

Circadian activity patterns, photoperiodic responses and population cycles in voles

I. Long-term variations in circadian activity patterns

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Summary. Patterns of above-ground activity were recorded in two free-ranging populations of *Microtus agrestis* (L.) and one population of *M. arvalis* (Pall.) over several years by means of passage counters. Long-term variations of the circadian pattern were observed, but did not repeat themselves in a 12-month cycle. Variations in all three populations could be described by a sinusoidal function of an 18-month period. Maxima and minima of the sine-function were connected to distinct photoperiods (equinoxes and solstices). In a cyclic North Swedish population, the sine-function was superimposed by a second function which shows saturation behaviour. The relevance of these findings is discussed with respect to vole population cycles.

Key words: Microtines – Circadian activity behaviour – Long-term variations – Population cycles

Activity behaviour in voles is dominated by short activity bouts and rest periods both during daytime and the night, resulting in a polyphasic pattern (Szymanski 1920; Davis 1933; Ostermann 1956). Known features of this short-term rhythm, which does not match environmental cycles, have been discussed by Daan and Aschoff (1981). The polyphasic pattern is modified by the daily light/dark-cycle entraining an endogenous circadian mechanism (Lehmann 1976). It gives prominence to an activity phase either during daytime or during the night. The resp. positions of the activity phase seem to depend on season.

Phase-shifts have been observed both in laboratory (Ostermann 1956; Erkinaro 1961, 1969) and in the field (Bäumler 1975; Halle 1984). However, in some investigations, seasonal phase-shifts could not be observed (Lehmann and Sommersberg 1980; Wigger 1983). Moreover, it is obvious that activity behaviour in voles decisively depends on the particular environmental conditions. Voles kept in an enclosure of 12 m² were active during daytime, whereas voles kept in registration cages (25 × 30 cm) within the same enclosure were active only at night (Lehmann and Sommersberg 1980). Changes of the pattern caused by cages of different size (Lehmann 1976) have been reported as well as changes owing to different biotopes (Hooenboom et al. 1984; Wigger 1983) and owing to different social conditions (Halle 1984; Lehmann unpublished work). Thus, the complex organisation of vole activity behaviour

appears to enable a high degree of plasticity. This might reflect specific time schedules to match the challenge of fluctuating environmental conditions.

In consequence, only an analysis under undisturbed natural conditions can yield relevant information. Therefore, we employed the method of recording above-ground activity in voles by passage counters (Mossing 1975) for long-term studies in three free-ranging populations at two different latitudes (Rhineland/Germany, Västerbotten/Sweden).

Methods and material

The passage counters (Fig. 1) were modified after Lehmann and Sommersberg (1980). They were placed in discernible runways, so that “activity” only refers to above-ground locomotion within the runway system. The passages can be taken as representative for activity distribution, but are an unknown and varying proportion of all movements on the area covered. The proportion between all counts per daytime (sunrise to sunset, cL) and all counts per night (sunset to sunrise, cD) was expressed in percentage (Table 1b). To exclude the effect of the varying photoperiod, we divided the number of counts by the length of the respective phase, resulting in “activity intensity per hour in L or D” (Table 1c). To compare decades with different overall activity, the “activity intensity in daylight” (ai-L, Table 1d) was expressed in percentages. The difference of ai-L to 50% yields the index δ_{50} (Table 1e) which thus is a measure for the degree of predominance of “activity intensity” either in daylight ($\delta_{50} > 0$) or at night ($\delta_{50} < 0$).

Data reported derived from two populations of *Microtus agrestis* (L.) and one population of *M. arvalis* (Pall.).

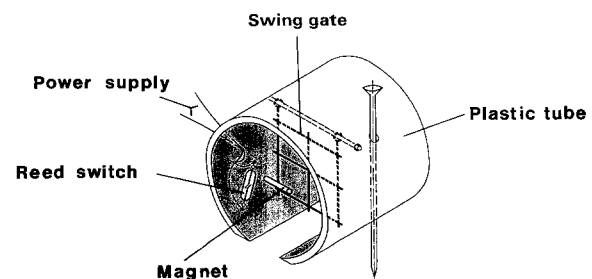


Fig. 1. Passage counter to record above-ground vole locomotion in the field. Power leads and reed switch are protected against corrosion. Passages are registered by event recorders

