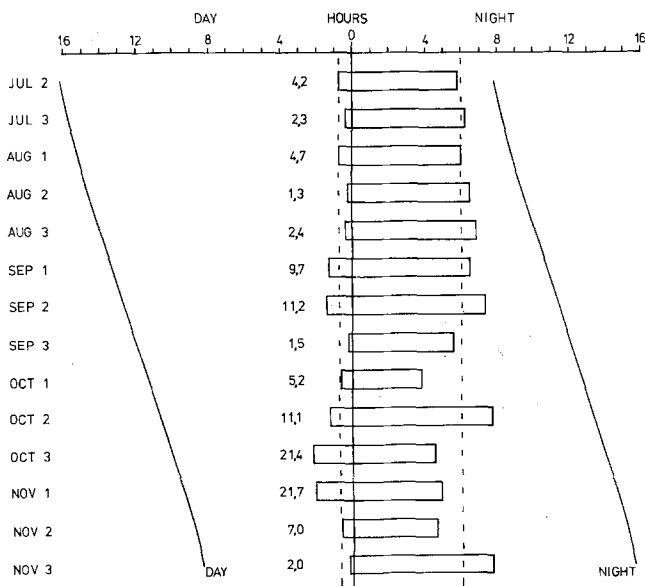


Fig. 11. Independence of the duration of wheel-running activity from the photoperiod, as evaluated from Fig. 9. Each column represents the respective duration of wheel-running activity (in h) per night and per daytime, given as mean values of ten-day periods. Dotted lines indicate the average duration of both daytime and night activity during the five months. The numbers show the percentage of wheel-running activity during daylight hours (*left*) and darkness (*right*). *Slanted lines*: duration of daylight hours (*left*) and darkness (*right*)

that although the beginning and the end of the night activity period is clearly correlated with the light-dark cycle, the amount of activity per night is constant. This is achieved by rest periods which the voles take with the lengthening of the night. One might speculate that this constant amount of wheel-running activity indicates the independence of this behaviour from an annual cycle, e.g. sexual activity.

As a further approach towards understanding the correlation in nature to the circadian wheel-running activity we offered a running-wheel to the voles in the enclosure as well, for a period of a month, from March 22 to April 18. The first time the voles used the wheel was on the third day after its installation. Although the subsequent pattern was not constant some features can be pointed out. A typical sequence of ten days is shown in Fig. 12.

1. The voles preferred running on the wheel during darkness. On most days wheel-running started at sunset and stopped at sunrise – an analogy to the behaviour of the cage voles. On some days, however, the wheel was used during the daylight hours to

