

Interindividual Influence on Diurnal Rhythms of Activity in Cycling and Noncycling Populations of the Field Vole, *Microtus agrestis* L.

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Summary. The effects of interaction among individuals with respect to wheel-running activity has been investigated in two geographically separated populations of the field vole *Microtus agrestis* L. In one of them, a northern cyclically varying population, a strictly nocturnal activity pattern is changed into a more or less short term 24 h pattern under conditions of increased contact among individuals. In the other population, south-Swedish, without population cycles, no such effects were observed. This indicates population differences in response to interindividual contact which might be of importance to the known differences in population dynamics.

Introduction

Much of our present knowledge of the behavior of small mammals comes from observations of animals in captivity. This is particularly valid for species like the field vole (*Microtus agrestis*) that spend most of the time in covered runways, and thus are utterly difficult to study in natural habitats. Activity and rhythmicity in different species of rodents have been extensively studied in laboratories using various types of experimental designs (for reviews see Johst, 1967; Bünning, 1967). However, only rarely have the effects of interaction between individuals on the different behavioural manifestations been considered. Calhoun (1963) as well as Crowcroft and Rowe (1963) and Bovet (1972) reported an influence of social rank on the distribution of general activity in mice. Fujimoto (1953) observed that male mice showed identical patterns of activity distribution when separated but dissimilar ones when caged together. Contrary to this, Kavanau (1963) found that female mice showed individually varying activity patterns when separated but similar ones when kept together.

It has previously been shown (Rasmuson et al., 1977) that two geographically separated populations of field vole differed in their amounts of activity, both with regard to single individual activity and to group activity. The differences between the two populations were more pronounced for males than for females

and greater when animals were grouped than when they were single. Breeding experiments showed that this behavioural trait had a genetic background.

The aim of the present study was to investigate whether the two populations also differed in activity distribution and whether contact between individuals affected the activity patterns. An experimental arrangement, which allowed observations of interindividual influence on the circadian patterns of wheel-running activity was used.

Material and Methods

The specimens of *Microtus agrestis* used in the present investigation were trapped in Longworth traps at two localities in Sweden, Degernäs near Umeå (N 63, E 21°) and Stensoffa Research Station near Lund (N 55°30', E 13°).

The northern population is a typically fluctuating population with cyclic density fluctuations of great magnitude, while the southern population except for seasonal variations is almost stable (Hanson, 1971 a, b). Studies of several allozyme systems (Nygren, in preparation) suggest considerable genetic differences between field voles from the two populations.

The experiments were carried out in a greenhouse under natural light conditions (see legend of Fig. 2). Animals of the southern population were collected in November 1976 and kept in

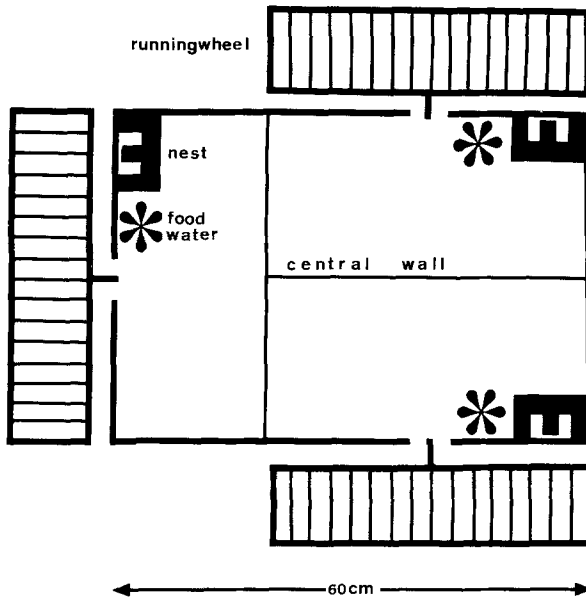


Fig. 1. Plan view of the experimental cage used for recording wheel-running activity. The central walls were changeable to permit the use of two types of walls, one of solid aluminum (thickness 6 mm), the other of perforated perspex (thickness 6 mm, densely spaced holes). The latter allowed auditory, visual, olfactory and physical contact. With the aluminum wall the contact between animals was restricted to an auditory and olfactory one. The walls facing outwards were made of perforated aluminum plate. A lever on the running-wheel activated a micro-switch connected to an event recorder (Esterline-Angus) which registered the beginning and duration of the events. Food pellets, lettuce, and water – was available ad lib. and nesting material was provided

