

# Seasonal change in the daily timing of behaviour of the common vole, *Microtus arvalis*

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**Summary.** 1. Seasonal effects on daily activity patterns in the common vole were established by periodic trapping in the field and continuous year round recording of running wheel and feeding activity in cages exposed to natural meteorological conditions.

2. Trapping revealed decreased nocturnality in winter as compared to summer. This was paralleled by a winter reduction in both nocturnal wheel running and feeding time in cages.

3. Frequent trap checks revealed a 2 h rhythm in daytime catches in winter, not in summer. Cage feeding activity in daytime was always organized in c. 2 h intervals, but day-to-day variations in phase blurred the rhythm in summer in a summation of individual daily records. Thus both seasonal and short-term temporal patterns are consistent between field trappings and cage feeding records.

4. Variables associated with the seasonal change in daily pattern were: reproductive state (sexually active voles more nocturnal), age (juveniles more nocturnal), temperature (cold days: less nocturnal), food (indicated by feeding experiments), habitat structure (more nocturnal in habitat with underground tunnels).

5. Minor discrepancies between field trappings and cage feeding activity can be explained by assuming increased trappability of voles in winter. Cage wheel running is not predictive of field trapping patterns and is thought to reflect behavioral motivations not associated with feeding but with other activities (e.g., exploratory, escape, interactive behaviour) undetected by current methods, including radiotelemetry and passage-counting.

6. Winter decrease in nocturnality appears to involve a reduction in nocturnal non-feeding and feeding behaviour and is interpreted primarily as an adaptation to reduce energy expenditure in adverse but socially stable winter conditions.

apart from the numerous studies with automatic recording in captivity, is based mainly on live trapping in the field (e.g., Brown 1956; Kikkawa 1964; Bäumlér 1975). In addition, a few studies have employed radio telemetry (e.g., Herman 1977; Leuze 1980; Shields 1976; Madison 1981) and direct observations in red light, either in the wild (Robitaille and Bovet 1976) or in terraria (Bovet 1972). Other techniques include the recording of passages at fixed points in the habitat (Osterberg 1962; Pearson 1960) or in enclosures (Lehmann and Sommersberg 1980). Nearly all these methods interfere to some extent with the natural behaviour pattern of the animal studied, and hence meet difficulty of interpretation. A comparison between methods would be useful to reveal how consistent various aspects of circadian behaviour are.

We have made a study of the seasonal change in daily rhythms in the common vole, *Microtus arvalis*, using mainly the two traditional techniques, live trapping and recording from cages. A vole species was chosen since voles show various characteristics of their circadian organization which demand functional understanding. Voles have been reported to be predominantly nocturnal in summer and more diurnal in winter, both in cages (Ostermann 1956; Erkinaro 1969) and in field trapping studies (Bäumlér 1975), although in an enclosure outside they were reported to be diurnal year round (Lehmann and Sommersberg 1980). They further exhibit a remarkable short-term rhythm in their foraging activity in cages (Lehmann 1976), which again has also been observed in trapping studies (Daan and Slopsema 1978; Raptor group RUG/RIJP 1982). An analysis of common vole behaviour was of further interest to us, as it turned out to affect the foraging behaviour of one of its predators, the European kestrel (*Falco tinnunculus*) which was studied simultaneously by our research group (Rijnsdorp et al. 1981; Daan and Aschoff 1982). A species with systematic variations in its tendency to be either nocturnal or diurnal, e.g., on a seasonal basis, should provide insight in the adaptive meaning of circadian patterns more readily than species which are exclusively nocturnal or diurnal in any condition. In this descriptive paper we aim at elucidating a number of factors possibly responsible for the seasonal change in diurnality of the common vole.

## 1 Introduction

Small mammals have been widely used in laboratory studies of the endogenous clocks which generate circadian activity rhythms. The functional interpretation of such rhythms is impeded by a lack of knowledge of the behaviour of small mammals in the wild, due to the difficulties in continuous field observation in animals with a secretive and often nocturnal life style. Knowledge of daily rhythms in small ro-

## 2 Methods

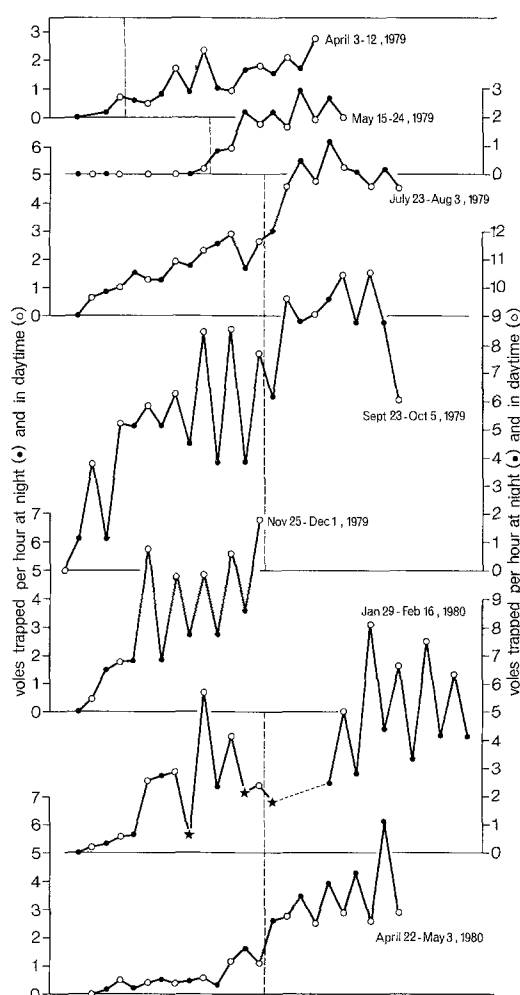
Live trapping. The field study was carried out in the "Lauwersmeer", a polder in the northern Netherlands (53°20' N, 6°17' E), which largely underwent a natural development since its reclamation from the sea in 1969 (see

Joenje 1978). Two study sites of ca. 0.5 ha each were selected. These will be henceforth referred to as MW (Marnewaard) and ZK (Zoutkamperplaat). The MW trapping site was sandy and covered with a low, grassy vegetation; the ZK habitat was dominated by reeds on a clay soil. Vegetation is described in section 5.4. The site MW was inhabited by common voles, common shrews (*Sorex araneus*), and wood mice (*Apodemus sylvaticus*), site ZK in addition to these species by harvest mice (*Micromys minutus*) and water voles (*Arvicola terrestris*). Trapping was done year-round in 1976–1978 (ZK) and in 1979–1980 (MW). In addition, a few other trapping data obtained at ZK in 1979 and 1980 and at a third grassland (Ezumakeeg EK) will be included in the evaluation. In each trapping period, 196 Longworth traps were placed at 5 m intervals in the same grid of 14 × 14 fixed stations. Traps were filled with hay and baited with grain and carrots, and inspected at sunrise and sunset for 8 to 10 days in sequence. After cursory inspection of closed trap doors, which took ca. 10 min for the whole grid, those voles, which had been captured at inspection time were sexed, weighed, marked individually by toe-clipping, and released. In the MW study, grid trapping was usually followed by another 8–10 day period during which traps were positioned not at the fixed trapping stations but as close as possible to burrows and/or runways within 2.5 m from the station. Trapping periods were usually terminated by a 24- or 48-h series of frequent (once per 20 min) trap checks, in which several observers participated, to determine short-term fluctuations in trap catches.

The vegetation present in each trapping period at the Marnewaard was evaluated by establishing in 7 “permanent quadrats” (2 × 2 m<sup>2</sup>) the % area covered by green plants projected at right angles to the ground (Londo 1975). Samples of fresh plants were collected and subjected to chemical analysis for crude protein and holocellulose content. Crude protein content (N × 6.25) was assayed with the micro Kjeldahl method followed by Nessler reaction (Allen 1974). Holocellulose content was determined by means of a delignification process of the plant material (Allen 1974). Holocellulose is the first-stage product in the cellulose isolation and consists of a mixture of cellulose and hemicellulose.

Faecal analysis was done by comparing epidermal fragments present in the faecal pellets with a reference collection of the epidermal cells of the plants in the Marnewaard area. For this purpose faeces were collected in each trapping period from the live-traps and stored in 80% alcohol. From each trapping period at least 10 slides, each containing 2 faecal pellets and coloured with an epidermis stain, Mayer’s haemalum (Hansson 1970) were analysed under a stereomicroscope by 10 × 40 magnification. Numbers of different fragments coinciding with each of 10 × 36 points in an ocular micrometer grid were counted. The relative abundance of epidermal fragments in each faecal sample reflects both diet composition and differential digestive breakdown of the epidermal cells. However, we expect shifts in diet composition to be reflected qualitatively in the faecal fragment composition.