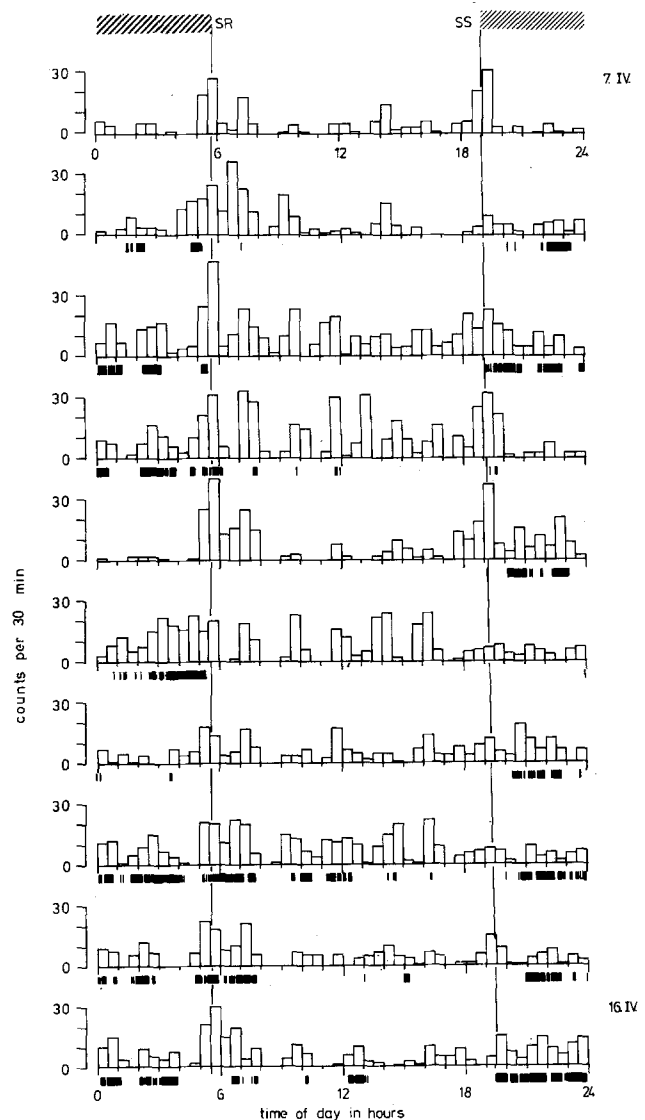


Fig. 12. Activity pattern of the colony of *Microtus arvalis* in the enclosure as recorded by passage counters (*columns*) and from the running-wheel (shown in black below each corresponding day). For details see text. *SR* sunrise; *SS* sunset

a remarkable extent (e.g. April 14). We could not detect any reason for this occasional change in the pattern.

2. During the nights with a significant amount of wheel-running the proportion of counts from the passage counters always increased markedly. This is due to the fact that the voles frequently interrupted wheel-running for short visits to the feeding site. This behaviour is also in accordance with the behaviour recorded in cage voles (Lehmann 1976a, b).

3. In the enclosure wheel-running activity was always suppressed by rainy weather. In the cage voles we could not observe this, because the cage was sheltered against rain.

4. During the period of investigation we could easily discriminate between an old male, an old female and their offspring (6 voles born in August 1978). Therefore it became evident by observation that wheel-running was a privilege of the old male which he defended jealously against the young voles. When the old male ran on the wheel he was never disturbed – when a young vole ran on the wheel it immediately left it on the appearance of the old male. At the end of the annual cycle reported in this paper we placed two running-wheels in the enclosure. The old male claimed both wheels, running from one wheel to the other to chase off other voles trying to use a wheel.

Thus, these experiments revealed similarities between the circadian pattern of wheel-running of both enclosure and cage voles. The fact that wheel-running in the enclosure was obviously a privilege of dominant specimens leads us to assume that it is not primarily motivated by fear or an urge to escape.

Discussion

The most outstanding feature of the voles' activity pattern is the short-term rhythm – at least from the circadian point of view. If “zoologists have come to understand circadian rhythms as innate programs matching the day outside in an adaptive manner” (Daan and Slopsema 1978) the problem with respect to the short-term rhythm arises, namely, to which periodic feature of the voles' environment should a behavioural rhythm of ca. two-hour periods refer. The most obvious approach to this problem derives from the fact that the short-term activity is essentially a feeding rhythm. This is without doubt evident for cage voles (*Microtus agrestis*: Lehmann 1976a; *Microtus arvalis*: Daan and Slopsema 1978; Lehmann unpubl.) as well as for *Microtus arvalis* in our enclosure. The close correlation to metabolic demands becomes also evident through the dependence of the short-term period length on the body weight. This was demonstrated by Daan and Slopsema (1978) who analysed data from 7 species of *Microtinae*. This does not mean, however, that metabolic demands directly control the short-term rhythm. There are striking similarities to the concept of circadian oscillators (Erkinaro 1973). Our knowledge of the endogenous controlling mechanism has been recently considered by Daan and Aschoff (1980).

Independent of these considerations, however, the question arises as to what might be the functional meaning of the short-term rhythm and its presumed adaptive value for vole survival. Daan and Aschoff (1980) stress the point that a regular pattern of stomach filling might guarantee an optimal breakdown of celluloses with the help of microbial enzymes in the gastrointestinal tract. Thus, for animals feeding like voles on poor nutritional vegetable matter, regular foraging could be advantageous for physiological reasons. From this approach the voles' short-term activity can be understood as a strategy to overcome long and dangerous daylight periods – to ensure a regular food intake at intervals

dependent on physiological properties on the one hand, and to reduce the risk of predation by synchronized surface activity to achieve “safety in numbers” (Daan and Slopsema 1978) on the other hand.

There is good evidence for this concept, deriving from several observations. Controlling a series of traps at intervals of 20 min throughout the day, Daan and Slopsema (1978) revealed a significant gap in trappings for about one hour after sunrise and before sunset. They point out that this makes up an optimal pattern to reduce time spent above ground. Beginning and ending daytime with a rest period leads to five activity bouts within the short-term rhythm during daytime in September. In the enclosure, however, we recorded a contrast in temporal distribution: the voles clearly exhibited distinct peaks after sunrise and before sunset – thus they had seven activity peaks during daytime in September (Figs. 4, 5). This is an important contrast between the two experiments.