the laboratory at 16° C, in artificial light, L:D, 18 h:6 h. Before the start of the experiments the animals were kept for 3 weeks in the greenhouse. The northern voles were trapped in January 1977 and treated in the same manner. The animals were kept isolated from each other until the experiments started. Adult reproductively active males of about similar size were chosen for the experiments. The cages used in the experiment are shown in Figure 1.

Three males of each population were studied with respect to activity patterns under two experimental conditions—"contact" and "isolation". The males were placed singly in the compartments of the cages and their wheelrunning activities were recorded (registration of activity events, Fig. 2). Between day 1 and 29 and between day 40 and 49 the animals were separated by solid aluminum walls, "isolated" conditions, and between day 29 and 40 and between day 49 and 54 by transparent, perforated perspex walls, "contact" conditions.

Results

The experiment can be divided into five phases: I, early part of the first interval (day 1–29); II, late part of the same interval; III, the second interval (day 29–40); IV, the third interval (day 40–49); V, the fourth interval (day 49–54). From each of these, five representative days were taken out for statistical analysis. The average numbers of activity events are shown in Table 1a. During the first two phases the activity for all six animals is distinctly concentrated in the dark period. This is expected since field voles have previously been shown to be preferentially nightactive with respect to this kind of behavior (Erkinaro, 1961). An analysis of variance, performed separately for each population, shows that the variation among individuals is significant in the southern population (Table 1 b). In the northern population there is a highly significant difference ($P < 0.001$) in mean activity between the two repeats, due to a higher nocturnal activity of the animals during phase II. This difference between phases in nocturnal activity manifests itself as a significant interaction between repeats and light conditions. There are also differences among the three northern males with respect to the increase in nocturnal activity, which leads to a significant ($P < 0.01$) interaction between individuals and light conditions (Table 1 b).

Table 1a. Averages (with standard errors) of activity events calculated for the light and dark period, respectively, of 5 days during each phase. Phases I, II, and IV represent "isolated" conditions; phases III and V "contact" conditions. Further information is given in the text

	Phase	Southern population	Northern population
Light	I	2.6 ± 0.75	1.5 ± 0.49
	II	3.0 ± 1.54	1.5 ± 0.36
	III	2.3 ± 0.71	11.9 ± 2.00
	IV	1.7 ± 0.47	8.0 ± 2.92
	V	1.6 ± 0.39	31.3 ± 7.67
Dark	I	20.4 ± 1.15	13.9 ± 1.05
	II	17.2 ± 0.75	21.2 ± 1.63
	III	14.4 ± 1.80	21.9 ± 0.68
	IV	16.7 ± 1.49	15.7 ± 1.39
	V	16.6 ± 1.27	16.9 ± 1.59

Table 1b. Analyses of variance of number of activity events between two repeats of "isolated" conditions, phases I and II

	df	Southern population MS	Northern population MS
Between light-dark	1	3872.067***	3856.017***
Among animals	2	174.067***	28.80
Between repeats	1	29.40	198.017***
Interaction repeats \times individuals	2	12.80	64.067**
Interaction repeats \times light-dark	2	48.60*	198.017***
Interaction individuals \times light-dark	2	28.467	16.267
Interaction individuals \times repeats \times light-dark	2	50.45*	93.733**
Error	48	10.233	11.683

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2a. Mean percentages of activity events during daytime calculated for five days. Phases I, II, and IV represent "isolated" conditions, III and V "contact" conditions