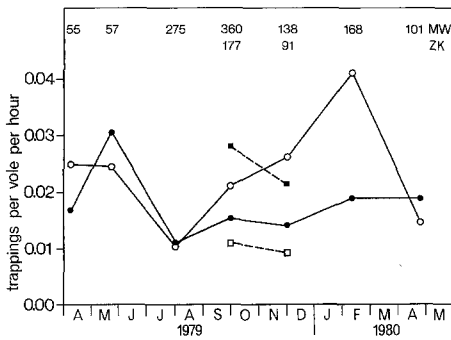
Cage activity. Seven recording cages (24 × 24 × 30 cm high) each containing a nest box and hay, a running wheel (Ø 22 cm), water bottle and food rack, were placed in an outside shed near the laboratory. They were sheltered against rain and wind but otherwise fully exposed to natural daylight and meteorological variations. Common voles,



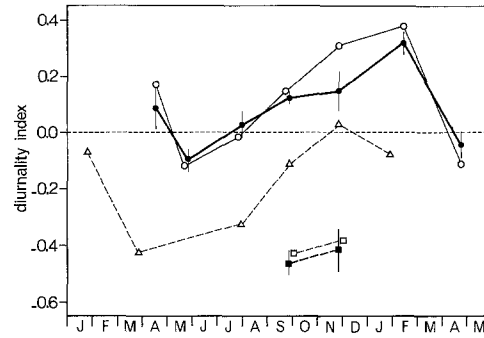
**Fig. 1.** Absolute vole capture frequencies per h in the Marnewaard trapping grid (196 traps) in daytime (○) and at night (●). Dotted lines mark the day when traps were shifted from the fixed trapping grid station to a nearby burrow or runway. Asterisks indicate nights with malfunctioning of traps due to frost and snow

captured in the Lauwersmeer (ZK) were kept individually in these cages for up to 13 months. Running wheel revolutions and presses on a microswitch-mounted bar in front of the food rack were continuously recorded automatically on an Esterline Angus event recorder. Records were pasted in standard actogram format albeit with food and run records alternating (see e.g., Fig. 4). Slow chart speed (1 inch/h) precluded precise quantification of the number of wheel revolutions and bar presses, but their temporal distribution could be analysed by visual inspection. The voles were fed on ad lib rat chow (Muracon®) replenished at irregular intervals, except in some experiments with alternative feeds (see Sect. 5.3), and generally remained in good health. The main analysis concerns the records of six individuals. Three were trapped as adults in spring 1978 and entered the recording cages in July; three others were born in the laboratory on October 4, 1978 and were recorded from October 21 onwards. The two groups were labeled “old” and “young”. Except for one vole in the “old” group which died in April 1979, all survived till the end of the experiment in August 1979. A fourth vole in the old group turned out to be blind and was treated separately (see Fig. 5).

Telemetric recording in an outdoor enclosure. An enclo-



**Fig. 2.** Relative capture frequencies per vole per hour in daytime (○) and at night (●). Numbers indicate total number of individually marked voles in each grid (ZK □, ■; MW ○, ●) per period



**Fig. 3.** Seasonal change in diurnality index for trappings at Zoutkamperplaat (Δ: 1977/78; □: 1979) and Marnewaard 1979/80 (○). Open symbols represent population indices, solid symbols means (± 1 s.e.) of individuals caught at least 4 times

sure of 15 × 15 m was built in a meadow in the laboratory gardens and provided with a grid of 2 × 11 overhead wire antennas, 1.5 m apart, according to Chute et al. (1975; see also Herman 1977). Voles were released in the enclosure (Fig. 18) and at a later stage trapped and provided with small (1.5 gram) neck collar transmitters (27 MC). Although we had difficulty in getting this system to work properly in most animals, reliable information on above ground movements was obtained for three voles by continuously selecting the x- and y-antenna's receiving the maximal signal. Reduced signal strength at a constant level and from constant position was interpreted as coming from underground and this was usually in the localized central burrow system of each animal (\* in Fig. 18).

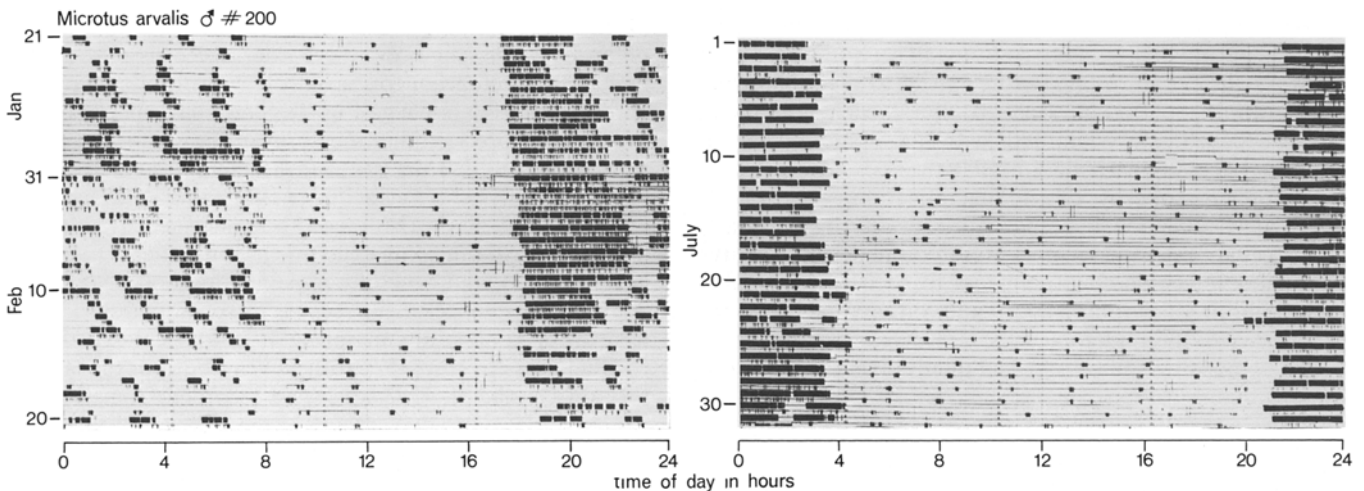
Observations in indoor enclosures. Some time budget observations were obtained in two cages (250 × 150 cm, with 75 cm high smooth walls and open top), each in a light- and temperature-controlled room (18 °C; LD 10:14; lights on from 9 a.m. till 7 p.m. in cage 1, from 11 p.m. till 9 a.m. in cage 2). Four dark red incandescent lamps illuminated each cage from above continuously, which just allowed visual observation of voles active on the surface. Each cage was divided in two halves by a smooth separation wall, which was removed half way through the experiment. Cage floors were covered with 10 cm of soil and a low grass

vegetation. As the grass was gradually eaten away, a large carrot was offered as replacement. In each cage division two wild caught voles (♂, ♀) were released in October 1981, and continuous observations were made after 3 days of accommodation, each day from 8 a.m. till 8 p.m. during 7 days. Surface presence and behaviour (Eat, Run, Dig) were recorded every minute for each of the eight individuals (identified by fur clippings on the back) by shifts of observers.

### 3 Seasonal change in diurnality

#### 3.1 Live trapping

In all trapping periods there was a marked increase in the frequency of captures, expressed in the number of voles trapped per h (Fig. 1). This increase, presumably related to a gradual decay of trap shyness, seemed to be accelerated when traps were moved to new positions near burrows and runways. After several days conspicuous differences between night and day usually emerged (Fig. 1). Capture rates varied considerably between trapping periods, obviously related to seasonal changes in population density in the area. The number of trapped and marked individuals per period varied in the Marnewaard from 55 in April to 360 in October. For the marked part of the population the individual cap-



**Fig. 4.** Sample records of wheel running and feeding in vole #200 in winter and summer. Wheel running and feeding records are pasted alternatingly below each other. Note the considerable reduction in nocturnal wheel running and the constancy of diurnal meal timing in winter

ture frequency (captures/voles present  $\times$  h of trap exposure) was calculated. Nocturnal capture frequencies were rather constant throughout the year except for a higher rate in May (Fig. 2). In contrast, capture frequencies in daytime had a minimum in July and a maximum in February. It should be noted that at high population densities trap saturation may have occurred, suppressing the catch frequency per individual. In September 1979 total catches went up to 123 voles caught per night in 196 traps.

For further analysis we defined a “diurnality index” ( $D$ ) as a simple descriptor of the tendency of being trapped more frequently in daytime than at night.

$$D = \frac{C_D/T_D - C_N/T_N}{C_D/T_D + C_N/T_N}$$

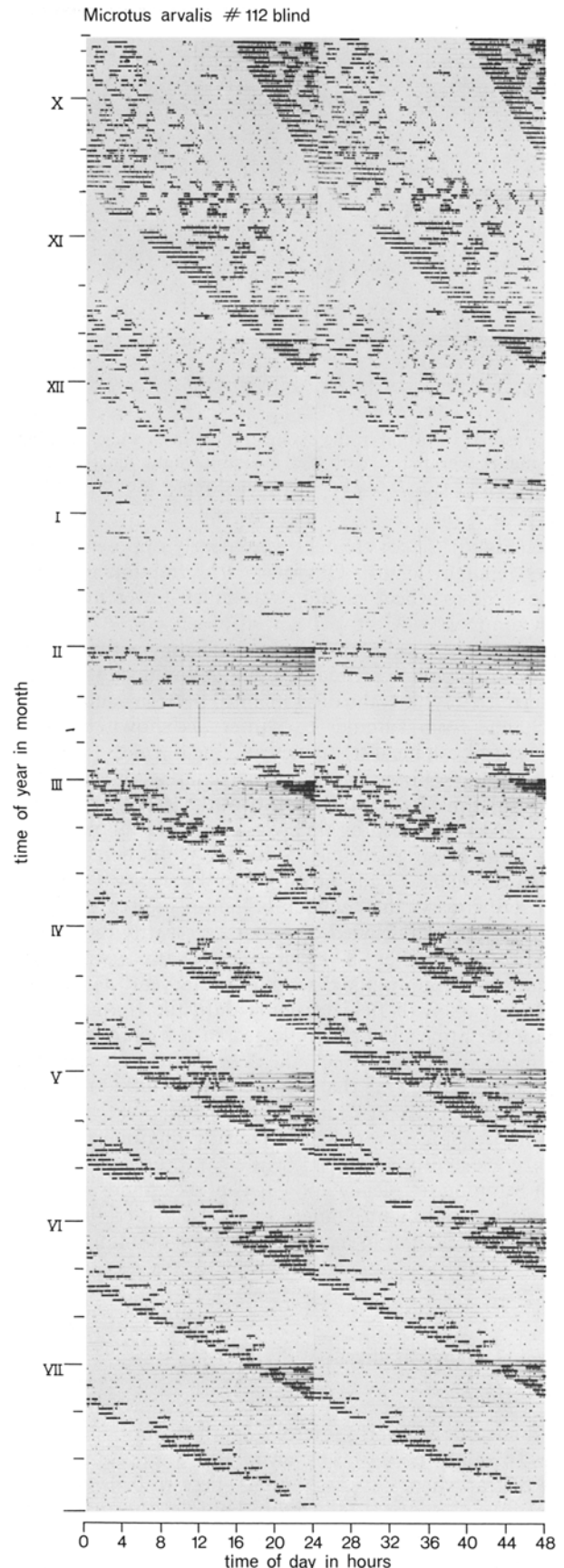
where  $C_D$  and  $C_N$  are captures in daytime and at night, respectively, and  $T_D$  and  $T_N$  are the corresponding trap exposure times. This index is symmetric around 0 and runs from  $-1$  (no daytime captures) to  $+1$  (only daytime captures). The index can be computed both for the population present and for individuals that were frequently captured (we used four captures per period as a minimum), thus permitting an estimate of interindividual variance.