Further evidence that the short-term rhythm is a strategy to overcome critical daylight hours derives from the fact that it only stands out during daylight hours. At night feeding activity occurs in frequent, but short bouts at rather irregular intervals. This pattern has been recorded consistently in cage voles as well as in the enclosure. This indeed strongly suggests that the presumed adaptive function of the short-term rhythm is related to daylight hours. Daan and Slopsema (1978) and Daan and Aschoff (1980) put forward the hypothesis that the crucial point here is the predation risk an active vole runs on the surface during daylight hours. These considerations about the functional background of the short-term rhythm basically infer that the voles' surface activity at daytime is enforced by foraging demands, and further, that the “true” phase of activity is at night, presumably because of a lower risk of predation. However, there are several reasons for questioning this point of view.

If the voles' short-term rhythm is conceived to be a strategy to ensure food intake during dangerous daylight hours, major feeding activity should be expected to occur at night. But there is no experimental evidence for this assumption. In the enclosure we recorded only few visits to the feeding site during the night and the amount of food taken was also low. Both the reduction of recorded visits and the reduction in estimated food intake were down on daytime values by about 80%. As can be evaluated from the records, cage voles definitely spend more time feeding during daylight hours than in darkness (e.g. Lehmann, 1976a). The proportion of food intake as measured in our laboratory was 45% at night and 55% during the daytime (Wessels unpubl.). These data suggest that food intake of the common vole is more probably decreased than increased during the night.

Moreover it must be emphasized that a short-term rhythm of feeding activity does not imply a need for activity above ground. Voles are well known to store food and in our enclosure they did so to a large extent. Thus they could easily feed underground and were not forced to go on foraging trips on the surface during daylight hours. This is clearly demonstrated by the voles' behaviour on cold and wet days, when they did not leave the burrows for several days in succession (Fig. 8). Nevertheless, under normal weather conditions they were active on the surface as regularly as the cage voles which were completely prevented from storing food. In the field, of course, food will hardly be available as easily and as plentifully as in the enclosure. But except for during the climax of a population cycle, food should always be available in surplus, thus allowing storage. This holds true at least for our investigation region.

In addition, we recorded other activities in our enclosure like running through the pathways, burrowing and storage, all nearly

exclusively during daytime. This suggests that extended activity on the surface during daytime is quite common – to a far greater extent than the minimum necessary for a guaranteed food supply. It follows from this that we must question the conventional assumption that the voles' main activity phase is at night. Our information about the circadian activity pattern of *Microtus arvalis* derives from three types of experiment:

1. Caged voles exhibit maximum locomotor activity during darkness. Measured as wheel-running activity it was demonstrated to be controlled by an endogenous circadian rhythm (Lehmann 1976a; Daan and Slopsema 1978). For *Microtus agrestis* it has been shown that this circadian rhythm is entrained by the light-dark cycle and that the overt activity is suppressed beyond a threshold of light intensity during the dark phase of the LD-regime (Lehmann 1976a).

2. Through controlling traps in the course of the day, some authors recorded best trappability at night, whereas others recorded significantly more catches during daytime (Hatfield 1935; Hamilton 1937; Brown 1956; Daan and Slopsema 1978).

3. In our enclosure we recorded minimum surface activity at night. This low activity was in fact related to short foraging trips, whereas no activity in the pathway system was detectable. This is in accordance to the observations of Frank (1954) who also reported that the voles in his enclosure were predominantly active during daytime. On the other hand, with a running-wheel available, the voles in the enclosure exhibited a significant amount of activity at night, too. Thus, the information available on vole activity behaviour at night is rather contradictory.

We assume that these contradictions can be understood only if we consider the voles' activity pattern in the context of their social structure. This is primarily characterized by strict territorial behaviour, which is made obvious by the well developed pathway-systems as well as by large fluctuations in number, which result in the typical population cycles. On the one hand, this makes it necessary for the voles to resolutely control and defend their territory and on the other, with increasing number, for them to venture into and to explore the surroundings and probably to extend their territory. We would like to put forward the hypothesis that the complex activity pattern of the voles can be conceived as a strategy to overcome social competition during population cycles.