Table 1. Method example for calculating the indices under discussion, as derived from decades XI/1 ('84, '85) depicted in Fig. 2 (100% = all counts over 24 h per decade). For explanation see text

Decade XI/1, 1984		Decade XI/1, 1985	
a)			
Sunrise: 7.35	hL = 9.4	Sunrise: 7.35	hL = 9.4
Sunset: 17.00	hD = 14.6	Sunset: 17.00	hD = 14.6
b)			
cL = 485 = 66.2%		cL = 31 = 13.5%	
cD = $\frac{248}{733} = 33.8\%$		cD = $\frac{198}{229} = 86.5\%$	
c)			
$\frac{cL}{hL} = 51.6$ counts/h		$\frac{cL}{hL} = 3.3$ counts/h	
$\frac{cD}{hD} = 17.0$ counts/h		$\frac{cD}{hD} = 13.6$ counts/h	
d)			
$ai-L = \frac{51.6}{51.6 + 17.0} \cdot 100 = 75.2\%$		$ai-L = \frac{3.3}{3.3 + 13.6} \cdot 100 = 19.5\%$	
e)			
$\delta_{50} = +25.2$		$\delta_{50} = -30.4$	

1. Sophienhöhe (50° 54' N, 6° 24' E)

Dense open grassland of ca. 3 ha in an extended reclaimed lignite area in the open cast mining district near Cologne. Vegetation was dominated by *Festuca spec.*, *Lolium perenne* and *Poa pratensis* as gramineas, and the herbs *Trifolium spec.*, *Sanguisorba minor* and *Lathyrus pratensis*. The meadow was colonized by *Microtus arvalis*. Activity was recorded continuously from May '84 until April '86 (72 decades).

2. Haus Österle (50° 51' N, 6° 32' E)

A glade of ca. 1 ha in a woodland area 7 km distant from Sophienhöhe. Vegetation cover was dense and homogeneous, dominated by *Calamagrostis epigeios* and *Urtica dioica*. It had not been mown for several years and was inhabited by *Microtus agrestis*. This population was under survey continuously from February '84 to March '85 (40 decades).

3. Torpet (63° 35' N, 19° 50' E)

This area is situated in the North Swedish province of Västerbotten, 30 km south of Umeå. It encloses ca. 2 ha old pasture land, abandoned since the '50s. Very dense vegetation cover is formed by *Deschampsia caespitosa*, *Alopecurus pratensis*, *Filipendula ulmaria* and *Anthriscus sylvestris* and, additionally, by some shrubs of *Salix spec.* and *Betula spec.*. This habitat, typical for the whole region, offers optimal conditions to *Microtus agrestis* (Hansson 1971). As shown by Halle (1985), the general trend of population cycles observed in Northern Scandinavia (Myllymäki 1977; Hörnfeldt 1986) is also followed by the population at Torpet. Recording of activity was partially accompanied by investigations of population structure during summer months. There are data for four separate periods with a total of

