

Short-Term and Circadian Rhythms in the Behaviour of the Vole, *Microtus agrestis* (L.)*

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Summary. The activity behaviour of the vole, *Microtus agrestis*, has been recorded in order to investigate the relationship between short-term rhythm and circadian rhythm. A simple device was developed, allowing separate monitoring of the time spent in or outside the nest, wheel-running, eating and drinking. Under natural light conditions during summer, a distinct differentiation between a short term rhythm of eating and drinking during the day-time and a circadian rhythm of wheel-running during the night was observed. The short-term rhythm depends closely on metabolic demands (hunger, thirst, excretion). Control of these demands by an endogenous oscillation could not be substantiated. The circadian rhythm of wheel-running activity is, however, controlled by an endogenous oscillation, synchronized by light conditions. It is subjected to seasonal variations. a) The threshold of light intensity below which wheel-running occurs is lowest during summer (< 0.5 lx) and is higher during spring and autumn (> 5 lx). b) Wheel-running is controlled by a circadian oscillation during summer only whereas it is an integrated part of the short-term rhythm during spring and autumn (experiments during the winter have not yet been performed). Experiments gave evidence that the properties of the cage can deeply influence the amount and pattern of wheel-running activity. It is concluded that wheel-running reflects a certain level of excitation, which may be caused by different behavioural intentions. The seasonal changes of the control of wheel-running activity are discussed with respect to this assumption. The relevancy of locomotor activity patterns as usually recorded in the laboratory to reveal the physiological and ecological significance of endogenously controlled behavioural patterns is discussed.

Introduction

Activity patterns of captive field voles (*Microtus agrestis*) and of other *Cricetidae* are rather complex. The basic temporal structure is a *short-term rhythm*: activity

* Supported by the Deutsche Forschungsgemeinschaft

bursts and rest times alternate more or less regularly in periods of about 2–3 h (Crowcroft, 1954; Brown, 1956; Ostermann, 1956; Aschoff, 1962; Erkinaro, 1969). This short-term rhythm is influenced by the light conditions during the 24 h-cycle: the duration of activity time in relation to rest time is altered either during day-time or during the night; this yields a *24-h-rhythm*. Whether diurnal or nocturnal activity is dominant depends on an *annual rhythm*: the voles are nocturnal in summer but diurnal in winter (Ostermann, 1956; Erkinaro, 1961, 1969, 1972 b, 1973 a; Stebbins, 1975).

The control of all these rhythms by exogenous and endogenous factors as well as their ecological significance is not yet completely understood. This applies especially to the short-term rhythm which cannot correspond directly to a geophysical cycle. One may wonder therefore, how it is adapted to the 24 h-cycle. The investigations reported in this paper have been designed due to the assumption, that mere “activity” recording may not be sufficient to analyse the complex temporal structure of the activity behaviour. Therefore, the behaviour was recorded more in detail, monitoring the periods spent in the nest, eating, drinking, and wheel-running. Special efforts have been made to avoid disturbances of the behaviour of the captive voles by cage-conditions.

Material and Methods

All specimens of *Microtus agrestis* were captured at the same place near Cologne. Most of them were used for experiments immediately after capture, otherwise they were kept under natural light conditions.

Experiments under artificial light conditions (bulbs, stabilized low-voltage supply) were carried out in a light- and soundproof chamber with constant temperature (20° C). Activity under natural light conditions was recorded in a greenhouse; some irregular illumination during the night from buildings in the vicinity could not be avoided completely, but intensity was lower than 0.01x. Temperature was controlled (20° C), but could increase up to 25° C on sunny days.

The experimental cage is shown in a plane view in Figure 1. Square dimension is 25 to 30 cm, height is 25 cm, the walls are constructed from opaque plastic. The nest is a closed wooden box,

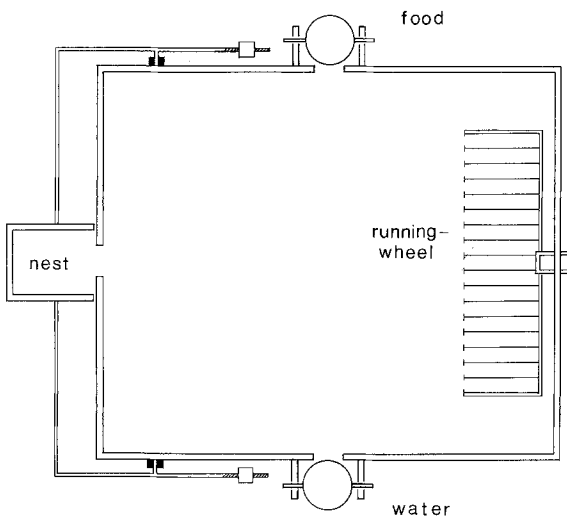


Fig. 1. Plane view of the experimental cage for monitoring periods spent in the nest, uptake of food and water and wheel-running. For details see text

balanced on a tip contact which is closed when the vole is inside the nest. The balance can be adjusted so that movements of the vole inside the nest can be recorded with different sensitivity. Nesting material is always provided.

Food and water are accessible from two glass tubes, attached like pendulums to the side-walls of the cage. Each time the animals eat or drink, the tubes are deflected and begin to swing. A small magnet on the tubes then activates a reed switch. The cylindrical food pellets (altromin Diät, Fa. Altrogge, Lage) are piled up in the tube and can be gnawed through a wire-mesh at the end. Thus the voles can eat only in small portions directly at the tube, but cannot catch a pellet and then eat elsewhere. By these arrangements eating and drinking can be recorded rather accurately. It stores an amount sufficient for 3 days.

