

# BURROWING BY COMMON VOLES (*MICROTUS ARVALIS*) IN VARIOUS SOCIAL ENVIRONMENTS

by

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## Summary

Female common voles live in groups in large burrows whereas males are probably solitary and promiscuous. At high population density, when burrows become a limiting factor, some females are forced to emigrate from their group. To investigate whether these emigrants could share new common burrows with unrelated neighbours, we analysed in the laboratory burrowing and social behaviour in dyads of unrelated wild females before and during their cohabitation. They were compared to wild male dyads.

In solitary voles, no sexual difference in burrowing pattern was observed but females built a burrow more quickly than males. In both sexes, the first encounters happened in one of the burrow and were of aggressive nature; during them intruders used burrowing during offensive approaches. While males displayed hierarchy and nested for themselves, females rapidly became friendly and nested together. They reshaped their burrows in response to social nesting and had more complex burrows than solitary females or intolerant males. We may conclude that in common voles at least unrelated non breeding females may contribute to the formation of social groups.

To investigate whether, within a matriarchal group, females may co-operate with their own daughters in building a new common burrow, we analysed burrowing behaviour in dyads comprising either an experienced wild mother with one of her naive daughters or two naive familiar daughters. No co-operative behaviour could be detected but experience in burrowing speeded up the building. The results strongly suggest that, within a short time, young females may improve their burrowing.

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## Introduction

In Europe, common voles are known to display high annual and multi-annual population fluctuations (Frank, 1953). During winter, non breeding common voles live in large groups, of mixed ages and sex (Chelkowska, 1978). In spring, individuals migrate from these groups to suitable fields where an appropriate food supply allows a rapid increase in the density of local populations. From summer to autumn, individuals disperse in adjacent fields (Frank, 1953). At high population density, they may become a major agricultural pest (Jobsen, 1988).

Ecological data (Frank, 1954; Boyce & Boyce, 1988a, b) indicate that common voles' social organisation is based on the territoriality of grouped breeding females. Most reproducing females live in exclusive groups of 2 to 6 (median: 2) and share large burrow systems with several nests and food storage chambers, with interconnecting tunnels and 2 to 14 entrances connected by surface runways (Liro, 1974; Goszczynska & Goszczynski, 1977; Boyce & Boyce, 1988b). At low population density, most grouped females breed synchronously.

The integration of breeding males in female groups is poorly known. As their home ranges extensively overlap those of several females (Reichstein, 1960), they are probably promiscuous. For some authors (Mackin-Rogalska, 1979; Blumenberg, 1986), males remain with females on a long-term basis but for Boyce & Boyce (1988a) they seem to visit females only for the short period of fertilisation and to nest solitarily in small burrows.

## Experiment 1: Behaviour of dyads of unrelated voles before and during social cohabitation

### *Introduction*

The dispersion behaviour of common voles is poorly known. Young males emigrate from their natal group presumably before sexual maturity whereas young and old females do so at high density probably because of the limited size of the burrows (Mackin-Rogalska *et al.*, 1986; Boyce & Boyce, 1988b). These emigrants either disperse far away or nest near their natal territory and reproduce solitarily in small burrows that cannot be extended because the soil is less suitable.

Dispersal in a remote suitable habitat raises the question on the origin of grouped females. Do dispersing animals (1) settle alone or with close relatives in new burrows, (2) settle into new groups with other unrelated emigrant females, or (3) join already established groups? It seems that both related and unrelated individuals may contribute to group formation (Chelkowska, 1978; Blumenberg, 1986). Since breeding females are known to behave aggressively towards unfamiliar conspecifics (de Jonge, 1983), the latter hypothesis makes the assumption that most groups of unrelated females stem from initially familiar neighbours.

The present laboratory work tested these hypotheses indirectly by analysing social relations and burrowing behaviour within dyads of unrelated wild females that had been initially neighbours. The experiment was then extended to wild males to unravel any sexual difference. Indeed females seem to be the main diggers (Blumenberg, 1986). Moreover, as in other digging species the burrow is the main site of social interactions (Flannelly & Lore, 1977; Rozenfeld & Denoël, 1994), we may expect voles to reshape their burrows in response to their social organisation. Non pregnant females would be less aggressive than males, settle together in the same nesting area and reshape a common complex burrow. Males, on the contrary, would be intolerant and nest on their own.