The mean diurnality index for the MW trappings was usually positive, and gradually increased from spring to winter followed by a sharp drop towards the next spring (Fig. 3). At the ZK-site, the diurnality index was considerably lower at any time of year but followed the same seasonal trend, with a minimum in spring and a maximum in winter. Group and mean individual index (MW) were mostly close together. Hence method of calculation is not the cause of the difference between the two sites. It can also not be attributed to climatic conditions since trappings on the Zoutkamperplaat simultaneous with the MW-study in autumn 1979 again revealed much lower diurnality indices (Fig. 3). Apparently, habitat differences contribute to the degree of diurnality as revealed by live trapping (see 5.4).

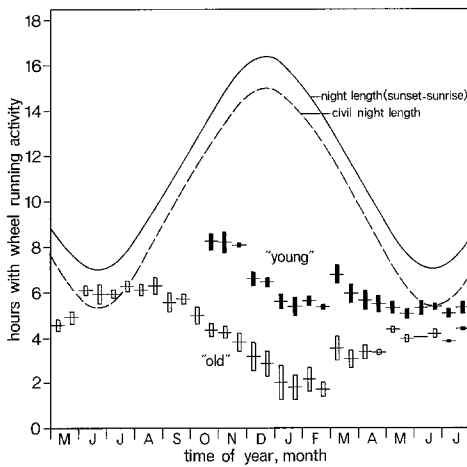
### 3.2 Cage activity

Wheel running activity of voles in captivity was virtually exclusively nocturnal throughout the year. Feeding activity occurred both in daytime and at night although in different patterns. In daytime, feeding was organized in discrete meals usually spaced 1 to 3 h apart. At night feeding was dispersed through the longer episodes of running activity (see Fig. 4). One accidentally blind animal ( $\text{♀}$  # 112) had a clear free running circadian pattern for 14 months and appeared totally insensitive to any zeitgeber cues from natural meteorological variations (see section of the record in Fig. 5).

In the amount of wheel running activity at night, considerable seasonal variation was observed. Wheel running appeared more intense during summer than winter nights. Indeed the total of all nocturnal 6 min intervals with running gradually decreased from August till February in the “old” group of voles and increased again towards the summer



**Fig. 5.** 10-months record of wheel running and feeding in a blind vole (no. 112). For clarity, the record is reproduced twice. Notice the absence of synchronization even in natural meteorological conditions and the reduction in wheel running activity during the cold winter months



**Fig. 6.** Seasonal variation in the extent of nocturnal wheel running (h per night), compared with the available night length. Half-monthly means ( $\pm 1$  s.e.m.) for the *old* and *young* group of voles

solstice (Fig. 6). These changes were nearly opposite to the changes in night length. Obviously, the fraction of night time devoted to wheel running was much lower in winter than in summer.

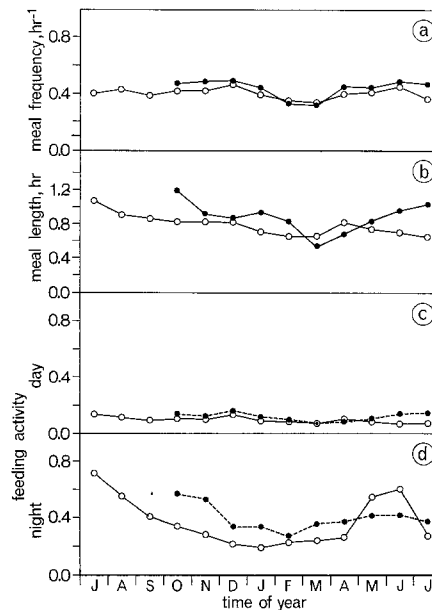
The analysis of seasonal changes in feeding activity from these records is made difficult by the day-night differences in pattern. In daytime, the discrete meal patterns underwent little change from summer to winter, as shown by near constancy of both meal frequency and meal length (Fig. 7a, b). The fraction of time the voles engaged in feeding activity thereby remained rather constant around 10% throughout (Fig. 7c). At night, feeding time was considerably increased during summer (Fig. 7d), as compared with minima observed in January ('old' group) and February ('young' group). Obviously, the number of 6 min intervals during which food intake occurred does not necessarily reflect the amounts of food eaten. These may for instance well have been constant for nights throughout the year. However, for comparison with field trapping data the frequency of food hopper approaches as reflected in the percentage of 6 min intervals during which these occurred is a relevant measure. It is interesting that this frequency shifted towards reduced nocturnality in winter as did the trap catches. Yet night-time feeding never dropped below daytime feeding, as was consistently found in winter trapping. Thus, although trapping frequency and cage activity underwent the same relative day-night changes in the course of the year, cage activity deviated in as much as wheel running hardly occurred in daytime and feeding was always less frequent in daytime.

#### 4 Seasonal change in ultradian rhythms

##### 4.1 Live trapping

A more detailed description of the distribution of trap catches through the day is given in Fig. 8, containing the results of trap checks every 20 min. These records confirm the general difference in diurnality between the two study sites. Capture frequencies at ZK were usually lower in daytime than at night, at MW higher. The difference is most striking in the lower panels of Fig. 8, showing results obtained simultaneously at the two sites.

Considerable short-term fluctuations were found in

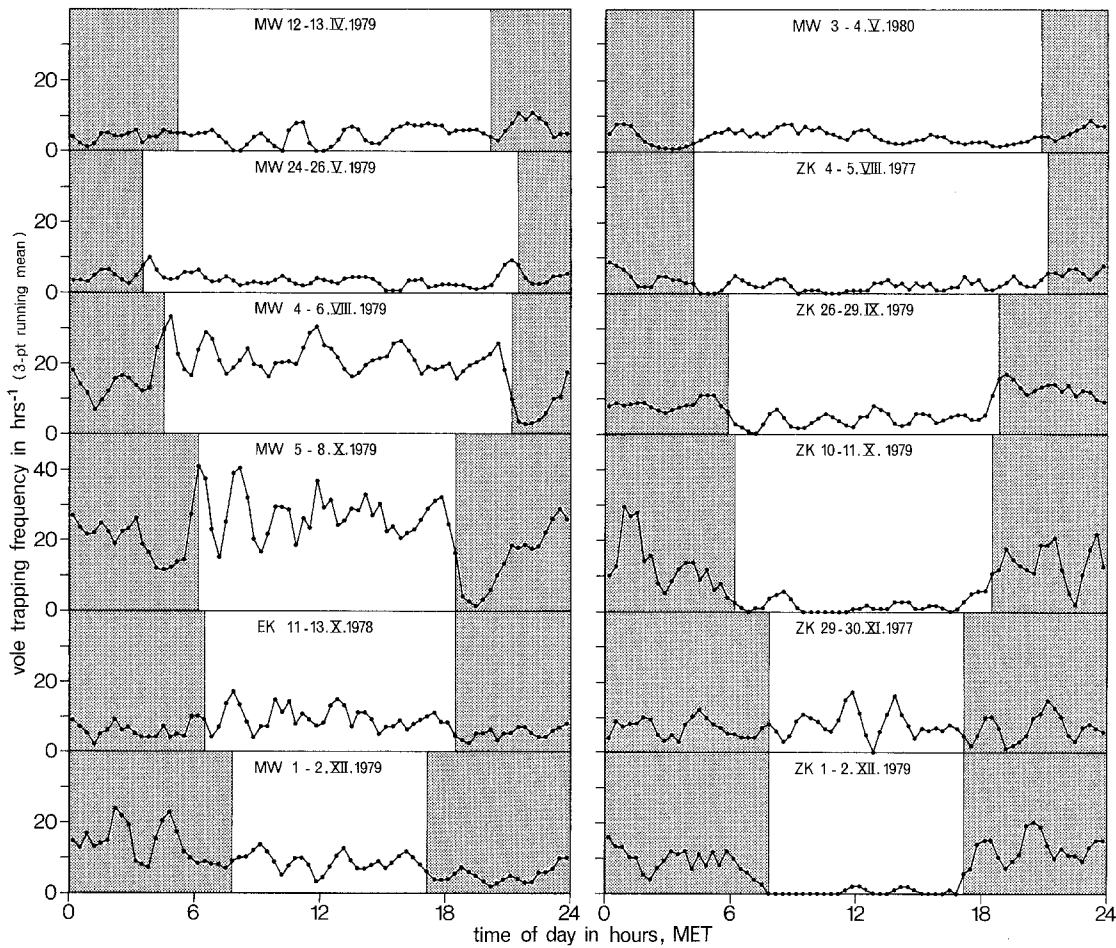


**Fig. 7a-d.** Seasonal variation in various time parameters of feeding activity in captive voles of the 'old' (○) and 'young' (●) groups. **a** Monthly averages of meal frequency in daytime. **b** Average meal durations. **c** and **d** Average fractions of 6' intervals in which feeding activity occurred in daytime **c** and at night **d**