The running wheel has a diameter of 20 cm. Once during each revolution a magnet on its axis outside the cage activates a reed switch.

The bottom of the cage consists of an inflexible wire-mesh (mesh-size 0.5 cm) without litter. Feces and urine fall through the mesh into a container so that the bottom is always clean.

All activities monitored were recorded by an Esterline-Angus event recorder. Thus, beginning and duration of the events could be evaluated, but not the amount of activity. Chart speed was varied from 20 mm/h to 200 mm/h.

Results

The Short-Term Rhythm

From Figure 2 it is evident, that "activity" of *M. agrestis* during day-time is quite different from "activity" during night. Between dawn and dusk the voles leave the nest in regular intervals only for eating and drinking. It never happens that they turn around the wheel during day-time in summer. Thus the short-term rhythm is closely correlated with metabolic requirements. This is also supported by observations that the voles usually first excrete when they have left the nest and then eat and drink. (Feces are only exceptionally found in the nest of *M. agrestis*.)

The properties of the short-term rhythm were investigated by analysing sequences of the periods without wheel-running activity. The frequency distributions of the duration of the activity time α' (time spend outside the nest), of the rest time ρ' (time spend inside the nest) and of the periods τ' , composed of α' plus succeeding ρ' as shown in Figure 3 are representative for all 10 specimens tested during summer. The mean period length is 129 ± 11 min, rest time averages 112 ± 9 min and activity time 17 ± 6 min. The period length as well as the duration of α' and ρ' show no regular variations during the day-time, except the first rest time and period, which are shorter than the mean. Therefore some information whether the short-term rhythm is controlled by an endogenous oscillation or by metabolic demands can be expected from a correlation analysis: a long τ' should be compensated by a succeeding short τ' (and vice versa), resulting in a negative correlation, when the rhythm is controlled by an oscillation. Negative correlations should be expected also between succeeding α' and ρ' and between succeeding ρ' and α' , if the period length is controlled. The results of the analysis (Table 1), however, reveal no uniform trend to negative correlations. On the contrary, between succeeding periods, especially those composed of ρ' plus α' , positive correlations are indicated. A tendency for negative coefficients is observed merely between the duration of a rest time and the succeeding activity time. This is in agreement with the results of Erkinaro

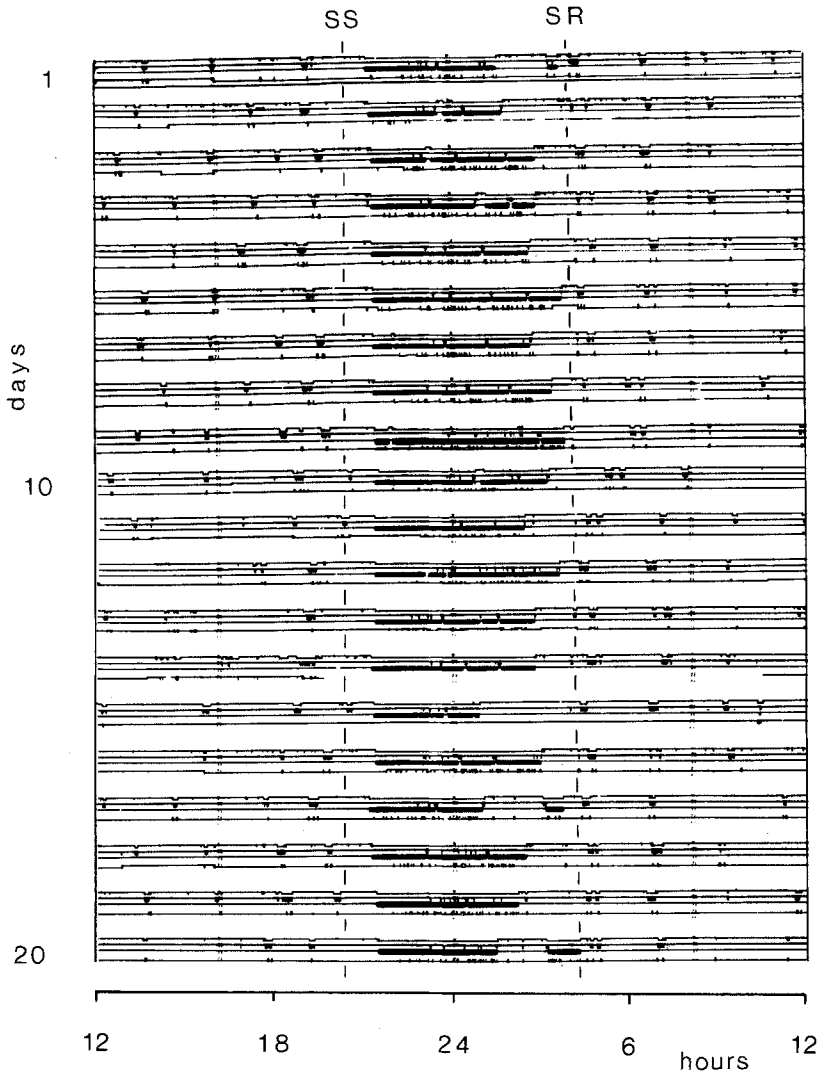


Fig. 2. Original Esterline-Angus records of the activity behaviour of *M. agrestis* under natural light conditions during summer (24.6.–14.7. 1975). The figure shows the short-term rhythm of eating and drinking during the day and the circadian rhythm of wheel-running during the night. Successive days are mounted one beneath the other. Channel 1: periods spent in the nest; channel 2: eating; channel 3: wheel-running; channel 4: drinking. *SS* sunset, *SR* sunrise