### *Method*

#### Subjects and experimental enclosures

All voles were wild adults caught in late autumn in southern Belgium. As they came from five distant places, they were presumed to be unrelated and unfamiliar individuals. After being treated against ecto-parasites (Bromocyclen, 15.1 g/l), voles were kept isolated for at least 30 days before testing in  $36 \times 25 \times 15$  cm polycarbonate cages with peat as litter, soft paper as nesting material and a  $20 \times 4$  cm PVC tube as refuge. Commercial rat, mouse and hamster pellets as well as water were provided *ad libitum* and supplemented with carrots or lettuce twice a week. Rearing and experiments were performed at a temperature of 17-20°C, with a relative humidity of 69-92% and a light cycle of 16L:8D, similar to spring conditions (dispersal season). Dim condition (set on at 17:30) implied two 60-W yellow bulbs; light condition, four 120-W white bulbs.

The observation pens were made of two contiguous enclosures as illustrated in Fig. 1. Each enclosure consisted of a foraging area (F) and a burrowing area (B), connected by a glass tube of  $10 \times 4$  cm (T) considered as part of the burrowing area. Hereafter it will be called the tube.

The foraging area measured  $60 \times 50 \times 50$  cm. Three of the walls, including the removable common partition (P), were aluminium sheets, the fourth being a glass window. The aluminium floor was lined with unprinted newspaper. Water (w) and food (f) were placed along the common partition (P). To make the animals come out of their burrows more

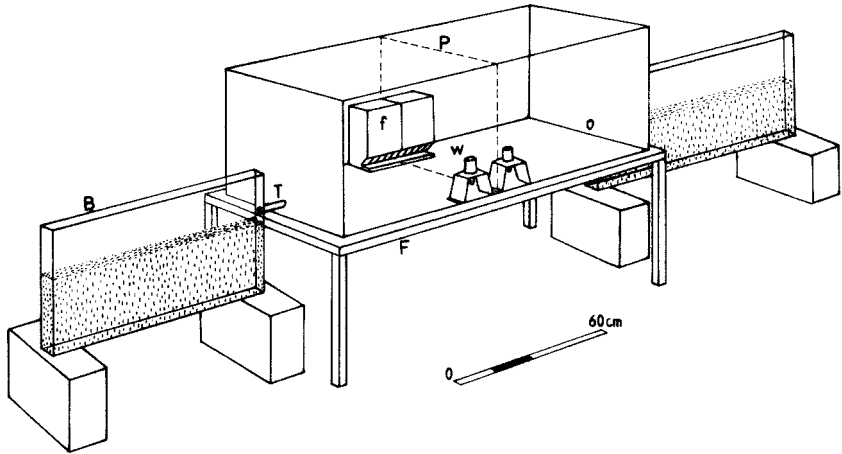


Fig. 1. Design of two contiguous experimental enclosures separated by a common partition (P). Each one includes a burrowing area (B, a vertical terrarium) connected through a glass tube (T) to a foraging area (F) containing water (w) and food in a trough (f). In experiment 2, two animals are put in a single enclosure.

frequently, pellets were provided in a trough from which they could not be taken away to be stored.

The burrowing area was a narrow terrarium, with two vertical glass walls ( $80 \times 40$  cm) through which underground behaviour could be observed. The 3-cm gap between the windows was filled with 25 cm of a tightly packed mixture of peat (5 L), water (2.5 L) and expanded clay beads (63 g =  $\sim 100$  beads, 7 mm in diameter). These beads were used to retain humidity and to simulate a heterogeneous soil. The burrowing area was darkened with two black screens, except during observations.

#### Experimental procedure

As a notable difference in weight may influence the outcome of fights (Drickamer *et al.*, 1973; de Jonge, 1983), 24 hours before testing, voles were weighed to the nearest 0.05 g and matched so that the median weight difference was less than 6% for females and 2% for males. The voles were then individually marked by fur clipping. At the end of each experiment, voles were weighed again.

Each experiment lasted eight days (days 0 to 8) and was organised in two 4-day phases. (a) Neighbouring phase: Two unfamiliar voles of the same sex were transferred, with their refuge tube to either foraging area of two contiguous enclosures. The common partition, through which voles could only hear and smell each other, simulated the presence of a neighbour. The refuge tubes were removed when the voles entered the burrowing area for the first time. (b) Cohabitation phase: The common partition was removed, providing both voles with a common enlarged foraging area.