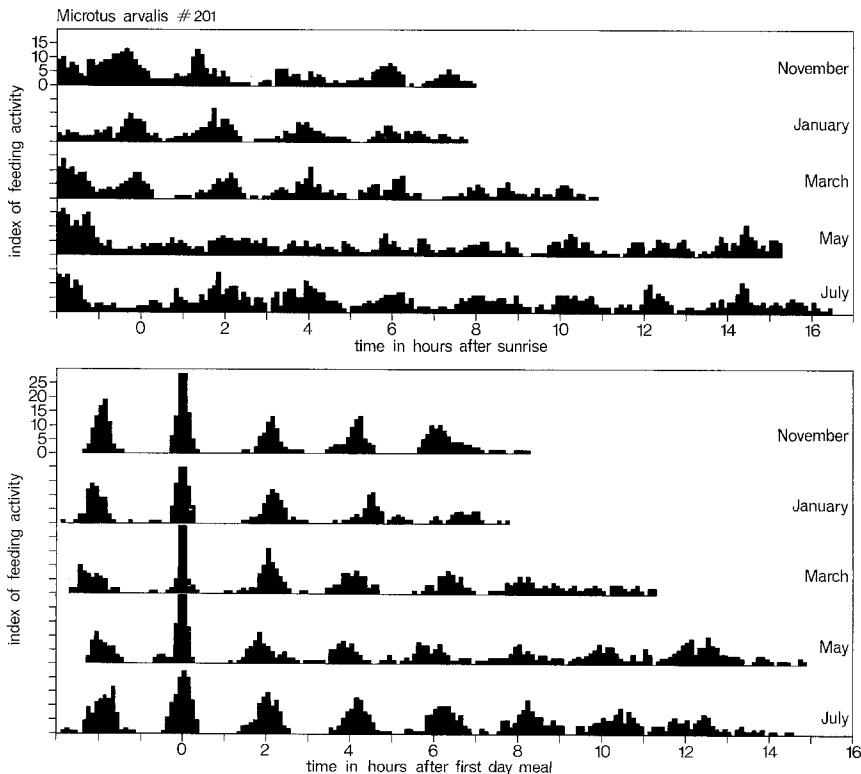
some of the data. A sharp decrease in vole captures was observed just after dusk civil twilight in several of the MW records. Periodic fluctuations seemed to occur during the night but we have observed no systematic nocturnal pattern. During daytime, high and low capture rates often alternated with a period of about two, especially in the first half of the daylight. This periodicity was most consistent during autumn and winter records, at least when diurnal capture rate was sufficiently high. The short-term fluctuations kept a rather stable phase relationship with dawn civil twilight (c.t.), with the first morning peak in vole trappings following c.t. by c. 120 min (Daan and Slopsema 1978; Rijnsdorp et al. 1981). They are caused by considerable synchrony in trappability of individuals in the population. This synchrony fades out towards the afternoon. If such short-term rhythms in trappability were also present in individuals in spring and early summer, it must be concluded that they were less synchronous at that time of year than in the fall and winter.

##### 4.2 Cage activity

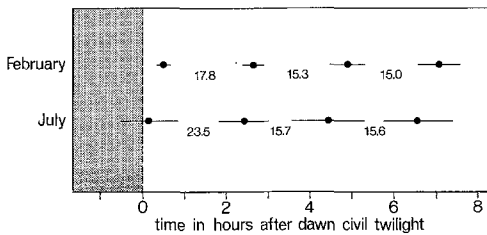
The sample records (Fig. 4) suggest that in daytime a short-term rhythm in feeding activity occurred both in summer and winter. This contrasts with the trapping data, where trap catches in summer were fairly uniformly distributed over the daylight period (Fig. 8). Pooling the individual feeding records per month leads to a similar scattered distribution of feeding times with respect to sunrise in summer, while in winter pronounced rhythmicity remains (Fig. 9A). Apparently, meal times were less synchronous from day to day in summer than in winter. Loss of synchrony in summer may either be due to more variation in the period of the short-term rhythm or in its phase relative to the light dark cycle. Pooling the same data with respect to the first meal of the day instead of sunrise corrects for day-to-day variation in phase, and leads to a different picture,



**Fig. 8.** Distribution of vole captures over day and night, as established by frequent (once per 20 min) trap checks, and smoothed by adding numbers in three consecutive checks. Letters indicate three different trapping areas: *MW* Marnewaard, *ZK* Zoutkamperplaat, *EK* Ezumakeeg. Shaded areas represent darkness between civil twilights



**Fig. 9A, B.** Day-to-day synchrony of daytime meals in sample records of an individual vole (no. 201) in different months. **A** Fraction of 6 min intervals with feeding activity plotted with respect to sunrise. Notice the loss of synchrony from April onwards. **B** Fraction of 6 min intervals with feeding activity plotted with respect to the midpoint of the first daytime meal

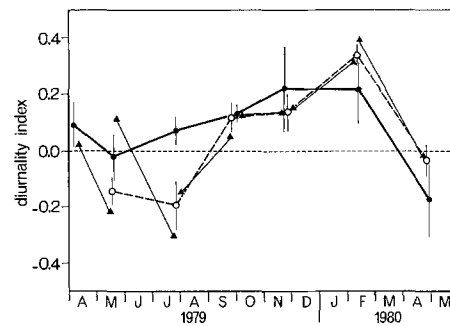


**Fig. 10.** Average meal times ( $\pm 1$  standard deviation) for voles in February and July. Numbers indicate the standard deviations (in minutes) of the meal-meal intervals. Notice the increased variation in the absolute times, not in the intervals, in July

with pronounced rhythmicity also in summer (Fig. 9b). This analysis shows that the scatter of meal times in summer was primarily due to a larger variability in the time of the first daytime meal. This is corroborated by a comparison of meal times in February and July in all voles (Fig. 10): meal to meal intervals were as variable in winter as in summer, but clock times varied more during the warmer season. What reduces the day-to-day synchrony in summer remains a matter of speculation. With longer days, light will hit the light sensitive part of the circadian phase response curve more than with shorter days (Pittendrigh and Daan 1976; Daan 1982). Alternations between activity and rest around the end of the night may lead to chance variations in the phase of the circadian cycle illuminated each day and thus contribute to more variation in circadian phasing in summer. Be this as it may, the seasonal changes in the short-term rhythm of trap catches seems adequately explained by increased variability in phasing and synchrony of the short-term meal cycle in summer.

## 5 Factors affecting daily activity patterns

Many factors may be held responsible for the seasonal changes in vole activity patterns. On the basis of trapping data alone, only a general correlative analysis can be made. Yet it is useful to analyze the patterns with respect to such variables as population structure, food availability and climatic conditions which change considerably with time of year, and to compare this with the evidence available from captivity.



**Fig. 11.** Seasonal change in diurnality index  $D$ , for new ( $\bullet$ ) and old ( $\circ$ ) animals in the field, and for voles present in two consecutive trapping periods ( $\blacktriangle$ ). Means ( $\pm 1$  s.e.) of individuals caught at least four times

### 5.1 Age and reproductive state

The vole population in the trapping grids underwent sizable changes in the course of the year. Juvenile and subadult voles entered the trappable population throughout the summer and it might be presumed that the changes in diurnality were the result of the changing age composition. To investigate this we have computed mean diurnality indices in each trapping period for two age groups of voles: those which had, and those which had not been trapped prior to that trapping period. These indices were not consistently different (Fig. 11) although a slightly increased diurnality was observed in the 'new' group in one trapping period (July). Both groups followed the same general seasonal change. Also, changes in diurnality index for groups of individuals present in two consecutive trapping periods ran parallel to the overall average indices, decreasing in spring and increasing in autumn. These results imply that the change in diurnality was not due to individuals entering and leaving the population, but to changing individual behaviour.

There is further evidence in the data that individuals shifted their diurnality index in the same direction as the population did. This is suggested by positive rank correlations between the deviations of individual indices from the mean index for a particular period (Table 1). Pooling all successive pairs of deviations yielded a highly significant rank correlation for both females and males.