(1973a, b) showing that variation of the period lengths in *Lemmus lemmus* is smaller in periods composed of ρ' plus α' than in periods of α' plus ρ' . This may be an indication for the control by an oscillation, but it may also indicate that the duration of a rest is controlled by metabolic demands: rest time is long when the vole is not hungry or thirsty and subsequently does not need much food. However, α' means the duration of eating but not the amount of food-intake, which would be the relevant parameter. Therefore, this analysis

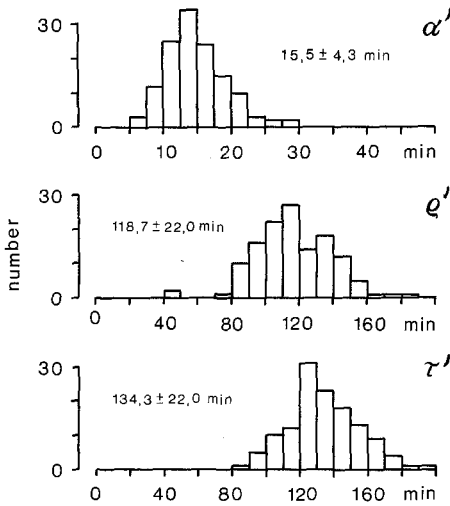


Fig. 3. Frequency distribution of the duration of the short activity times α' , of the short rest times ρ' and of the short periods τ' ($\alpha' + \rho'$) of *M. agrestis* as evaluated from the experiment in Figure 2 (Periods without wheel-running activity only)

Table 1. Coefficients of correlation between the parameters of the short-term rhythm of *M. agrestis*. Experiments during summer (May–September) under light-dark conditions (LD) and constant conditions (LL). α' : short activity time, ρ' : short rest time, τ'_1 : short period $\alpha' + \rho'$, τ'_2 : short period $\rho' + \alpha'$

Experiment		No. of the Periods (τ)	Coefficients of correlation			
No.	Light cond.		$\tau'_1 - \tau'_1$	$\tau'_2 - \tau'_2$	$\alpha' - \rho'$	$\rho' - \alpha'$
1	nat. LD	57	-0.08	-0.18	-0.15	-0.28 ^a
2	nat. LD	130	-0.10	+0.09	-0.06	-0.43 ^c
3	LD 14:10	50	-0.09	+0.08	-0.36 ^b	-0.39 ^b
4	LL 0.01 lx	100	-0.14	+0.10	-0.19	-0.31 ^b
5	LL 0.01 lx	95	+0.19	+0.22 ^a	+0.19	-0.08
6	LL 0.5 lx	63	+0.01	+0.03	-0.03	-0.16
7	LL 0.5 lx	132	+0.30 ^c	+0.24 ^b	+0.22 ^a	+0.11
8	LL 0.5 lx	52	+0.20	+0.39 ^b	+0.12	-0.18
9	LL 5 lx	58	-0.08	+0.06	-0.01	-0.37 ^b

^a Indicates significance at the 5% level

^b At the 1% level

^c At the 0.1% level

does not appear to allow a clear interpretation, whether the short-term rhythm is controlled by an endogenous oscillation or not.

The Circadian Rhythm

The circadian rhythm of *M. agrestis* derives from wheel-running activity only (Fig. 2). Wheel-running has a clear-cut start about 1 h after sunset, when light