Nesting material (20 strips of unprinted newspaper ( $20 \times 2$  cm) and 2.5 g of cotton wool) was introduced into the foraging area 24 hours after the beginning of an experiment in order to keep voles from building a surface nest before burrowing.

Six dyads of females (F + F) and six dyads of males (M + M) were used in this first experiment. As a control, the burrows were compared with those dug by five other dyads of females (F//F), kept for eight days in contiguous enclosures without removing the common partition.

#### Data recording and analyses

All manipulations were carried out at 10:30 and subsequent observations ended at most at 17:30. On day 0, we video recorded the first 20 min of burrowing. We analysed with our own designed software the number of grooming sessions and of crossings through the tube as well as the frequency and the duration of four burrowing behaviour: digging (pulling out compact soil with incisors) or with alternate movements of front legs and throwing the loosened soil away by kicking), kicking (while moving, accumulating loosened soil under the belly with brief alternate movements of front legs and getting rid of it by striking it backwards with both hind feet), heading (pushing peat forwards with the muzzle), burying (burying itself under the loosened earth and moving the soil with shoulders).

On day 4, after the two pens had been merged, we video recorded the exploration of the foreign area and the first 20 min of physical encounter. On day 7, as voles interacted far less frequently, we manually recorded social and non social behaviour during 280 min.

For the social behaviour, the number of agonistic behaviour and huddling was analysed. Only those behavioural elements that have not been identified in previous rodent studies (Grant & Mackintosh, 1963; Colvin, 1973; Rozenfeld & Denoël, 1994) are defined here. Eight types of agonistic acts were observed and, according to Bowen & Brooks (1978), five of them were considered as positive ones: offensive approach, attack with and without biting, chase and fighting; the other three were regarded as negative: flight, retreat and freezing (staying motionless in response to the approach of an opponent). On day 4, a vole was regarded as aggressive if more than 50% of its agonistic acts were positive. On day 7, any dominance was assessed according to Bowen & Brooks' index.

Three types of non social behaviour were analysed: duration of sniffing (nostrils within 1 cm) during exploration, number of crossings through the tube and burrowing (the four acts previously described were pooled). On day 7, the spacing behaviour was also estimated by recording the number of times each animal stayed for more than 10 min in the foraging area and in each burrowing area.

The burrow complexity was estimated on days 1, 4, 7 and 8 by the sum of the number of segments and chambers in a burrow (Meadows, 1991). A segment is an unbranched gallery linking intersections, dead-ends or exits. A chamber is a widened segment of gallery used as a resting place for at least 10 min. We considered that an elementary burrow existed when at least one gallery was excavated.

All statistical analyses performed were non parametric tests. When not otherwise noted, the tests are two-tailed. For independent variables, we used the Mann-Whitney *U*-test (called *U*-test). Chi-square test was used to compare aggression frequencies between sexes. For dependent variables, we used the Wilcoxon matched-pairs signed ranks test.

## Results

### 1. Burrowing behaviour in solitary neighbouring voles

On day 0, once voles discovered the burrowing area, they immediately performed some digging mainly at the far end of the terrarium. Within 20 min

TABLE 1. *Behaviour of solitary females and males during the first 20 min of digging in experiment 1*

Behaviour	Median number [range]				Median duration in s [range]			
	Females		Males		Females		Males	
Digging	113	[41-247]	80	[74-147]	1.4	[1.1-2.0]	1.6	[0.8-2.5]
Kicking	183	[24-304]	139	[110-284]	0.8	[0.5-0.9]	0.7	[0.5-1.0]
Heading	26	[4-42]	31	[15-39]	0.8	[0.4-1.4]	0.9	[0.7-1.3]
Burying	7	[1-32]	1	[0-18]	1.6	[0.4-4.2]	0.95	[0.6-2.1]
Total (Burrowing)	308	[138-398]	317	[205-460]	1.0	[0.4-4.2]	0.9	[0.5-2.5]
Crossing	8	[0-25]	< 24	[2-46]	–		–	
Grooming	15	[5-27]	10	[6-31]	6.4	[3.3-15.2]	4.5	[2.8-16.5]

Median number and duration of behaviour performed by nine solitary females and seven males during the first 20 min of digging on day 0 in experiment 1. There is no sexual difference (“<” indicates a statistical tendency, Mann-Whitney  $U$  test,  $p = 0.07$ ).

of burrowing, nine females out of 12 (75%) and seven males out of 12 (58%) had already dug an elementary burrow. As shown in Table 1, we found no significant sexual difference in burrowing behaviour ( $U$ -test,  $N_1 \times N_2 = 63$ ,  $U > 17$ ,  $p > 0.20$ ).