If individual changes in behaviour are involved in the seasonal shift in diurnality a next hypothesis to be considered is that this shift is associated with reproductive behaviour. Winter populations differ from summer populations in having no reproductively active voles (except for a few

**Table 1.** Spearman rank correlation coefficients between individual diurnality indices (expressed as deviations from average) in consecutive periods. Based on individual voles captures at least twice in each period. Numbers of individuals in parentheses

Periods	Males		Females		Total	
April–May '79	0.00(6)	n.s.	0.54(11)	$P < 0.05$	0.37(17)	$P < 0.01$
May–July '79	0.50(5)	n.s.	-0.21(7)	n.s.	-0.02(12)	n.s.
July–Sept. '79	0.05(7)	n.s.	-0.06(21)	n.s.	0.02(29)	n.s.
Sept.–Nov. '79	-0.11(30)	n.s.	0.01(41)	n.s.	0.03(77)	n.s.
Nov.–Febr. '80	0.37(23)	$P < 0.05$	0.64(15)	$P < 0.01$	0.49(39)	$P < 0.005$
Febr.–April '80	0.26(21)	n.s.	0.07(35)	n.s.	0.11(56)	n.s.
Total	0.31(118) $P < 0.001$		0.21(144) $P < 0.01$		0.30(277) $P < 0.0001$	

**Table 2.** Diurnality indices among sexually active and inactive voles. Mean  $\pm$  s.d. ( $n$ ) for individuals with more than 3 captures per trapping period. Males and females pooled as they had virtually identical mean indices in each group. Significance of difference tested by two-tailed  $t$ -test

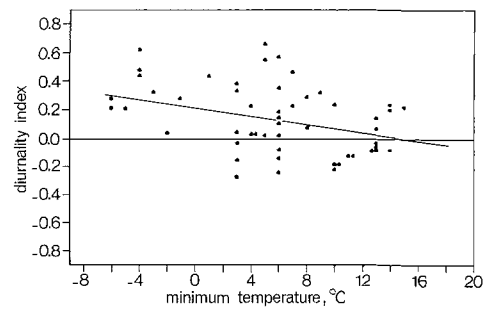
Reproductive status	Active	Inactive	
Summer	0.00 $\pm$ 0.38 (185)	0.12 $\pm$ 0.43 (169)	$P < 0.01$
Winter	0.05 $\pm$ 0.41 (11) not sign.	0.25 $\pm$ 0.47 (194) $P < 0.01$	not sign.

active males in October). During summer, reproductively inactive voles were indeed more diurnal than active voles (Table 2). The difference is small, however, and reproductively inactive voles in summer were less diurnal than those in winter (Table 2). Apparently a change in reproductive state, as far as can be judged from external inspection, can account only partly for the seasonal change in behaviour.

In captivity, the seasonal change in nocturnal locomotor activity, with a minimum in winter, was apparently superimposed on a long-term trend. 'Old' voles were considerably less active in their second than in their first summer (Fig. 6). 'Young' voles showed consistently more wheel running than the 'old' group and reached the same level in their first summer as the 'old' group had a year earlier. This difference is consistent with the general decrease in locomotor activity with age in small rodents (Aschoff 1962), but has no parallel in our field data.

### 5.2 Temperature

A factor previously held responsible for the seasonal change in diurnality of the common vole is ambient temperature. Ostermann (1956) suggested that in winter it might be energetically advantageous for voles to shift their activity to the warmest part of the day. Our data on this point are ambiguous. Comparing group diurnality index per period with the average daily minimum temperature yields a negative rank correlation which is not significantly different from zero with the small number ( $n = 7$ ) of values compared (Table 3). The correlation is significantly negative when



**Fig. 12.** Dependence of group diurnality index on daily temperature minimum ( $t$  °C) in the Marnewaard. Diurnality index was calculated from night catch and subsequent day catch and plotted against the minimum temperature for that night. Line is the linear regression  $D = 0.212 - 0.0144 t$  ( $P < 0.05$ )

daily indices are compared with daily temperature minima, giving a larger  $n$  ( $n = 56$ ; see Fig. 12). This correlation is indeed largely due to seasonal changes in temperature since it disappears when the seasonal effect is excluded by normalizing daily indices and temperatures to the means for each trapping period.

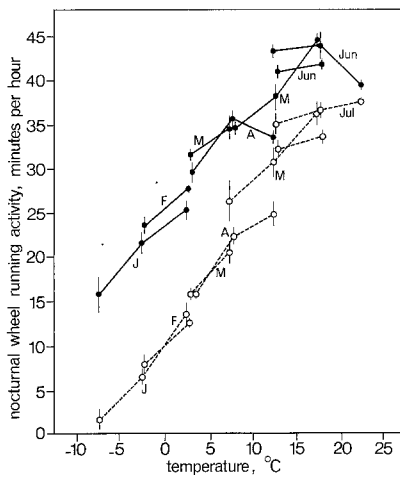
Thus the field data do not provide firm support for the hypothesis that daily trapping pattern and temperature are closely associated. While maximum diurnality was found at the lowest ambient temperature in February, vole trappings were most predominantly nocturnal in May, before the warm nights of summer. If temperature has a causal influence, it presumably is only one of several factors contributing to seasonal change.

In contrast, much of the seasonal variation in nocturnal wheel running activity in cages can be explained by direct influences of ambient temperature. From  $-10$  till  $+15$  °C there was in any month of the year a clear positive correlation between temperature and the fraction of time devoted to wheel running (Fig. 13). Variation between days within the same temperature class in different months was negligible. At the extreme low temperatures in February only the 'young' voles did any significant wheel running. Above  $15$  °C virtually the whole night was devoted to wheel running, and no further temperature dependence was observed. The pattern corresponds qualitatively with the field trap-

**Table 3.** Common vole diurnality indices and some environmental variables.  $R_s$  indicates Spearman's coefficient of correlation between diurnality index and variable. For correlations with crude protein and holocellulose, August data were excluded since grasses contributed little to the diet of this month

	1979					1980		$R_s$ ( $n$ )
	April	May	Aug.	Oct.	Nov.	Febr.	May	
Diurnality index	0.174	-0.110	-0.012	0.148	0.302	0.366	-0.126	-
Green cover (mean %)	11	41	80	84	16	2	14	0.43 (7) n.s.
Crude protein (% of dry weight $\pm$ S.D.)								
Festuca rubra	-	6.3 $\pm$ 4.9	3.6 $\pm$ 0.9	4.8 $\pm$ 1.1	7.1 $\pm$ 1.1	11.4 $\pm$ 4.5	11.8 $\pm$ 4.0	-0.10 (5) n.s.
Poa pratensis	-	6.6 $\pm$ 6.8	5.6 $\pm$ 2.3	3.8 $\pm$ 1.3	7.6 $\pm$ 1.8	11.2 $\pm$ 2.9	9.3 $\pm$ 3.6	0.30 (5) n.s.
Holocellulose (% of dry weight)								
Festuca rubra	-	15.4	41.7	60.8	52.8	22.4	14.0	0.60 (5) n.s.
Poa pratensis	-	16.6	66.3	67.0	45.0	22.2	36.1	0.10 (5) n.s.
Mean minimum temperature (°C)	3.3	9.6	13.2	4.1	6.8	-3.9	4.5	-0.571 (7) n.s.





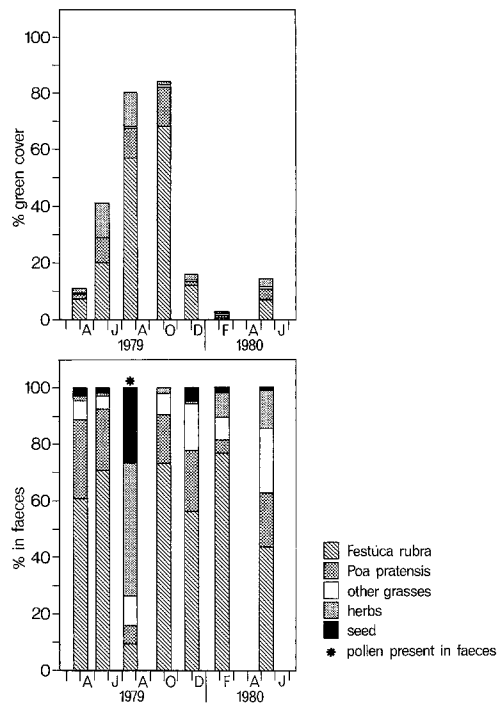
**Fig. 13.** Nocturnal wheel running time in different months separated in 5° C classes of ambient temperature for the *old* (o) and *young* (●) groups of voles. Vertical lines are of length 2 s.e.m.

ping data where minimal nocturnality was recorded at the lowest temperature in February, while summer patterns were not obviously related to temperature.

It is of interest that with the absence of nocturnal wheel running due to low temperature in the 'old' group of voles, a two-hour rhythm of discrete meals emerged at night (Fig. 4, left panel), just as it is always seen in daytime.

**5.3 Food**

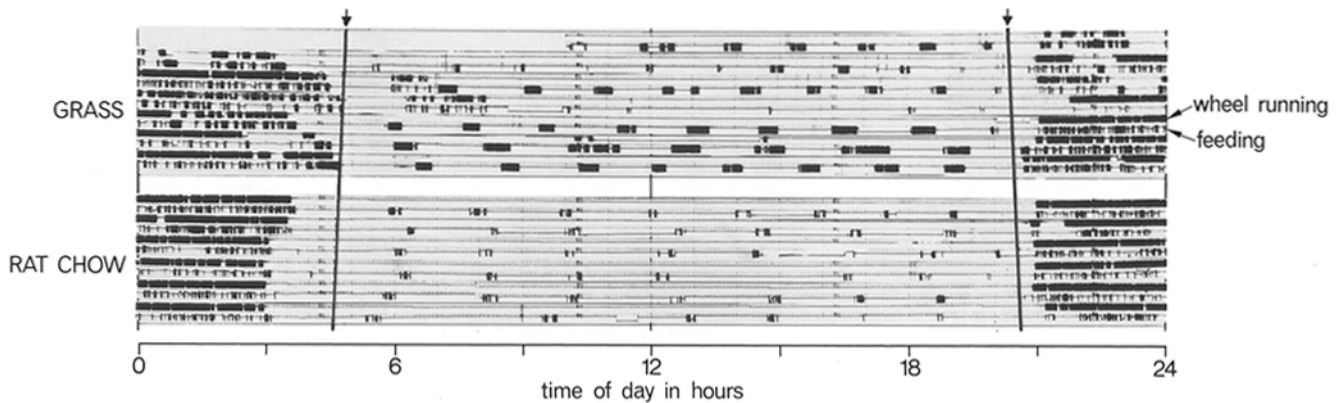
Other variables possibly contributing to seasonal change in diurnality of the common vole concern its food. The availability of green plants changes dramatically in the course of the year (Fig. 14 upper panel). The percentage green cover was highest from July till October, lowest in winter (November till February). The dominating plant species were Red Fescue (*Festuca rubra*) and Smooth Meadow grass (*Poa pratensis*). The selection of plants by the common voles as analyzed from faecal pellets is shown in Fig. 14 (lower panel). Monocotyledons comprised the major portion of the common vole diet (>85% of identifiable remains in faeces), except in July/August. In July/August they mainly fed on dicotyledons (47%) and seeds (28%). Remarkable is the presence of pollen in the faeces at this time of the year.