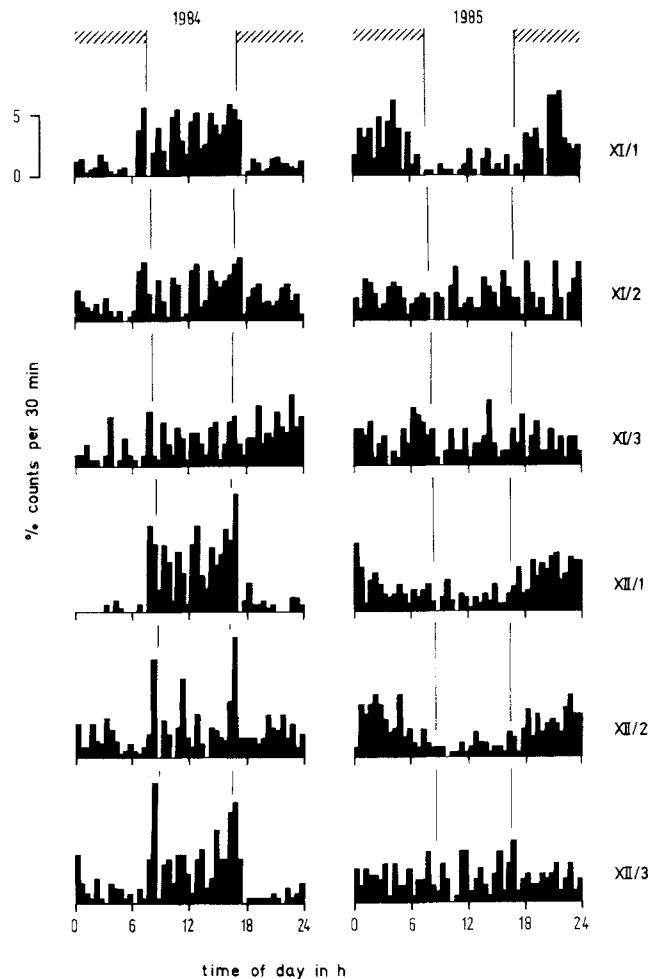


Fig. 2. Example of activity patterns of *M. arvalis* as recorded during November and December (decades XI/1 – XII/3) 1984 and 1985 at Sophienhöhe. The patterns are evaluated on counts per 30 min, then calculated as percentage of counts per 10-day period (= 100%)

67 decades: June to December '81 (peak phase), May to September '82 (decrease and low phase), June '84 to January '85 (peak phase) and May to September '85 (decrease and low phase).

Results

Long-term variations in the activity patterns recorded were quite obvious in all three populations. Surprisingly these variations did not correlate with seasons as can be seen for *M. arvalis* at Sophienhöhe (Fig. 2) – between both years in corresponding seasons the patterns are markedly different. In '84, diurnal activity is predominant and a clear-cut short-term rhythm stands out during daytime with peaks at sunrise and sunset. In '85, nocturnal activity is predominant and no distinct peaks can be seen at dawn and dusk. Environmental influences which could be correlated to these changes (e.g. habitat structure or climate) were not detectable.

Inspecting the index δ_{50} for the whole period of investigation (Fig. 3) it became obvious that it oscillates in a regular pattern and can be fitted by a sine-function (to test the quality of approximation, a correlation analysis was performed for the field data plotted against the calculated

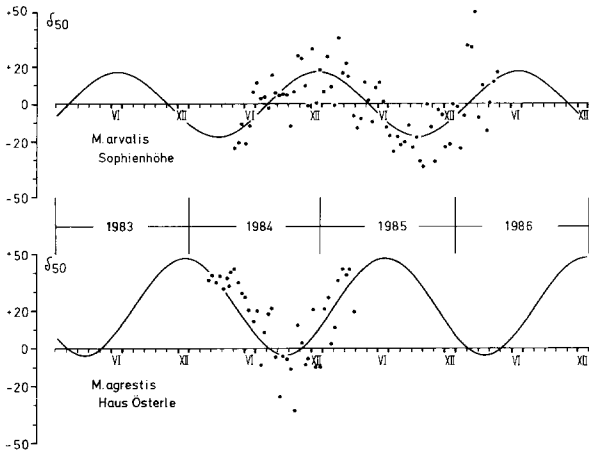


Fig. 3. Temporal course of δ_{50} in the Rhineland populations during the period under survey. If $\delta_{50} > 0$, activity intensity in daylight is predominant; if $\delta_{50} < 0$, activity intensity at night is predominant. δ_{50} pictures the degree of predominance. The parameters of the approximated sinusoidal graphs are given in Table 2

values, Table 2). An overview of the patterns recorded in the other two populations yielded similarities with respect to both position of maxima and minima at about the equinoxes and solstices and to the period length, although one year out of line with Sophienhöhe. Therefore, we performed similar approximations for all three populations, keeping in mind that owing to the short observation period (Haus Österle) and discontinuous records (Torpet) approximations cannot be totally substantiated, although they nevertheless demonstrate that our assumptions need not be rejected.