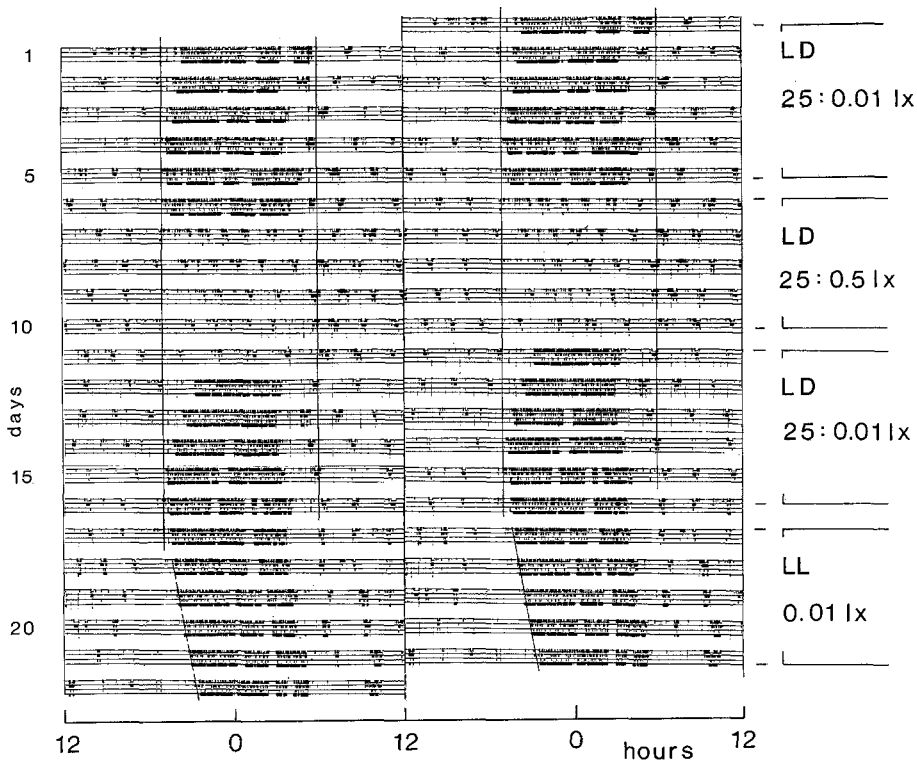


Fig. 4. Activity patterns of *M. agrestis* under sinusoidal light-dark regimes (days 1–17) and under constant conditions (days 17–22) during the summer (13.6.–5.7. 1975). Lines indicate 0.5 lx at dawn and dusk or the spontaneous period of the free-running rhythm, resp. Channel 1: periods spent in the nest; channel 2: eating; channel 3: drinking; channel 4: wheel-running

intensity is <0.01 lx. The end is always before sunrise, but varies much more than the beginning. From May until September there is either one long continuous burst of about 4–7 h duration during the night, or wheel-running activity is splitted up into a long initial burst of about 4 h duration and a second and shorter one before sunrise. With lengthening of the nights during September the long initial burst is followed by 2 or 3 shorter periods of wheel-running, separated by rests in the nest (Fig. 8). During wheel-running activity the voles drink frequently in irregular intervals. Food intake occurs not as frequent, but the intervals are irregular, too. Thus the short-term rhythm is not detectable during night, neither for eating and drinking nor for wheel-running.

In the beginning of almost each nocturnal activity period the voles run the wheel immediately after leaving their nest. It is observed exceptionally only that they eat or drink first, and in most of these cases they then retire into the nest again for a moment, before they start wheel-running. Then about 1 h later interruptions of wheel-running for drinking become frequent, and intensified eating is recorded even later. This sequence of events gives the impression that wheel-running does not extend an activity burst of the short-term

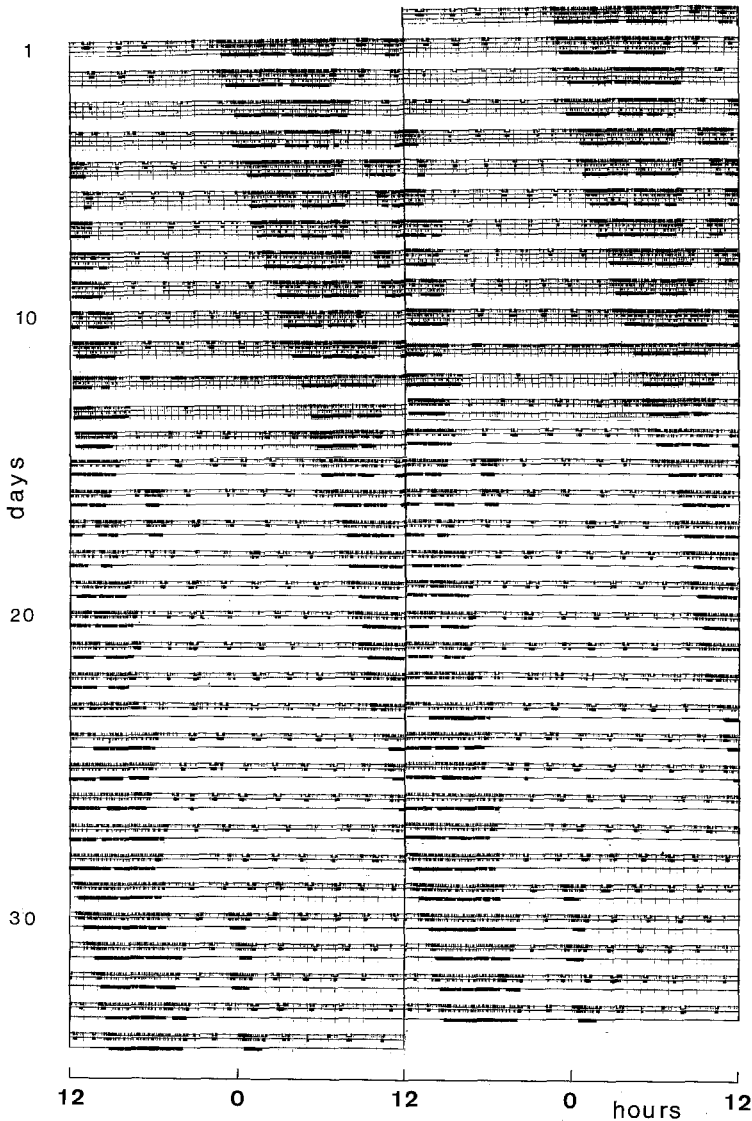


Fig. 5. Free-running rhythm of wheel-running activity of *M. agrestis* during the summer (24.7.–26.8. 1975) under constant conditions (LL 0.01 lx). Channels see Figure 4. Days 12/13: failure of channel 1 (nest); days 14–34: failure of channel 3 (drinking)

rhythm. Obviously the voles leave the nest intentionally for wheel-running which seems to be controlled by a circadian rhythm independent from the short-term rhythm of metabolism. To investigate the control of wheel-running activity, the behaviour of *M. agrestis* was recorded under various artificial light conditions.