**Fig. 14.** Seasonal change in the percentage green cover of the vegetation (upper panel) and the composition of diet remains in vole faecal pellets (lower panel)

Apart from quantitative changes there are qualitative seasonal changes in the food. The common vole's forage has a low caloric value and contains a relatively low proportion of protein (Allen 1974). White (1978) showed the importance of the protein content of the forage. It is generally accepted that crude fibers decrease the digestibility and quality of food (Maynard and Loosli 1956). Therefore protein and crude fibres are important variables determining the quality of forage.

The quality of the food of our common voles was estimated by measuring the dry weight percentages of crude protein and holocellulose in the two main food plants, *Festuca rubra* and *Poa pratensis* (See Table 3). Crude protein in both grasses had highest values in February and May 1980, thus at times when extreme maxima and minima in the diurnality indices were found. Holocellulose fractions were highest in autumn, coinciding with the maximum



**Fig. 15.** Effect of food quality on the pattern of feeding. Grass and herbs diet resulted in frequent long meals in daytime, Murakon rat chow in shorter, less frequent meals

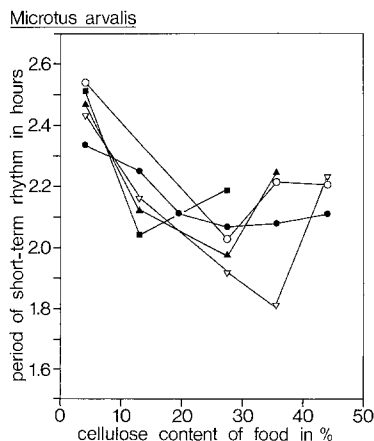
**Table 4.** Effect of food on feeding activity during day and night and on the frequency of meals during the day. Results of two experiments where standard rat chow was temporarily replaced by a 1:1 mixture of Muracon and lucerne (I) and by a mixture of fresh grass and herbs. Significance indicated by two-tailed t-test

	I (16–24.8.1978); (n=4)			II (6–16.5.1979); (n=5)		
	Muracon	<u>Muracon</u> lucerne	P	Muracon	grass + herbs	P
Feeding activity:						
% of 6' intervals						
Day	12.5 ± 0.5	16.3 ± 0.9	<0.025	10.2 ± 1.0	26.2 ± 1.2	<0.005
Night	41.3 ± 7.4	52.8 ± 5.1	n.s.	45.6 ± 9.0	53.2 ± 4.6	n.s.
Diurnality index	-0.50 ± 0.08	-0.52 ± 0.05	n.s.	-0.59 ± 0.05	-0.33 ± 0.05	<0.005
Meal frequency (h <sup>-1</sup> in daytime)	0.44 ± 0.01	0.49 ± 0.01	<0.05	0.42 ± 0.02	0.49 ± 0.02	<0.05
Nocturnal wheel running % of 6' intervals	74.6 ± 7.5	63.0 ± 13.9		77.4 ± 5.5	63.4 ± 11.6	

green cover and with the gradual rise in diurnality. Thus, none of the parameters of food quantity and quality we have analysed had a significant relationship with the vole diurnality index.

There are two shortcomings in the analysis to be pointed out at this stage. Firstly, it is likely that faecal remnant analysis gives a biased impression of the vole's diet due to differential resistance to digestion. Yet the predominance of two grass species in the vegetation as well as in the faecal remains (except in midsummer when seeds were abundant), combined with the fact that this vegetation supported a dense vole population throughout the year, suggests to us that these grasses were dominant in the diet also. Secondly, protein and holocellulose contents were established in whole plants. It is again likely that the voles have selected for instance proximal parts, differing considerably in chemical composition from the rest. A thorough food selection study would be necessary before any firm statement about the effects of food availability on the degree of diurnality can be made. We are presently restricted to the conclusion that food availability, if contributing to the seasonal change in the daily distribution of field activity is again unlikely to be the sole factor responsible.

In caged animals, we have done several experiments



**Fig. 16.** Effect of cellulose content of the diet on the period of the short-term rhythm of food intake. Diets were made by mixing rat chow and lucerne in different quantities. Symbols represent data from five different individuals

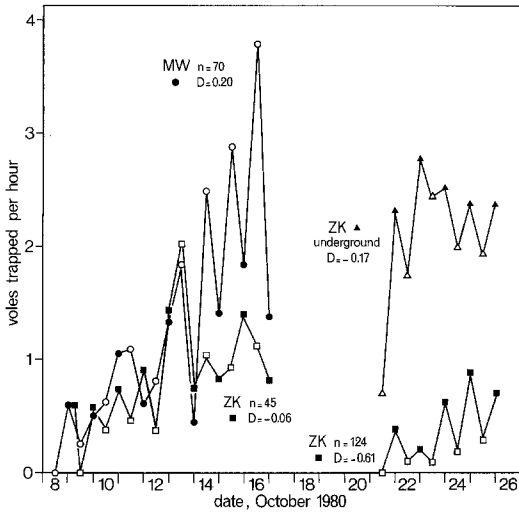
bearing on the effects of food quality on temporal activity patterns. Such effects are exemplified by the record in Fig. 15. When fed with natural grasses and herbs voles showed increased diurnal feeding and reduced nocturnal wheel running as compared with their behaviour when maintained on standard rat food. The same effects were observed when standard food (Muracon®), was replaced by a mixture of Muracon and dried lucerne (Table 4). Furthermore, the addition of various amounts of lucerne had a clear accelerating effect on the short-term rhythm of feeding in daytime (Fig. 16). It is possible that such influences of food quality may also contribute to the pattern of diurnality in field circumstances, although precise information on the responsible chemical compounds and their relevance for the natural diet is not available. At any rate, such findings underscore the artificiality of activity patterns recorded in captive conditions where animals are held on unnatural diets.

### 5.3 Habitat structure

Apart from the seasonal variation, considerable differences in diurnality existed between two trapping sites (Figs. 2, 3 and 4). The two sites differ considerably in soil and vegetation. An important aspect of the habitat at ZK is the clay soil, which is rooted up with vole tunnels at a depth of ca. 5–20 cm. In the tunnels food may be available as the ground is full of roots and young offshoots of Reed (*Phragmites australis*). At MW the soil is firm and more sandy, a similar tunnel system is absent and burrows are clearly marked by concentrations of holes.

To understand the possible role of this difference in habitat structure an experiment was done by M.P. Gerkema in October 1980. At MW and ZK a trapping program was executed in the usual way, i.e., with 196 traps at fixed trapping stations for 9 days. At ZK this was followed by 5 further trapping days, using 196 extra live traps. Within 2.5 m from each trap station a tunnel was opened and the entrance of one extra trap was inserted in the hole (the "underground traps").

The results are summarized in Fig. 17. Initial capture frequencies at MW (0.0183 captures per individual per hour) and ZK (0.0191) did not differ much. They also were similar to the frequencies in the trapping period in October 1979 at MW (0.0179) and ZK (0.0194). Subsequent trap-

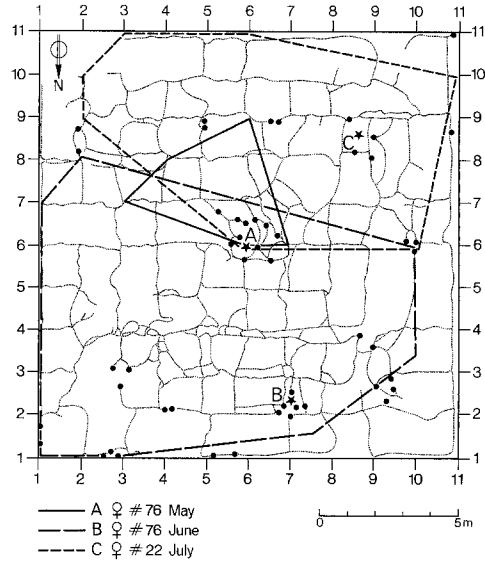


**Fig. 17.** Variation in night and daytime trapping frequencies in two habitats (MW  $\circ$  and ZK  $\square$ ) and within a habitat between traps placed 'underground' in tunnels (ZK  $\Delta$ ) and on the surface ( $\square$ ). Solid symbols indicate nocturnal, open symbols diurnal trapping frequencies

ping in the tunnels revealed the presence of 79 unmarked individuals at ZK in addition to 45 which had already been marked during surface trapping. With the extra traps total catch frequency per individual (0.0207) did not change importantly but in this situation 85% of the trappings were underground.

Captures at MW were considerably more frequent in daytime ( $D=0.20$ ), while at ZK they were again slightly more frequent at night ( $D=-0.06$ ), confirming the difference found in 1979. After the 'underground' traps had been added, ZK trappings became even more nocturnal, especially in the surface traps.