1. *Sophienhöhe* (Fig. 3, Table 2)

In spite of high variance (indicated by the standard deviation) the sine-function fits well; the limit for significant correlation is clearly exceeded. The most interesting feature

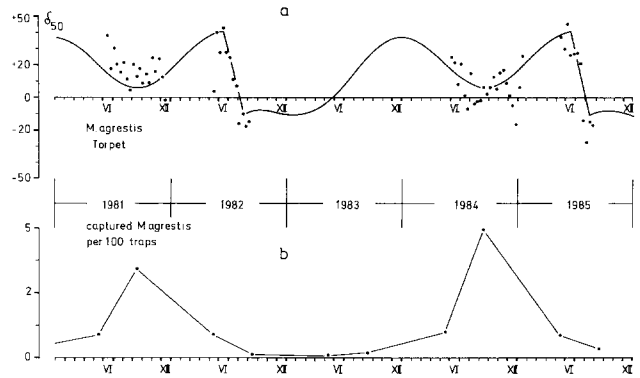


Fig. 4. **a** Temporal course of δ_{50} in the cyclic North Swedish population (δ_{50} as in Fig. 3). **b** Development of population density after Hörnfeldt (1986) data for the whole province of Västerbotten

of the sine, however, is the fact that it repeats itself after 54 decades, i.e. after 18 months.

The phase relation between sine-function and photoperiod is such that maxima are reached alternately at the solstices (June and December) and minima at the equinoxes (March and September).

2. *Haus Österle* (Fig. 3, Table 2)

The same sine-function as evaluated for Sophienhöhe approximates the data equally well, but the amplitude is enlarged and the zero axis is shifted. Therefore, there is a consistent predominance of “activity intensity in daylight”. The relation between phase and photoperiod is the same as at Sophienhöhe (minimum in September), but with the one year difference.

3. *Torpet* (Fig. 4, Table 2)

Fitting of the data is complicated because activity patterns could not be recorded continuously. Another difficulty is

Table 2. Parameters for the approximation by sine-functions. The function of best fit is found if a) the parameters for linear regression ($y = a + b \cdot x$) are $a = 0$ and $b = 1$, b) the correlation coefficient r is up to a maximum and above the significance limit, and c) the standard deviation is as small as possible (Sachs 1969)

<i>Sophienhöhe</i> ($n = 72$ decades)	
Formula	$\delta_{50} = 17.5 \cdot \sin\left(\frac{360}{54} \cdot (t - 10)\right) - 0.11$
Linear regression	$a = 0.00 \quad b = 1.00$
Correlation	$r = 0.6676 > r_{70; 0.001} = 0.3798$
Stand. deviation	$s_{y,x} = 13.27$
<i>Haus Österle</i> ($n = 40$ decades)	
Formula	$\delta_{50} = 25.6 \cdot \sin\left(\frac{360}{54} \cdot (t - 19)\right) + 22.16$
Linear regression	$a = -0.01 \quad b = 1.12$
Correlation	$r = 0.7732 > r_{38; 0.001} = 0.5007$
Stand. deviation	$s_{y,x} = 13.24$
<i>Torpet</i> ($n = 67$ decades)	
Formula	$\delta_{50} = 16.8 \cdot \sin\left(\frac{360}{54} \cdot (t - 40)\right) + 48.3 \cdot (1 - e^{-0.05 \cdot t}) - \frac{48.3}{2}$
Linear regression	$a = 0.01 \quad b = 0.87$
Correlation	$r = 0.7087 > r_{65; 0.001} = 0.3931$
Stand. deviation	$s_{y,x} = 11.52$

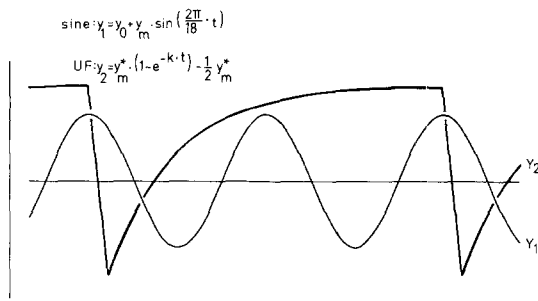


Fig. 5. Graphic representation of the two functions sine and UF (Unknown Factor), which produce the curve shown in Fig. 4a. For explanation see text

the obvious influence of the two population cycles during the course of investigation (Fig. 4b). However, there are striking similarities between corresponding cycle phases. During peak phases in '81 and '84 a minimum of δ_{50} was revealed in August/September. After declines in '82 and '85, δ_{50} was very high in June. Then phase-shifts occurred, so that in August δ_{50} was about -15 . The data can be fitted by the curve given in Fig. 4a, with a hypothetical description in the periods without observation.