In Figure 4 the vole was first exposed to a sinusoidal light regime. Maximum of light intensity was 25 lx (measured at the bottom of the cage) at noon,

and 0.5 lx were reached at 19.00 (6.00 resp.). During days 1–6 illumination decreased further to 0.01 lx and was constant between 19.30 and 5.30. The vole was readily entrained by this light regime. As in natural conditions a short-term rhythm of eating and drinking was recorded during the light period and extended wheel-running during the dark period. At day 7 the light regime was altered in such a manner that the intensity could decrease only to 0.5 lx and was then constant between 19.00 and 6.00. The pattern of illumination between 6.00 and 19.00 remained unchanged. The effects of the increased light intensity during the dark period are striking: wheel-running is suppressed immediately and completely with the exception of two very short bursts during the first period. Although movements of the vole within the nest are more frequent during the first dark period and indicate increased restlessness it leaves the nest only for eating and drinking, and the typical short-term rhythm stands out clearly.

From day 12 to 17 light intensity was again 0.01 lx between 19.30 and 5.30. The circadian pattern of wheel-running activity appears immediately. However, it takes three transient periods until the onset has reached the previous phase relationship to the light-dark cycle. From day 17 the vole was kept in constant conditions of LL 0.01 lx. A clear-cut endogenous rhythm of wheel-running activity with a spontaneous period length of ca. 24.5 h duration stands out (see also Fig. 5).

Similar results are obtained from experiments during April and May (Fig. 6). But during this season wheel-running is not suppressed immediately by 0.5 lx LL, but it is persistent for some days, during which a vague circadian rhythm with a period length shorter than 24 h can be recognized. The duration of a wheel-running time is rather short and the onset is less precise as compared to Figures 4 and 5. When wheel-running has disappeared after 7 days in LL 0.5 lx, a regular short-term rhythm without circadian variations is recorded. After 15 days with LL 0.5 lx, light intensity was lowered to 0.05 lx (indicated by the arrow, Fig. 6, day 15). This causes wheel-running again, and a circadian rhythm is discernible. The short duration of a wheel-running period as well as the vague period length and the altered sensitivity to light intensity indicate that the endogenous oscillation controlling wheel-running is subjected to seasonal variations. From Figure 7a and b it becomes evident that these seasonal influences may have drastic effects upon the activity behaviour. First, the threshold of light intensity which suppresses wheel-running is markedly increased: during LL 0.5 lx *M. agrestis* still intensively runs the wheel, whereas 5 lx are effective. Later on light intensity must be even >5 lx in order to suppress wheel-running. Besides this seasonal variation of the sensitivity to light, the control of wheel-running obviously has changed. There is no indication of a circadian rhythm in constant conditions, but wheel-running is now an intergrated part of the short-term rhythm.

Experimental Manipulation of Wheel-Running Activity

The distinct differentiation between a short-term rhythm which is correlated with metabolic requirements and a circadian rhythm of wheel-running which

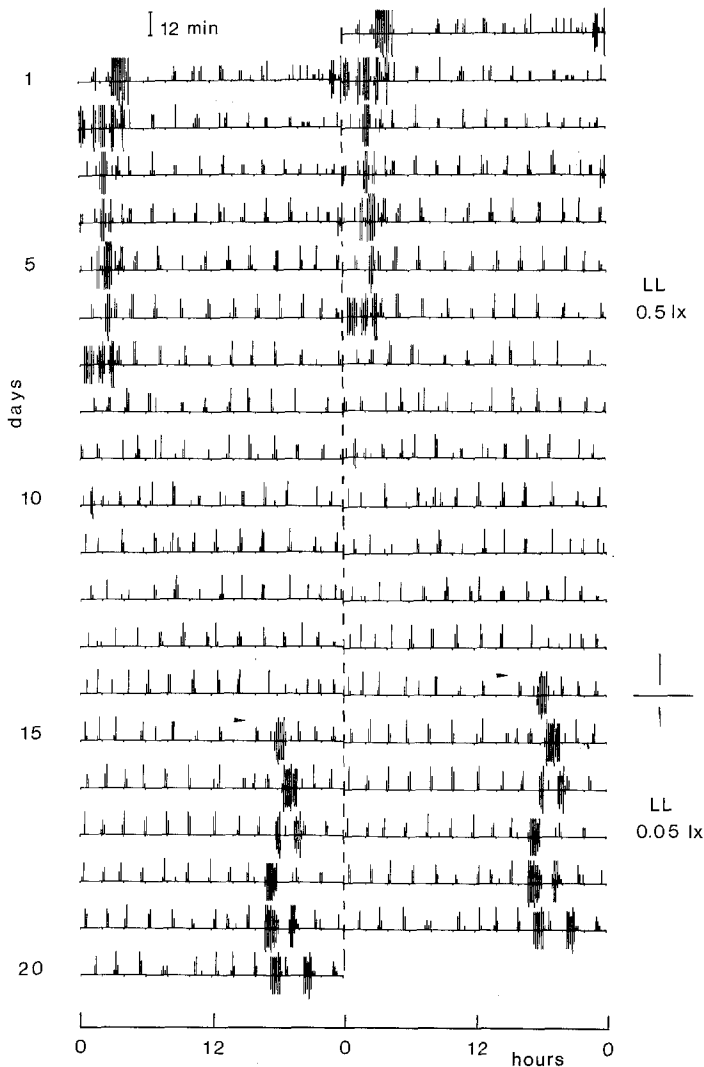


Fig. 6. Activity behaviour of *M. agrestis* under constant conditions with LL 0.5 lx and LL 0.05 lx during late spring (3.-22.5. 1975). Lines above the abscissa: time the vole spent outside the nest evaluated in 12 min successions; lines below the abscissa: duration of wheel-running in these successions. During LL 0.5 lx the circadian wheel-running activity fades out after 7 days. With the introduction of LL 0.05 lx it occurs again