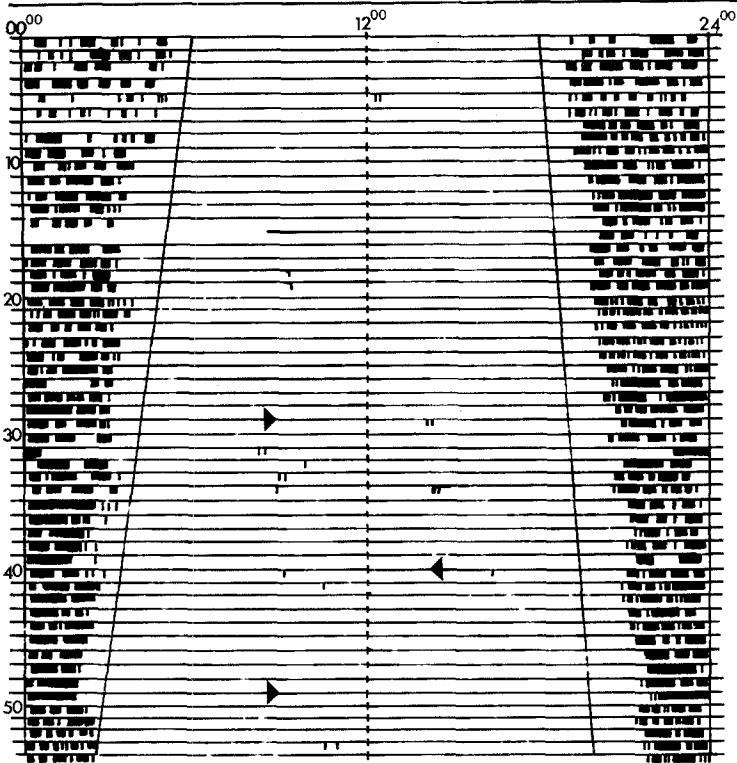
Phase	Southern population	Northern population
I	9.3 \pm 2.22	8.5 \pm 2.69
II	13.9 \pm 5.20	7.0 \pm 1.64
III	21.3 \pm 6.42	32.2 \pm 3.25
IV	7.4 \pm 1.86	24.2 \pm 5.13
V	7.8 \pm 1.69	55.9 \pm 4.34

Table 2b. Analyses of variance of angular transformed percentage of light activity events

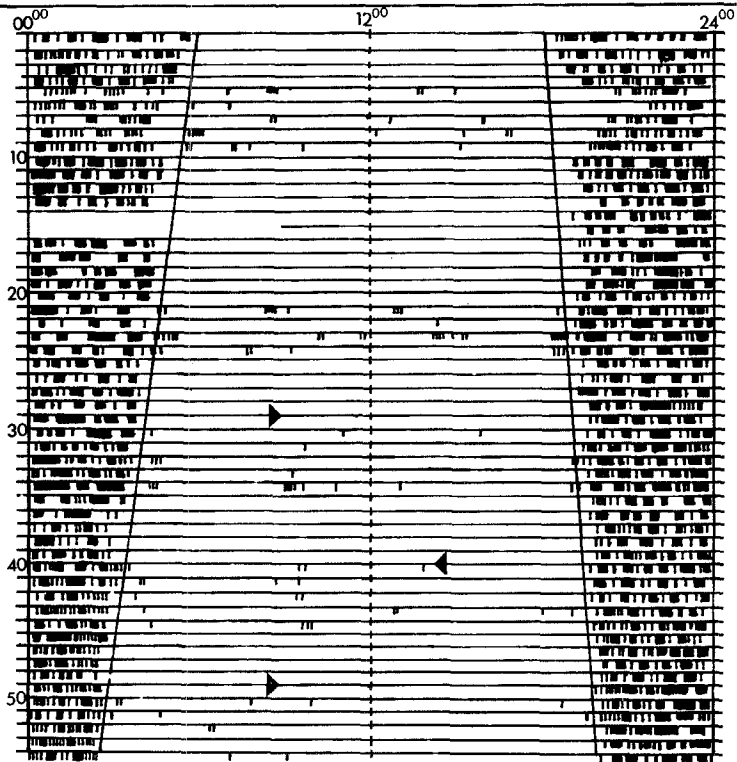
	df	Southern population MS	Northern population MS
Between testing conditions ("contact-isolation")	1	42.2017	12,422.8871***
Among animals	2	1,381.8550**	259.8347
Between testing repeats	1	278.7277	714.3571**
Interaction individuals \times testing condition	2	752.0058*	294.0441
Interaction repeats \times testing condition	1	173.8083	833.6553**
Interaction individuals \times repeats	2	441.6572	117.7907
Interaction repeats \times test. cond. \times indiv.	2	129.3862	20.8019
Error	48	166.0374	90.9315