On day 1, all females (including the 10 control females) except one (95%) had dug a burrow whereas only eight males out of 12 (67%) had done so; the other voles had only moved some soil. As it can be seen in Fig. 2, on day 1 females had built more complex burrows than males ( $U$ -test,  $N_1 \times N_2 = 264$ ,  $U = 66$ ,  $p = 0.015$ ) but there was no difference any more on day 4 whereas one male had still no burrow.

The structure of burrows markedly varied from one animal to another, ranging from a single short gallery leading to a nest chamber to a complex network of galleries with two or more apertures. Some burrows included cycles that allowed an animal to come back to a given intersection without passing twice along the same gallery. Twenty-six burrows (79%) contained at least one central nesting chamber and two escape tunnels leading from the nest cavity to each end of the burrowing area. During the construction of their burrows, voles transported excavated soil from the burrowing area to the foraging area by heading. A crescent mound was formed in front of the tube. By continuously moving through this mound during foraging, the animals eventually made two paths leading to food and to water source.

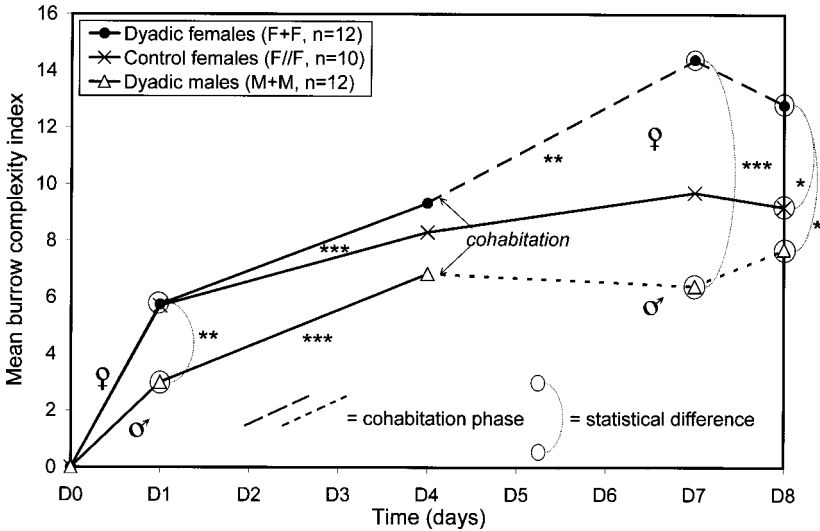


Fig. 2. Modification of the mean burrow complexity index (number of galleries and chambers in a burrow) built during experiment 1 by female dyads (F + F) and male dyad (M + M) during four days neighbouring followed by four days cohabitation (dotted lines). Control females remained in neighbouring during eight days (F//F). Wilcoxon and Mann-Whitney  $U$  tests were used (\*:  $p < 0.050$ , \*\*:  $p < 0.025$ , \*\*\*:  $p < 0.010$ ).

## 2. Social behaviour and burrowing in cohabitating females (F + F)

On day 4, after the common partition had been removed, only one female in each dyad left her burrowing area before the first encounter, which occurred in the burrow of the other female. Before entering into her neighbour's burrow, the intruder sniffed at the mound in front of the tube (during 94 s [24-122]) and at the surface of the soil in the terrarium (51 s [9-237]). Then, she cautiously explored the different galleries until she detected the owner, which, by that time, remained motionless in her nest (freezing). After an aggressive interaction, five out of six residents chased the intruder out of her burrow. The intruder, however, repeatedly returned to the resident's burrow and retreated in response to the intolerance of the resident. During the 20 min of observation, the resident never left her burrow to pursue the invader or to escape (Table 2, crossing). In one dyad, females became friendly after 10 min of interaction without any positive aggression and huddled in the resident's nest. All residents but one were defensive (Fig. 3). During agonistic encounters, mainly intruders burrowed (Table 2).