In our view the synchronized short-term activity during daytime is intended to maintain the territory of a kin. The voles move within a pathway-system where they are known to have excellent spacial orientation and therefore a good chance to escape from day-active raptors. The pathways lead to the feeding sites and thus allow foraging in relative safety. However, through these regular foraging trips, they control their territory as well, and most probably leave scent marks at the same time. This may simply happen through surface contact when running through the pathways, but also by marking with excreta. This is indicated by the fact that cage voles always excrete at the beginning of an activity bout, and it is also indicated by the distinct excretion sites spread over the territory. Only during very unsuitable weather will the voles excrete in the immediate vicinity of an exit. Evidence suggesting that the short-term activity in daytime is in fact essentially related to repeated controls of the territory, derives from the voles' behaviour in our enclosure. The normally concurrent patterns of foraging and using the pathways were disjuncted by the availability of food at only the one feeding site. It can be well seen from the records that under these circumstances the voles visited the feeding site immediately after emergence, but then used the pathways leading to other sites in the enclosure. In continuation,

we suggest that the obvious synchronization of the short-term activity directly results from the necessity to defend the territory – it may certainly be advantageous to be present when the neighbours are active and there is a danger that they might extend their territory.

Evidence for a functional interrelationship between territoriality and activity pattern has been pointed out in kangaroo rats (*Dipodomys microps* and *Dipodomys merriami*) by Kenagy (1976). Comparing the onset of activity in a free-ranging population with the onset of activity of several isolated captive kangaroo rats he found a surprisingly small variation in the population, but a very broad distribution in the caged specimens. He discussed this difference with respect to competition and the establishing or maintaining of exclusive utilisation of space. If these considerations of the functional role of the circadian rhythm hold true, they offer a convincing explanation of how the short-term activity pattern of about two hours could have come about without reference to an environmental cycle.

Although the reasons for the regular vole population cycles are still under discussion (Charnov and Finerty 1980) it is quite clear that growing competition during population increase leads to a differentiation between residents and dispersers. After the cycle climax, the population is reestablished by the surviving residents. These residents will most likely be specimens which could defend their territory and therefore their food supply. If regular and well-timed controls of the territory are advantageous in the competition for space, these specimens will have an increased chance to survive and to establish a new population. Under these conditions the temporal activity pattern would be strongly favoured by selection. This could explain the evolution and maintenance of the endogenously controlled short-term rhythm without substantiation by an environmental cycle.

The circadian pattern of night-activity, on the other hand, could be then considered as exploratory and dispersal activity outside the pathways and probably outside the territory, as is indicated by some observations. The first observation refers to the circadian variation of trappability. If activity at night is characterized by movements outside the pathways – whereas activity at daytime is characterized by movements within the pathways – the position of traps can be expected to have a great influence on trapping success during a 24 h cycle. Traps inside the pathways should show highest trappability in the daytime, whereas traps outside the pathways should be more successful at night.

Unfortunately, we are not aware of any investigation which has explicitly tested the effect of the trap position, but it is most likely that contradictory results of trapping observations result from differences in the trap position. In our field investigations (Sommersberg 1979), the traps in the pathways accounted for as much as 87% of all catches during daytime, whereas Daan and Slopsema (1978) who placed the traps in grid pattern, revealed significantly more catches at night than at daytime.

Further confirmation that night activity represents exploratory behaviour may be drawn from the observation that captive voles frequently interrupt wheel-running for short visits to the feeding site (Lehmann 1976b). This can be seen from records of cage voles as well as from records in our enclosure. In the enclosure it was evident that the voles visited the feeding site, but did not really feed. This suggests, that wheel-running represents locomotor activity rather intended to discover food than to forage for it.

The reduced activity at night in the enclosure thus could be due to the fact that only one kin formed a colony. There was neither competition for space nor necessity to explore the vicinity of the pathway-system for food after the voles had once explored

it. The use of the running-wheel in the enclosure – mainly by the dominant male – might therefore reflect an innate motivation to explore, which had been previously suppressed by the special conditions of the enclosure.

This hypothesis of the functional meaning of the voles' complex activity pattern is an attempt to piece together those observations so far available. The role of the short-term activity rhythm as a requirement to establish and maintain territories, thus enabling the voles to survive the climax of a population cycle, appears fairly conclusive to us. The hypothesis seems less convincing with respect to the function of the night-activity within the circadian pattern – in both captive and free-ranging voles. Thus the evaluation of more reliable information on the circadian activity rhythm within the course of the year is of particular interest. This would enable deeper insight into the ecological significance of the temporal structure in vole behaviour.

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