The graph in Fig. 4a results from superimposition of two functions (Fig. 5):

$$y_1 = y_0 + y_m \cdot \sin\left(\frac{2\pi}{18} \cdot t\right) \quad (1)$$

This is the same function as that fitted to the populations at Sophienhöhe and Haus Österle.

$$y_2 = y_m^* \cdot (1 - e^{-k \cdot t}) - 1/2 y_m^* \quad (2)$$

This function displays a saturation behaviour. We call it UF, because an Unknown Factor modifies the basic sine-function. If y_2 nearly reaches the maximum value $1/2 y_m^*$ and if y_1 of the sine is in its maximum, a collapse occurs which takes two months and leads to zero again. Because of the term " $-1/2 y_m^*$ " the curve runs symmetrically to the zero axis. Seen in sequence, UF resembles a relaxation oscillation. It must be stressed, however, that this is only a seeming likeness. The time of collapse is determined by extrinsic parameters and not by an inherent periodicity.

The resulting approximation seems acceptable (Table 2). The maximum positive item offered by UF yields 24.15 which is of the same magnitude as observed at Haus Österle (22.16). The amplitude is nearly identical to that found at Sophienhöhe.

Discussion

Despite some uncertainties, the long-term observation of activity patterns in three different populations yielded fundamental similarities:

- the voles shift between predominantly diurnal and nocturnal activity (calculated as "activity intensity" in L or D),
- the extreme values of both diurnality and nocturnality are observed at distinct times of the year (equinoxes and solstices),
- the basic course of events is repeated in periods of 18 months.

Phase-shifts of vole activity patterns have been reported several times, but they have been discussed against the back-

ground of seasonal dependency (Ostermann 1956; Erkinaro 1961, 1969; Bäumlér 1975; Rowsemit et al. 1982). Most of these investigations were carried out with caged specimens, and the annual pattern was derived by combining the records of different individuals from successive experiments. Our long-term records from undisturbed free-ranging populations thus seem reliable, seen in the light of the assumptions mentioned above.

However, interpretation of variation in circadian patterns as a sequence with 18-month periodicity raises several questions. It must be considered that this span involves several successive generations. This infers that all members of the population undergo the same variation of their circadian system, i.e. synchronization between individuals, irrespective of age and weight, is necessary. In *Mus booduga*, Viswanathan and Chandrashekarán (1985) demonstrated that the mother's absence/presence pattern acts as a zeitgeber which determines the phase of circadian activity in the juveniles. In voles, social synchronization of the short-term rhythm is quite plain – the regular sequence of activity bouts in populations as established by trapping in 20 min-intervals (Daan and Slopsema 1978) and by our method (Fig. 2) cannot be explained otherwise. Therefore, social synchronization of the circadian patterns and transmission of long-term variations between generations seems probable, too.

The basic sine-function obviously underlies modifications in different populations. On the one hand, we assume an influence of the environmental state, because weather conditions (Lehmann and Sommersberg 1980) as well as snow and vegetation cover (Halle in prep.) have been proved to change activity patterns. These influences probably cause deviations of the computed activity intensity in L or D between successive decades.

On the other hand, in order to describe long-term variations in the cyclic populations at Torpet, the UF-Function had to be introduced. This function explains the shift of the patterns towards diurnal activity (Fig. 4a). The same mechanism might be responsible for predominant day activity at Haus Österle. UF indicates a steady influence. As it is correlated to population cycles, dependence on density and social conditions might be suggested.

In general, two oscillations with a period length of 12 months (i.e. photoperiod) and 18 months (i.e. sine-function) come in phase every third year. Both of the population cycles observed in North Sweden (Hörnfeldt 1986) were of 3-year periodicity. Therefore, during each phase of a cycle the relation between photoperiod and circadian system must have been different. Thus, we assume that *Microtus population cycles either cause or are caused by systematically changing phase relations between photoperiod and circadian system in the course of years.*

As derives from Fig. 3, the fitted sine-function of the populations at Sophienhöhe and Haus Österle are one year out of phase. This may demonstrate that vole population cycles are not triggered by overriding (e.g. climatic) conditions, but depend on population properties themselves. Thus it is plausible that cycles may be or may not be synchronized in different populations, as found, e.g., by Chitty (1952) and Godfrey (1955).