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

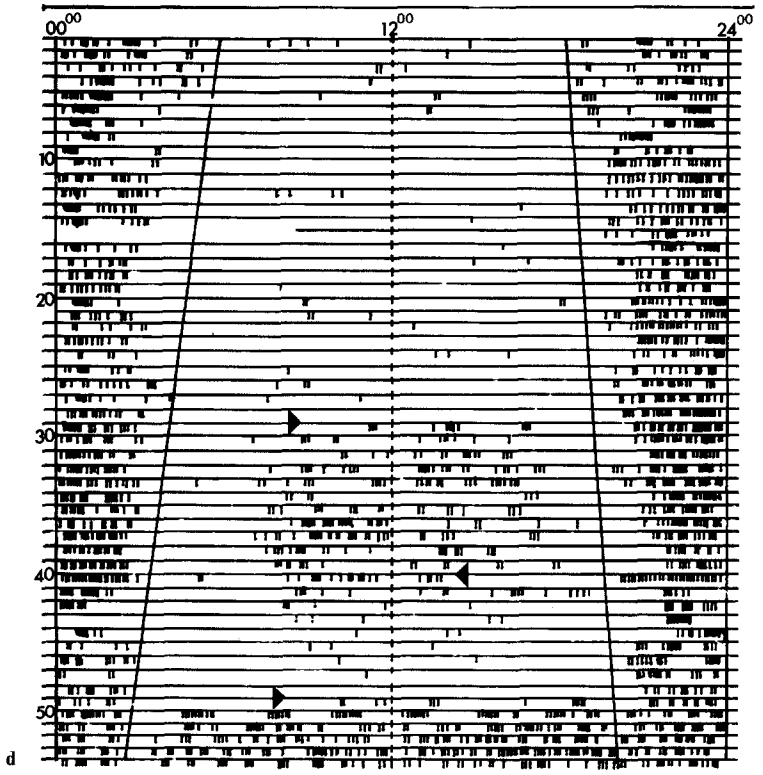
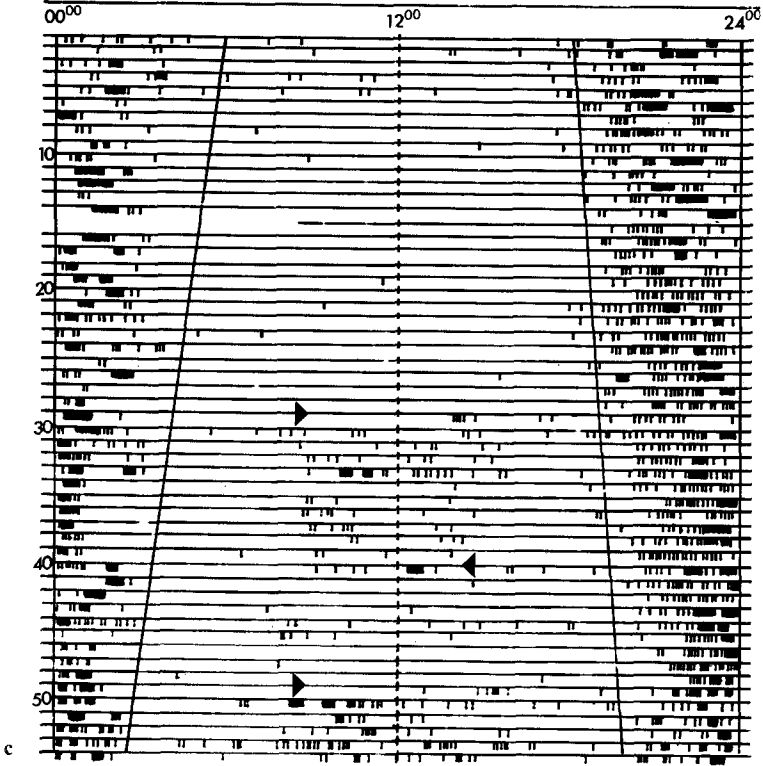
Fig. 2a-d. Original records of wheel-running activity behavior during natural light conditions. The figures show the activity patterns for two males, respectively, of the two field populations during the two different cage conditions, "contact" (days 29-40 and 49-54) and "isolation" (days 29-40 and 49-54). The changes are indicated by arrows. **a** and **b** show the patterns of males belonging to the southern population, **c** and **d** those of northern population males. The day number is given at the left margin. The vertical bars indicate schematically when light intensity rose above and fell below 5 lux, respectively. The daylength increased from 11.5 h at the start to 17 h at the end of the experiment. The temperature was set to 18°C, but could in sunny days rise to 24-26°C. The experiment was performed 15 March-10 May 1977