is controlled by light conditions has become obvious by the detailed monitoring of the "activity". Both components of the activity behaviour of *M. agrestis* can not be discerned by using recording devices for overall activity like spring-suspended cages (Ostermann, 1956; Aschoff, 1962; Erkinaro, 1969) or by counting passages over switching mechanisms (Erkinaro, 1961, 1969; Stebbins, 1974), but differences between this overall activity and the pattern of wheel-running

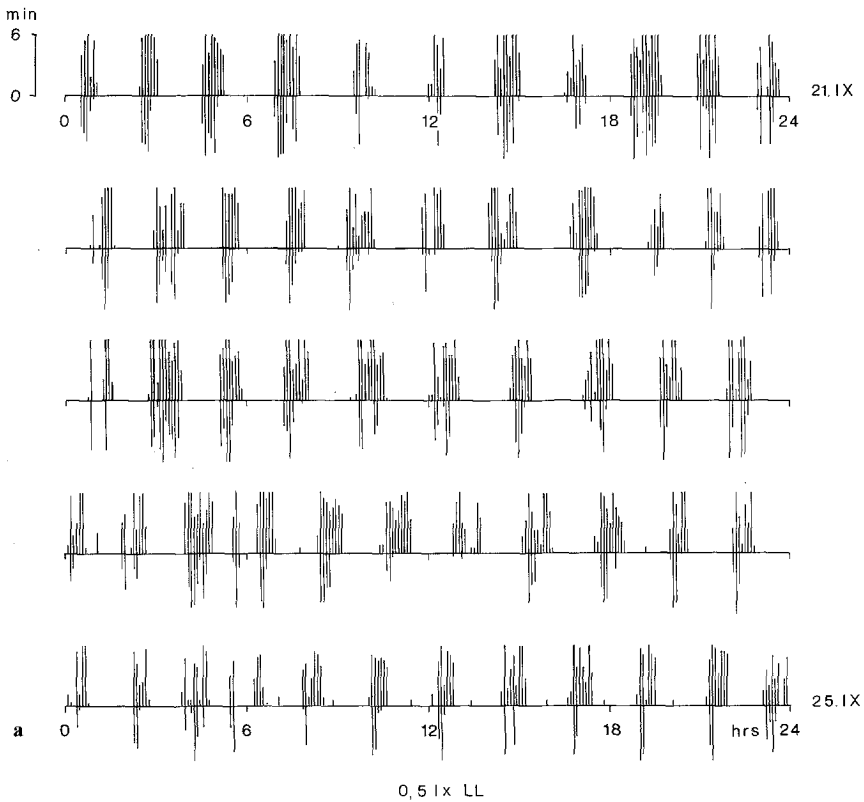


Fig. 7a and b. Activity of *M. agrestis* under constant conditions during autumn. Lines above the abscissa: time the vole spent outside the nest evaluated in 6 min successions; lines below the abscissa: duration of wheel-running in these successions. In LL 0.5 lx wheel-running occurs during each activity time, whereas in LL 5 lx it is suppressed immediately in the same specimen

should be expected. However, comparing records of wheel-running with those obtained from spring-suspended cages and switching-mechanisms Erkinaro (1969) found good agreements: in his device, *M. agrestis* run the wheel during each short activity time. This discrepancy must be independent from details of the monitoring technique, but indicates essential influences of the properties of the cage upon the behaviour. Therefore, some experiments were performed by modifying the cage.

In a first experiment, at the side of the running-wheel a compartment of 15 × 25 cm was separated by an opaque cross-wall. The wire-net at the bottom was covered with a board, nesting material was added, food (pellets, flaked oats, corn) and water were freely accessible. In this compartment only wheel-running could be recorded. When the vole was placed in the new surrounding it immediately started wheel-running for about 90 min (Fig. 8, day 5). Two h later a second activity burst was recorded and then the typical intensive wheel-