From the next day (day 5) until the end of the experiments, all females behaved friendly and aggression completely disappeared. They shared the

TABLE 2. *Non social behaviour during the first physical encounter and three days later in experiment 1*

		First encounter (20 min, day 4)			Three days later (280 min, day 7)		
Females	Intruder	<i>N</i> = 6	Resident	'Intruder'	<i>N</i> = 6	'Resident'	
Burrowing	15.5 [0-37]	**	0.0 [0-15]	1.5 [0-3]		0.5 [0-3]	
Crossing	13.0 [3-35]	*	0.0 [0-1]	14.0 [4-33]		12.0 [0-24]	
Grooming	2.0 [0-4]	*	0.5 [0-2]	1.5 [0-6]		0.0 [0-6]	
Males	Intruder	<i>N</i> = 6	Resident	Dominant	<i>N</i> = 4	Subordinate	
Burrowing	18.0 [0-185]	**	0.0 [0-9]	3.5 [0-20]		1.0 [0-7]	
Crossing	22.0 [9-89]	*	0.0 [0-10]	31.0 [18-52]		9.0 [4-20]	
Grooming	1.0 [0-15]		2.5 [0-8]	2.5 [0-6]		1.0 [0-5]	

Median number of non social behaviour in female and male dyads of experiment 1 during the first physical encounter (day 4) and three days later (day 7). Intruder is the burrow invader on day 4. Resident is the owner of the invaded burrow on day 4. On day 7, males were grouped according to their social status (see Fig. 3). Wilcoxon test was used (\*:  $p < 0.050$ , \*\*:  $p < 0.025$ ). The difference in burrowing is significant by grouping both sexes.

same nest and were often seen eating together. On day 7, females spent much of their time huddling in one of both burrows and very few burrowing episodes were observed. Five females were seen digging in their original burrow, two in the other burrow and one in both burrows. Both females spent as many long stays (> 10 min) in one than in the other burrow.

### 3. Social behaviour and burrowing in cohabitating males (M + M)

On day 4, in two dyads out of six, both animals came out of their burrow during the observation period, but the first male out was the future intruder. As in females, male intruders sniffed at the mound of their neighbour (18 s [0-71]) and at the surface of the burrowing area (45 s [0-97]). As in females, residents remained frozen in their nesting chamber until intruders came close to them. Contrary to the females, the male residents were the aggressive individuals (Fig. 3; Chi-square test,  $\chi^2 = 4.2$ ,  $df = 1$ ,  $p < 0.05$ ). However, only two residents went out of their burrow. As in females, burrowing during an offensive approach was performed mainly by intruders. By pooling both sexes, the difference in burrowing is significant between resident and intruder (Wilcoxon test,  $N = 12$ ,  $p < 0.026$ ). In males, however, burrowing by the intruder often ended in widening a gallery or, in half the cases, the aperture of the chamber in which the resident was. The resident responded by fleeing

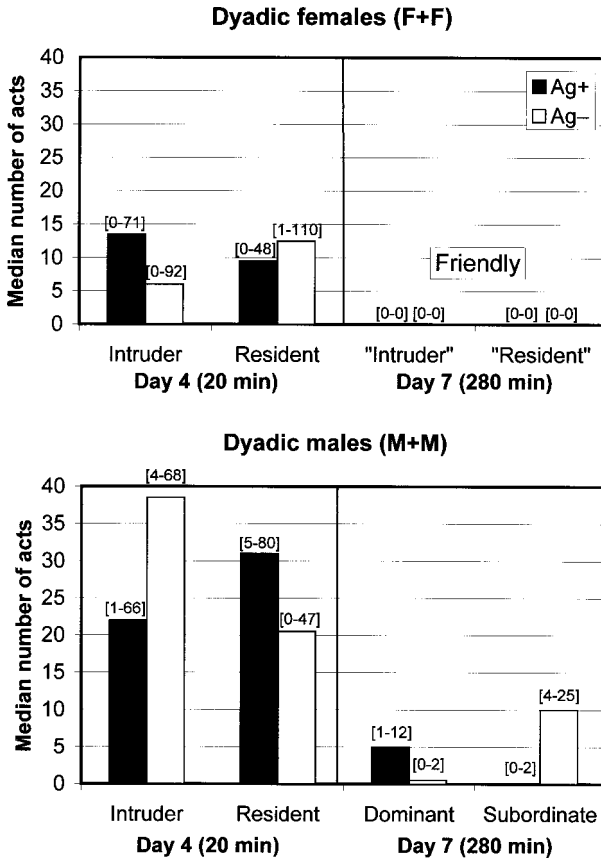


Fig. 3. Median number of positive and negative agonistic acts (Ag+ and Ag-) in female and male dyads (F + F and M + M) during the first physical encounter (day 4) and three days later (day 7). See Table 2 for the classification and the number of subjects. On day 4, intruders and residents showed an inverted pattern between both sexes.

away. Intruders entered or quit an area once per minute in median, which is more frequently than residents (Wilcoxon test,  $N = 6$ ,  $p < 0.05$ , Table 2).