These results suggest that there are two sources of considerable variation in the daily distribution of vole trappings: soil and vegetation structure and trap placement. The latter effect is usually excluded when trap placement is done in a rigid standard way. We have observed a similar effect when traps in the Marnewaard were moved from fixed stations to holes and runways (cf. Fig. 1). This led to a decrease in diurnality (hole trapping  $D=0.08 \pm s.d.$  0.49,  $n=498$ , as compared with station trapping  $D=0.29 \pm 0.61$ ,  $n=337$ ; all data pooled, two-tailed  $t$ -test  $P < 0.001$ ), similar to the underground trapping at ZK. The effect of



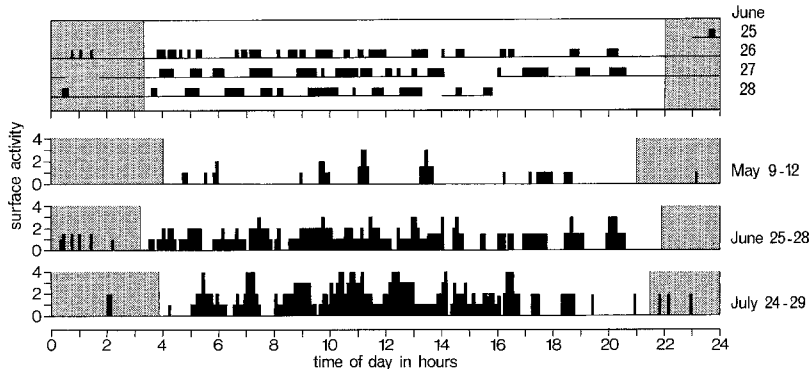
**Fig. 18.** Map of the outdoors enclosure for telemetric recordings of activity according to Chute et al. (1975) with home ranges (convex polygons) of three individually tracked voles. Black dots indicate entrances of burrows, numbers the overhead wire antennas and dotted lines vole runways

habitat structure suggests that the presence of burrow systems and vegetation cover, which both change in the course of the year, may have contributed to the seasonal change in diurnality, although we did not attempt to quantify such changes.

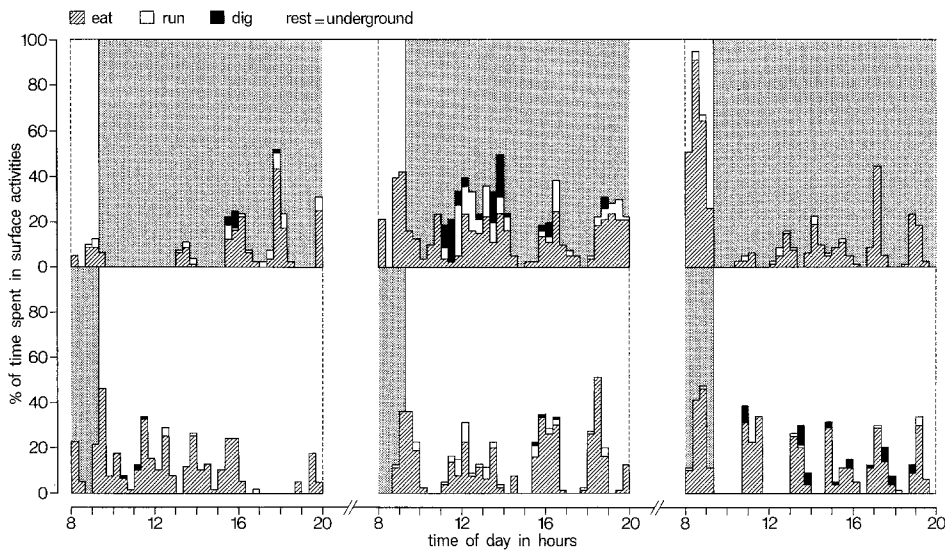
**6 Activity timing in seminatural conditions**

In addition to the year round assays of activity patterns in natural and cage conditions we obtained two restricted sets of data in seminatural circumstances in outdoor and indoor enclosures. These have no immediate bearing on the seasonal change but are of importance with regard to the interpretation of the data.

In the outdoor enclosure, designed for radiotelemetry studies, the voles built their runway system in such a way that most runways were directly underneath the antenna wires (1 m above ground), and rectangular patterns were formed (Fig. 18). In three voles equipped with small radio transmitters we found that movements above ground on the runway system occurred nearly exclusively in daytime (Fig. 19). At night surface activity was sharply reduced and occurred only very close to the main burrows occupied (\*



**Fig. 19.** Surface activity patterns of three radiotracked voles. Upper panel: activity of vole June 25–28 on three consecutive days. Lower panels: surface activity scores accumulated per individual over consecutive days. (May 9–12; June 25–28; C July 24–29)



**Fig. 20.** Time spent in three different behaviours above ground per 20 min interval, averaged over 4 voles on a normal LD 12:12 cycle (lower panels) and 4 on a reverse cycle (upper panels). At 9:00 on the second day a separation wall in each cage was removed exposing the voles to new territory and resulting in increased frequencies of running and digging

in Fig. 18). In most of the observation days a ca. 2 h activity rhythm on the surface was recognizable (Fig. 19). This was further confirmed by a second series of recordings (obtained by J. Hiemstra) using transmitters with photocell modulated frequencies to distinguish surface from underground positions of the voles.

In another approach to the natural behaviour of voles and its timing we obtained complete time budgets in large indoor terraria by scoring the behaviours of 8 individual voles each min for seven 12-h periods. Also under these circumstances a pronounced two-h rhythmicity was observed in surface activity during the light phase, and less conspicuously during darkness (Fig. 20). Surface activity was primarily devoted to feeding both during daytime and at night. Other behaviour (running and digging) occurred predominantly during the night. These behaviours were enhanced following the removal of separation walls between two compartments of each cage whereby new territory became available to each vole.

## 7 Discussion

### 7.1 Comparison of methods

Conform with many other small rodents, wheel running activity in caged common voles was nearly exclusively nocturnal. In conditions of an enclosure, Lehmann and Sommersberg (1980) found a predominance of surface activity in daytime. The method of recording clearly affects the activity pattern found. In this section we compare our own results from trapping and cages with those of Lehmann and Sommersberg (1980). The latter were obtained in an extensive year-round study using automatic passage recording in a 3 × 4 m enclosure outdoors.

With all three techniques a relative shift in activity patterns towards more diurnality in winter than in summer was observed. In cage conditions this was due to a decrease of nocturnal wheel running in winter, while no obvious changes in feeding distribution were observed. In the field individual trapping frequency during daytime increased from summer to winter, while nocturnal trapping frequency remained rather stable (Fig. 2). In the enclosure, the sea-

sonal change was primarily due to a reduction of nocturnal surface activity in winter (Lehmann and Sommersberg 1980; Fig. 5). Thus while the relative distribution of activity over day and night changed in the same direction with all three methods, the average levels of activity decreased from summer to winter in cage and enclosure, and increased when measured in the field. It is likely that the difference between methods reflects increased trappability of active voles in winter conditions in the field and not a basic difference in the daily organization of behaviour between natural and cage conditions. Capture frequencies per vole can be considered the product of trappability (captures per active vole per h) and activity (active fraction of time per vole). Both diurnal and nocturnal capture frequencies were minimal in midsummer (Fig. 2). If the rise in diurnal capture frequency towards midwinter was due to increased trappability, perhaps related to reduced natural food supply (Fig. 14), then a similar rise in nocturnal trappability would compensate for the drop in nocturnal activity expected from the experiments in captivity. Indeed nocturnal capture frequencies did not change significantly from July till February.

Temperature effects were present in all three approaches: in the cages, nocturnal wheel running was linearly dependent on temperatures between  $-10$  and  $+15^{\circ}$  C. In the enclosure nocturnal passage counts were suppressed at low temperatures (Lehmann and Sommersberg 1980; Fig. 8). In the field diurnality was lower at high temperatures, although this effect was not significant within seasons. Trapping is apparently too coarse and discontinuous a method of assay to detect such effects.

Age related variations in the daily activity pattern were established only in the wheel-running records. No evidence was found for age dependent diurnality in field trappings (3.3.1). It should be noted, however, that the caged voles survived till much higher ages than is usual in nature. In field trappings of *M. agrestis* Bäumler (1975) has indeed found increased diurnality in heavier voles. The enclosure setup of Lehmann and Sommersberg (1980) precluded detection of interindividual differences.

So far, the seasonal change in diurnality of field trappings and of passage counts might be adequately explained

by a gradual summer to winter reduction in the nocturnal behaviour corresponding with wheel running. This is, however, unconvincing since all enclosure studies (including our telemetric recordings and direct observations) revealed very restricted nocturnal activity compared with nearly continuous running in cages in summer nights. On the other hand there was close correspondence of both field trappings and passage counts (Lehmann and Sommersberg 1980) with cage feeding patterns. With all three methods a conspicuous 2-h rhythmicity was found during daytime in winter. Nocturnal feeding was diffuse and revealed an ultradian rhythm only when severe cold in winter suppressed wheel running. The day pattern was likewise diffuse during summer, both in field trappings and passage recordings. This pattern is apparently explained by the ongoing presence of a 2-h rhythm in food intake: in summer, this is under less precise phase control of the daily cycle (Fig. 10) so that feeding bouts in a population are no longer strongly synchronized. Further support for the existence of a 2-h rhythm in surface activity stems from close correspondence between trapping patterns and the hunting yield of raptors observed simultaneously (Raptor Group RUG/RIJP 1982).

Thus surface activity as assayed by trapping, passage counting, telemetric records and direct observation all reflected feeding patterns as observed in cages, sometimes in considerable detail. While any of the methods may itself have affected the activity observed, they probably more closely approach the natural surface activity patterns of voles in the field than running wheel recordings. It is then of interest to reflect on the biological meaning of wheel running in caged microtines.