All findings and the interpretations suggested need further confirmation. In particular, 4 and 5-year cycles should be studied with the focus on assumed correlation between photoperiod and circadian system. Our ideas of how the

18-month periodicity of circadian behaviour might come about and how it might control population cycles will be presented in Part II.

Acknowledgements. We are indebted to the Forestry Office of Rheinbraun AG for technical support allowing investigations of the populations at Sophienhöhe and Haus Österle, and to I. and O. Nilsson (Umeå) who enabled our investigations at Torpet. The investigations in Sweden have been supported by the DFG (Le 196/6). Special thanks are offered to P. Brenner, who did the field-work under extremely difficult conditions in 1985. C. Wesselborg helped us with the Fourier-analysis, R. Bieg with the illustrations. We are also indebted to G. Tomlin for correcting the English manuscript.

References

- Bäumler W (1975) Activity of some small mammals in the field. *Acta theriol* 20:365–377
- Chitty D (1952) Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936–9. *Phil Trans R Soc Lond, Ser B* 236:505–552
- Daan S, Aschoff J (1981) Short term rhythms in activity. In: J. Aschoff (ed.) *Handbook of Behavioural Neurobiology*, Vol 4: *Biological Rhythms*, Plenum Press, New York and London, pp 491–498
- Daan S, Slopsema S (1978) Short-term rhythms in foraging behaviour of the common vole, *Microtus arvalis*. *J Comp Physiol* 127:215–227
- Davis DHS (1933) Rhythmic activity in the short-tailed vole, *Microtus*. *J Anim Ecol* 2:232–238
- 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) and *M. oeconomus* (Pall). *Aquilo (Ser Zool)* 8:1–31
- Godfrey GK (1955) Observations of the nature of the decline in numbers of two *Microtus* populations. *J Mamm* 36:209–214
- Halle S (1984) Zusammenbruch einer Population der Erdmaus (*Microtus agrestis* L.): Dynamik, Populationsstruktur, Aktivitätsverhalten. Diplomarbeit Universität Köln
- Halle S (1985) Manifestation of the Västerbotten field vole cycle 1981–1984 in a small area. *Fauna Norrlandica* 1:1–20
- Hansson L (1971) Habitat, food and population dynamics of the field vole *Microtus agrestis* (L) in South Sweden. *Viltrevy* 8:267–378
- Hörnfeldt B (1986) Basinventering Gnagare (BIG). Rapport 20. Inst Ekol Zool., Universitet Umeå
- Hoogenboom I, Daan S, Dallinga JH, Schoenmakers M (1984) Seasonal change in the daily timing of behaviour of the common vole, *Microtus arvalis*. *Oecologia* (Berlin) 61:13–31
- 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
- Mossing T (1975) Measuring small mammal locomotory activity by passage counters. *Oikos* 26:237–239
- Myllymäki A (1977) Outbreaks and damage by the field vole, *Microtus agrestis* (L) since world war II in Europe. *EPPO Bull* 7:177–207
- Ostermann K (1956) Zur Aktivität heimischer Muriden und Gliriden. *Zool Jb (Physiol)* 66:355–388
- Rowsemitt CN, Pettersborg LJ, Claypool LE, Hoppensteadt FC, Negus NC, Berger PJ (1982) Photoperiodic induction of diurnal locomotor activity in *Microtus montanus*, the montane vole. *Can J Zool* 60:2798–2803
- Sachs L (1969) *Statistische Auswertungsmethoden*. Springer Berlin, Heidelberg New York
- Szymanski JS (1920) Aktivität und Ruhe bei Tieren und Menschen. *Z Allg Physiol* 18:105–162
- Viswanathan N, Chandrashekar MK (1985) Cycles of presence and absence of mother mouse entrain the circadian clock of pups. *Nature* 317:530–531
- Wigger F (1983) Untersuchungen zum tages- und jahresperiodischen Aktivitätsverhalten freilebender und gekäfigter Arvicolidae (*Microtus arvalis* und *Clethrionomys glareolus*). Diplomarbeit Universität Köln

Received October 10, 1986