a



b



When changing to "contact" conditions, phase III and V, the animals of the northern provenance increase their day light activity markedly, while the activity of southern animals is not unequivocally affected (Table 1 a). The difference in response between the two populations is highly evident from the proportions of activity events occurring during daylight (Table 2a). An analysis of variance after angular transformation of percentages (Table 2b) shows that the activity change between phases I and II versus III and V (isolation versus contact) in the northern population is highly significant ($P < 0.001$). As between the "isolation" phases I and II (Table 1 a) there is in the northern population a distinct difference between the "contact" phases III and V, the light activity being higher during the later phase (Table 1 a). The rather high frequency of day light activity events among northern males in "isolation" phase IV (Table 1 a) may possibly be a delayed effect of the preceding contact between the animals in phase III.

Discussion

In an earlier investigation (Rasmuson et al., 1977) a great difference in locomotor activity was observed between animals of northern and southern populations of field vole, the former ones being more active than the latter. In the present investigation with the same populations locomotor activity has been examined with the use of a running-wheel. Although wheel-running activity is a most artificial kind of locomotor behavior which is difficult to relate to any type of behavior under natural conditions (Lehman, 1976), one could speculate that it might reflect some spacing or exploratory activity. The results obtained in the present study indicate differences between the two populations as to the response to varying degrees of interindividual contact. Among the northern population males significant increase in daylight activity is observed when the isolation between animals is diminished. The night active pattern is more or less replaced by a short-term pattern (Fig. 2). Contrary to this, an increased contact among the animals of the southern population did not bring about any significant change in activity pattern.

A change in the activity pattern from a predominantly nocturnal activity into a pattern distributed over 24 h could be of importance for the population development. It may be significant that this induced change in activity pattern occurs only in the northern population, which has a cyclic population density. An alternation in behavior produced by increasing individual contact might be a contributive factor to this specific type of population development. In this connection it should be mentioned that behavioral interaction between individuals repeatedly has been shown to exert strong effects on growth and reproduction in confined populations of rodents (for review see Southwick, 1955 a, b; Christian, 1963).

For the sensitive northern population the experiment indicated a gradual increase in activity during the course of the experiment. This change is possibly

due to the continued lengthening of the photoperiod. The response measured in each phase may also to some extent be affected by the activity level present during preceding days. This is evident from a comparison between e.g. the two "high contact" phases III and V, in which the difference in activity is roughly parallel to that between the two preceding "low contact" phases II and IV (Table 1 a).

A question which arises is whether the change in activity distribution among northern population males is a general phenomenon in cyclic populations of *Microtus agrestis*. At present nothing can be said about this, but studies that will elucidate this point are planned for other northern populations. Another question is whether the disposition to the behavioral changes observed is generally present in animals of the northern population or is restricted to animals present under a specific part of the population cycle. This issue is essential as some studies of allozyme variation indicate that the genetic composition of the population changes during the course of the cycle.

The data now available do suggest a relation between behavioral characteristics and population dynamics.

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