On day 7 (Fig. 3 and Table 2), direct aggression between males markedly decreased. A clear dominance-subordination relationship was established in five dyads out of six (one of them was stopped on day 6 due to too high aggression). In three dyads, the initial intruder became dominant. The two residents that became dominants were the only residents having left their burrow during the first encounter on day 4. In the sixth dyad, both males were friendly and nested together. Each male spent more time in his own

burrow than in the other burrow and dominants stayed more often in the subordinate's burrows than subordinates in the dominant's. Subordinates avoided contact with dominants by spending 23.7% of their long stays (> 10 min) in the common foraging area.

#### 4. Complexity of burrows during cohabitation

As shown in Fig. 2, from day 4 to day 8, only the burrow complexity of F + F significantly increased (Wilcoxon test, one-tailed,  $N = 12$ ,  $p < 0.025$ ). On day 7, as we could expect, burrows were more complex in F + F than in M + M ( $U$ -test, one-tailed,  $N_1 \times N_2 = 120$ ,  $U = 21$ ,  $p = 0.005$ ). Moreover, F + F had dug more chambers than M + M and than F//F (1.8 [SD = 0.9] vs 1.0 [SD = 0.8] and 1.1 [SD = 0.3],  $U$ -test,  $N_1 \times N_2 = 120$ ,  $U = 30$ ,  $p = 0.032$  and 0.025). On day 8, F + F possessed more complex burrows than M + M and than F//F ( $U$ -test, one-tailed,  $N_1 \times N_2 = 120$ ,  $U = 32$  and 34,  $p = 0.035$  and 0.043).

#### 5. Changes in body weight

Only M + M and F//F significantly lost weight during the experiment (Wilcoxon test, one-tailed,  $N = 10$  and 7,  $p < 0.025$  and  $p < 0.05$ ). The subordinate males lost 10.1% [-4.1-14.1] of their initial weight whereas dominants lost only 4.7% [3.4-8.1].

### *Discussion*

Our data on the construction of a new burrow by solitary voles suggest no sexual difference except that, in the beginning, females appeared to be more prompt in burrowing than males. As females are known to be territorial (Boyce & Boyce, 1988b), they may be more motivated to dig a burrow rapidly than males who are supposed to be promiscuous and to spend much of their time visiting different female groups.

The analysis of social behaviour of dyadic voles shed some light on the proximal behavioural mechanism involved in (a) the defence against an intruder (b) the spacing between males and (c) the formation of new social groups in non breeding females.

(a) The cautious way in which a vole explores a burrow for the first time suggests that it detects its occupant either by the scent marks or by auditory cues. The resident reacted to an invasion of its burrow by a freezing

behaviour, until the invader was close to him. It probably detected the intruder by auditory cues. It is interesting that common voles adopt the same behaviour pattern in response to the silhouette of a kestrel (Gerkema & Verhulst, 1990) and, in the field, to the excavation of their burrow by a human observer (Boyce & Boyce, 1988b). In a natural burrow with a complex network of galleries, freezing is probably an efficient strategy to avoid harmful encounters with a potentially stronger competitor or to escape predators such as the weasel.

(b) Like in most studies, when two adult conspecifics met for the first time, they always interacted aggressively. However, as they were in their burrows, males and females acted quite differently. Resident males were far more aggressive than resident females. Some male invaders responded to this aggressiveness by burrowing and altering locally the structure of the resident's burrow. Digging associated to agonistic encounters has already been described in rodents but it was regarded as a displacement activity in animals tested in arena situations (Clarke, 1956; Grant & Mackintosh, 1963). In our semi-natural conditions, digging may have an aggressive aspect: It forces the resident to flee from its refuge. The friendship observed in one dyad of males could be explained by their younger age, as they were lighter than the other tested males, which drives to a tendency to aggregate (de Jonge, 1983).