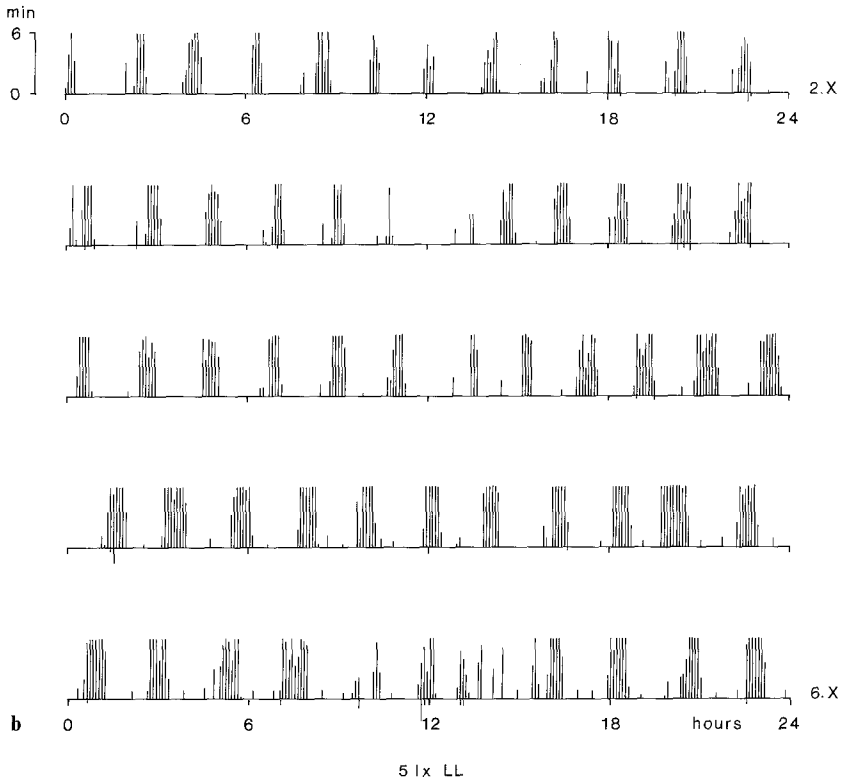


Fig. 7b

running during the night. At the following days, however, the vole run the wheel only occasionally during day-time, the circadian pattern of wheel-running activity was not influenced by this modification of the cage.

In a second experiment the space available for the vole was further limited. It was housed in a compartment with 10×10 cm square dimension only, with access to the running-wheel through a whole. Nesting material, food and water were supplied as in the previous experiment. In these conditions large bursts of wheel-running were recorded during the day-time as well as during the night (Fig. 8, days 9–12). It is not possible to decide, whether the vole is day-active or night-active.

At day 13 all modifications of the cage were removed. The vole withdrew into its separate nest and did not leave it until sunset. Then the typical circadian rhythm of wheel-running during night and the regular short-term rhythm of eating and drinking stands out again. The experiments indicate that the properties of the cage may influence the activity behaviour of *M. agrestis* markedly. Wheel-running during the day-time can in this season be enforced, when the vole is excited by disturbances and when the space available for sleeping and feeding is restricted.

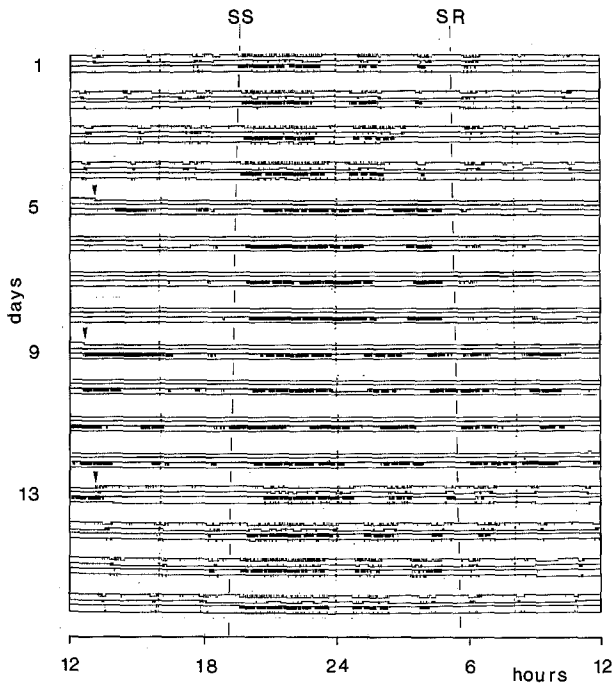


Fig. 8. Activity behaviour of *M. agrestis* under different cage conditions: the nocturnal pattern of wheel-running activity is disintegrated during the limitation of space to 10×10 cm (days 9–12). Days 1–4 and 13–16: original cage (see Fig. 1); days 5–8: space available for the vole limited to 15×25 cm. For details see text. Natural light-dark conditions (20.8.–4.9.1975). SS sunset, SR sunrise. Channels as in Figure 2

Discussion

The Short-Term Rhythm

The short-term rhythm has been conceived by some authors as an endogenous rhythm which is basic to functioning of the circadian rhythm; by other authors it has been suggested that it is mainly a feeding rhythm with the period depending upon food requirements, stomach capacity, and digestion rate (lit. see Stebbins, 1975). This investigation gives evidence that short-term rhythm and circadian rhythm in *M. agrestis* reflect different motivations and are controlled by different physiological mechanisms.

A close correlation between short-term rhythm and metabolic demands in *Microtus* has been pointed out already by Hatfield (1940). He recorded a regular eating activity in *M. pennsylvanicus*, which was independent from the light-dark cycle but could be influenced by temperature. Perhaps even more than on eating demands the 2 h-rhythm may be caused by the necessity to excrete. *Microtus* species obviously avoid excretion in the nest. In field experiments with *M. arvalis*, Frank (1954) observed during cold days, when the voles did not eat above ground, short excursions to the surface for excretion only. Excursions for excretion were also recorded by Pearson (1960) in his field study of *M. californicus*.