### 7.2 The significance of wheel running

Wheel running is not solely restricted to the condition of small cages where animals are kept in isolation. It occurs also in wheels placed in wider spaced colonies (*Microtus arvalis*: Lehmann and Sommersberg 1980; *Clethrionomys glareolus* and *Lemmus lemmus*: DeKock and Rohn 1971) and may even occur when wheels are offered outside to wild animals in the field (Rawson in Aschoff 1962; C.S. Pittendrigh pers. comm.). In most cases wheel running is virtually restricted to the night, and we would expect it to reflect a motivational state related to a naturally occurring nocturnal behaviour. We have not obtained convincing evidence for any such nocturnal behaviour using various techniques. The sudden sharp increase both in the trappable population and in the extent of nocturnality after traps had been placed in underground tunnels (5.4) suggests that a considerable part of the total activity escapes our attention when only activity on the surface is recorded and that this bias may well be different for day and night. Yet it is also possible that the behaviour reflected by wheel running is quite flexible and subject to variation between individuals and conditions. Using an ethological approach, DeKock and Rohn (1971) have suggested several factors affecting the use of the running wheel. They found it was frequently associated with scent marking in bank voles and lemmings. Wheel running was further enhanced in crowded colonies, suggesting escape behaviour, in new situations (animals transferred to a new colony) and in socially low ranking males. In contrast, Lehmann and Sommersberg (1980) report that in their colony it was a dominant male

which used the wheel mostly, and even defended it against intruders. Such information suggests that use of running wheels at night may reflect different motivational states, sometimes evidently in social context. While it possibly reflects territorial advertisement by refreshing chemical signposts in the runway system as hypothesized by Daan and Aschoff (1982) it may at other times be associated with exploratory and escape behaviour. The confinement of a small cage may have similar stimulating effects on such motivation as crowded conditions may have in nature. Finding little resemblance of nocturnal wheel running with various other methods of assaying natural activity patterns, makes any functional interpretation highly speculative. All we can presently say is that natural equivalents of nocturnal wheel running will probably be restricted to certain conditions which are likely to be dependent on food availability, crowding, and temperature.

### 7.3 Seasonal change in activity distribution

The night for a common vole then is a time where a variety of facultative behaviours may be carried out; the day appears nearly exclusively reserved for food intake in a systematic two-hour pattern. At night feeding is dispersed and an ultradian pattern condenses when in cages running wheel activity is suppressed. Feeding outside the burrow at night was virtually absent in the enclosure of Lehmann and Sommersberg (1980) where food hoarding relieved the voles of the need for nocturnal excursions.

Seasonal redistribution of the daily activity, observed with three different methods, was in all cases consistent with reduced nocturnal surface activity in winter (7.1). No evidence was found for changes in the pattern of activities associated with food intake.

Reduced nocturnal activity in winter has been found in several other microtine rodents (*Microtus agrestis*: Brown 1956; Bäumler 1975; *M. oeconomus*: Erkinaro 1969; *Clethrionomys rutilus* and *C. gapperi*: Stebbins 1975; Herman 1977). In these herbivorous animals, the seasonal shift can not be associated with a temporal redistribution of food availability as in some insectivorous bats where cold nights in spring and autumn lead to diurnal insect and bat activity (Nyholm 1965). Indeed food intake rates in *Microtus* species are nearly equal during day and night (Lehmann and Sommersberg 1980; Daan and Kenagy 1984), in accordance with equality of nocturnal and diurnal resting metabolic rates (Kenagy and Vleck 1982). We surmise that feeding both day and night guarantees maximal exploitation of bulk food. Winter reduction of nocturnal non-feeding activities would be one of the energy saving mechanisms (see Dark et al. 1983) contributing to the chances of survival in a season with low food supply and reduced interspecific interactions in a decreasing population density.

Causally, the seasonal redistribution of activity patterns is most probably the consequence of long- and short-term adaptive responses to factors as daylength (Rowsemit et al. 1982), food supply and temperature. Functionally, it appears to be geared to the annually fluctuating demands of a species group with dramatic annual changes in living conditions.

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## References

- Allen SA (1974) Chemical analysis of ecological materials. Blackwell Sc Publ Oxford
- Aschoff J (1962) Spontane lokomotorische Aktivität. Handb der Zool 8:30. Lief, Teil 11:1–74
- Bäumler W (1975) Activity of some small mammals in the field. Acta Theriologica 20:365–377
- Bovet J (1972) On the social behavior in a stable group of long-tailed field mice (*Apodemus sylvaticus*). II Its relation with distribution of daily activity. Behaviour 41:55–67
- Brown LE (1956) Field experiments on the activity of small mammals *Apodemus*, *Clethrionomys* and *Microtus*. Proc Zool Soc London 126:549–564
- Chute FA, Fuller WA, Harding PRJ, and Herman TB (1975) Radiotracking of small mammals using a grid of overhead wire antennas. Can J Zool 52:1481–1488
- Daan S (1982) Circadian rhythms in animals and plants. In: Brady J (ed) Biological Timekeeping. Cambridge Univ Press
- Daan S, Aschoff J (1982) Circadian contributions to survival. In: Aschoff J, Daan S, Gross G (eds) Vertebrate Circadian Systems. Springer, Berlin, pp 305–321
- Daan S, Kenagy GJ (1984) Daily energy balance of meadow voles with and without running wheels (submitted)
- Daan S, Slopsema S (1978) Short-term rhythms in foraging behaviour of the common vole, *Microtus arvalis*. J Comp Physiol 127:215–227
- Dark J, Zucker I, Wade GN (1983) Photoperiodic regulation of body mass, food intake, and reproduction in the meadow vole (*Microtus pennsylvanicus*). Biol Repr (submitted)
- DeKock LL, Rohn I (1971) Observations on the use of the exercise-wheel in relation to the social rank and hormonal condition in the bank vole (*Clethrionomys glareolus*) and the norwegian lemming (*Lemmus lemmus*). Z Tierpsychol 29:180–195
- Erkinaro E (1961) The seasonal change of the activity of *Microtus agrestis*. Oikos 12:157–163
- Erkinaro E (1969) Der Phasenwechsel der lokomotorischen Aktivität bei *Microtus agrestis* (L.), *M. arvalis* (Pall.) und *M. oeconomus* (Pall.). Aquilo Ser Zool 8:1–29
- Erkinaro E (1972) Seasonal change in the phase position of circadian activity rhythms in some voles, and their endogenous component. Aquilo Ser Zool 13:87–91
- Hansson L (1970) Methods of morphological diet micro-analysis in rodents. Oikos 21(2):255–266
- Herman TB (1977) Activity patterns and movements of subarctic voles. Oikos 29:434–444
- Joenje W (1978) Plant colonization and succession on embanked sandflats. Thesis, RU Groningen
- Kenagy GJ, Vleck D (1982) Daily temporal organization of metabolism in small mammals: Adaptation and diversity. In: Aschoff J, Daan S, Groos G (eds) Vertebrate Circadian Systems. Springer, Berlin, pp 322–338
- Kikkawa J (1964) Movement, activity, and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. J Anim Ecol 33:259–299
- Lehmann U (1976) Short term and circadian rhythms in the behaviour of the vole, *Microtus agrestis* (L.). Oecologia (Berlin) 23:185–199
- Lehmann U, Sommersberg CW (1980) Activity patterns of the common vole, *Microtus arvalis* – automatic recording of behaviour in an enclosure. Oecologia (Berlin) 47:61–75
- Leuze CCK (1980) The application of radiotracking and its effect on the behavioral ecology of the water vole, *Arvicola terrestris* (Lacépède). In: Amlaner CJ, MacDonald DW (eds) A Handbook on biotelemetry and Radio tracking. Pergamon Press, Oxford, pp 361–366
- Londo G (1975) De decimale schaal voor vegetatiekundige opnamen van permanente kwadraten. Gorteria 7:101–106
- Madison DM (1981) Time patterning of nest visitation by lactating meadow voles. J Mamm 62(2):389–391
- Maynard LA, Loosli JK (1956) Animal nutrition. McGraw Hill NY
- Nyholm ES (1965) Zur Ökologie von *Myotis mystacinus* (Leisl) und *M. daubentoni* (Leisl) (Chiroptera). Ann zool Fenn 2:77–123
- Osterberg DM (1962) Activity of small mammals as recorded by a photographic device. J Mammal 43(2):219–229
- Ostermann K (1956) Zur Aktivität heimischer Muriden und Gliriden. Zool Jahrb Allg Zool Physiol Tiere 66:355–388
- Pearson OP (1960) Habits of *Microtus californicus* revealed by automatic photographic recorders. Ecol Monogr 30:231–249
- Pittendrigh CS, Daan S (1976) A functional analysis of circadian pacemakers in nocturnal rodents. IV Entrainment: Pacemaker as Clock. J comp Physiol 106:291–331
- Raptor-group RUG/RIJP (1982) Timing of vole hunting in aerial predators. Mammal Rev 12:169–181
- Rijnsdorp AD, Daan S, Dijkstra C (1981) Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. Oecologia (Berlin) 50:391–406
- Robitaille JA, Bovet J (1976) Field observations on the social behaviour of the Norway rat, *Rattus norvegicus* (Berkenhout). Biol Behav 1:289–308
- Rowsemitt CN, Petterborg LJ, Claypool LE, Hoppenstaedt FC, Negus NC, Berger PJ (1982) Photoperiodic induction of diurnal locomotor activity in *Microtus montanus*, the Montane Vole. Can J Zool 60:2798–2803
- Shields LJ (1976) Telemetric determination of the activity of free-ranging rodents: The fine structure of *Microtus californicus* activity patterns. Ph D Thesis UCLA, pp 1–95
- Stebbins LL (1975) Short activity periods in relation to circadian rhythms in *Clethrionomys gapperi*. Oikos 26(1):32–38
- Taylor KD (1978) Range of movement and activity of common rats (*Rattus norvegicus*) on agricultural land. J appl Ecol 15:663–677
- White TCR (1978) The importance of a relative shortage of food in animal ecology. Oecologia (Berlin) 33:71–86

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