The question, whether the regularity of the short-term rhythm derives from these metabolic requirements or whether an endogenous oscillation is involved, cannot be resolved by the data available. So far, there are only indirect indications for a control by an oscillation with similar properties as the circadian oscillation (Erkinaro, 1972a, 1973a, b, c). They are mainly based on the detailed and accurate statistical analysis of the patterns of *Lemmus lemmus* and *Arvicola terrestris*. For *M. agrestis* the results of the correlation analysis are contradictory. Between the length of succeeding periods of an individual no uniform and significant trend of the correlation coefficients is obvious (Table 1). However, the mean period lengths of all individuals differ far less than the mean values of activity times and rest times. Thus comparing the individuals a significant negative correlation between α' and ρ' can be evaluated. It must be kept in mind, however, that the determination of the parameters (duration of activity time, rest time and period) is often difficult in spite of the apparent regularity of the rhythm. A quantitative analysis requires precise definitions which might be dubious with respect to individual variability as well as to diurnal and seasonal variations (see also Stebbins, 1975). Therefore, direct experimental evidence would be desirable. Experiments could concern influences of temperature, of short deprivation of food or water and changes of food quality as well as manipulation of the metabolic rate by drugs and the effects of light intensity.

Wheel-Running Activity

During the summer, nocturnal patterns of *M. agrestis* derive from wheel-running activity only. The control by an endogenous oscillation, synchronized with the light-dark cycle, is subjected to seasonal changes. The threshold of light intensity, below which wheel-running occurs, is lowest during summer and is increased markedly in spring and autumn. From winter time no data are available so far. It must be expected, however, that the threshold increases even more, thus allowing the diurnal activity pattern during winter as observed by Ostermann (1956) and Erkinaro (1961, 1969). Besides the variation of the threshold, the spontaneous patterns recorded during spring and autumn indicate that the control of wheel-running by the oscillator becomes less precise and may disappear completely. Either the oscillating system itself disintegrates in these seasons, or — most probably — it loses the control of wheel-running. An interpretation of this phenomenon requires consideration of the ecological significance of wheel-running, which is in fact a highly artificial kind of locomotor behaviour. The experiments in Figure 8 demonstrate that wheel-running can be caused by actual disturbances as well as by continuous unsuitable conditions. It seems to be a reasonable assumption therefore that wheel-running reflects generally and quite unspecifically a certain level of excitation. The conditions in the experimental cage the voles were exposed to in this investigation obviously fulfil at least a minimum of demands so that the voles do not feel stressed continuously. In these conditions wheel-running may represent natural nocturnal activities during the summer like exploratory and social behaviour (Shillito, 1963; Turner and Iverson, 1973). Turner and Iverson found a distinct annual cycle of intraspecific aggression in *M. pennsylvanicus* with a spring increase

and autumn decline, correlated with sexual activity. Home ranges were larger in summer than in winter. Thus, the coincidence between endogenous circadian control of wheel-running and the reproductive season suggests causal relationships. This hypothesis should be tested by investigating both activity behaviour and reproductive cycle.

The meaning of wheel-running during spring and autumn when it occurs during each short activity time cannot be deduced from the experiments performed so far. It is most probable, however, that it reflects other motivations than during the summer. A close context with the ecological meaning of the phaseshift from nocturnal to diurnal activity (and vice versa) must be assumed. Further observations of the behaviour under natural light-dark conditions and in constant conditions are necessary.

General Aspects

The interest in spontaneous activity patterns of animals derive mainly from two points of view: (1) to investigate the physiological basis of endogenous time-measuring mechanisms, which apparently control nearly all physiological processes in organisms, and (2) to understand the assumed ecological significance of endogenously controlled patterns. For both purposes extreme caution seems necessary when interpreting results obtained in the laboratory. Locomotion in a natural environment is no independent action, but will be always a means to realize intentions. It is obvious that these intentions may depend largely on the conditions offered to the animals. Even the basic distinction between day-activity or night-activity under LD—conditions may be obscured by the experimental arrangement (Figs. 4 and 8). To substantiate an ecological value of endogenous activity rhythms will require far more efforts to realize adequate conditions. Using social beings like voles adds further complication. The relevancy of activity records for investigating the mechanisms of an oscillator seems to be doubtful, too, although the differences between patterns obtained from various recording devices generally are not striking: the main character of the rhythms was apparent in all records (Pohl, 1968; Erkinaro, 1969; Aschoff et al., 1973). It has been demonstrated also that locomotor activity patterns are often synchronous with the patterns of physiological processes (Aschoff, 1967).

A convincing example that generally the pattern recorded does not depend on the monitoring technique, but can be obtained by measuring different kinds of activity is given by Kavanau (1963). In *Peromyscus maniculatus* all activities revealed the same circadian pattern. This indicates that essential differences as found in *M. agrestis* are not to be expected in all species. However, even small differences may be important as activity records are often used for very detailed quantitative analyses. Distinction between “spring-suspended oscillator” and “running wheel oscillator” (Aschoff et al., 1973) does not avoid the problem, whether alterations of a free-running rhythm by light conditions reflect responses of the circadian oscillator or whether they are due to unknown changes of the behaviour. In addition, it should be kept in mind in this context that clear-cut spontaneous activity rhythms are observed only in some species (especially birds and rodents) and only in certain conditions. In other species rhythmicity of spontaneous activity patterns is often vague and can be described also

as resulting from stochastic sequences (Lehmann et al., 1974; Kaiser and Lehmann, 1975; Lehmann, in prep.). Therefore, conclusions drawn from activity records should not imply a priori a close coupling between locomotor activity and endogenous oscillation.

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