(c) After a brief period of intolerance, females became friendly. Despite the fact that they had built their own burrow before interacting, they occupied both burrows but nested together in the same one. They reshaped their burrows by digging new galleries and in some cases by building a new chamber. These results support the hypothesis that groups of females may be constituted by related or neighbouring unrelated individuals. However in the presence of a male, these non-kin groups could break up because of hormonal changes, possible competition for some resources and the risk of taking care of unrelated pups. Our results may also suggest that even unrelated females could co-operate in reshaping their communal burrow. The next experiment was undertaken in order to investigate co-operation.

### **Experiment 2: Possible co-operation in burrowing between related females**

The results on unrelated females made us test the hypothesis that, if any co-operation in burrowing exists in this species, we may expect to observe it

at least between kin females. We thus observed the burrowing behaviour of dyads composed of an experienced mother and one of her naive daughters (F-D) with the aim to detect any co-operation in building a new burrow. These dyads were compared with D-D dyads, composed of naive sisters and with solitary animals used in experiment 1 (neighbouring animals before their physical encounter and control females: F + F, M + M and F//F). We expected to observe some behavioural differences between these groups and, more specially, that the F-D dyads construct a more elaborate nesting place than the D-D.

### *Methods*

In the ten F-D dyads, mothers were wild animals that had never been tested before. All young females were born in the laboratory from wild parents; they had been raised by their mothers only and were about 48 days old (SD = 4.0) when tested. The 11 D-D dyads (as well as all young that were not to be tested) were removed from their mother at 21 days. The sisters were kept together in a rearing cage with a refuge tube until testing. Other rearing conditions were the same as in experiment 1.

Each dyad was tested during eight days in an enclosure similar to one of the contiguous enclosures illustrated in Fig. 1, *i.e.* with only one foraging and one burrowing area. On day 0, the F-D and D-D dyads were transferred to the foraging area inside their refuge tube, which was removed as soon as both animals had discovered the burrowing area. Unlike in experiment 1, we recorded the burrowing behaviour of each female during the first four hours (from 13:30 to 17:30, *i.e.* at the end of the bright light period) by pooling the four behaviour described in experiment 1. In eight F-D dyads out of 10, we also analysed the modification of the burrow at 1-hour intervals during the next 16 hours (from 17:30 to 9:30, with the first recording beginning one hour after setting the dim light). For this long lasting record, we had to use a black and white time-lapse camera that unfortunately did not allow recognising each female individually at night. Among the 16 records, eight were made at night, *i.e.* during dim condition and eight others at 'daytime'. Moreover, during 10 min every hour, we also noted how many females were seen burrowing and where (at the surface of the soil or inside a gallery). On days 1, 4, 7 and 8, as in experiment 1, we estimated the complexity of burrows in both groups.

### *Results*

#### 1. First four hours of burrowing (on day 0)

In only four F-D out of ten, the first female to dig was the mother. During the 4-h observation, in eight (80%) F-D dyads and in six (54%) D-D dyads, both females were seen burrowing. In only two (20%) F-D dyads and three (27%) D-D dyads, both females were seen digging at the same moment but never at the same place. At the end of this period two distinct places of

burrowing were observed in five (50%) F-D dyads and in three (27%) D-D dyads. During this period, the females were never seen co-operating in digging. On the contrary, the presence of one female on the site of burrowing may interfere with the activity of the other.

## 2. Burrowing in mother-daughter dyads (F-D) during the next 16 hours

The first gallery was built by the F-D dyads, after a median time of 507 min [289-945 min], in the middle of the night. Burrowing behaviour was seen during 45% of observation sessions (58 out of 128) and was performed as frequently at night (in 26 sessions) as at daytime (32 sessions, Wilcoxon test,  $N = 8$ ,  $p > 0.05$ ). The light cycle had no influence on the digging place; as soon as a chamber was built 13% of their total burrowing activity was performed at the surface of the burrowing area both at night and at daytime.

In 34% of the burrowing observations ( $N = 20$ ), both females were seen burrowing at the same time. Thus, on average, if each female dug as much as the other one, a female dug alone only 50% of the time. During nine sessions only and in six dyads out of eight, both females were seen burrowing at the same place. On three sessions only, we noticed co-operative behaviour

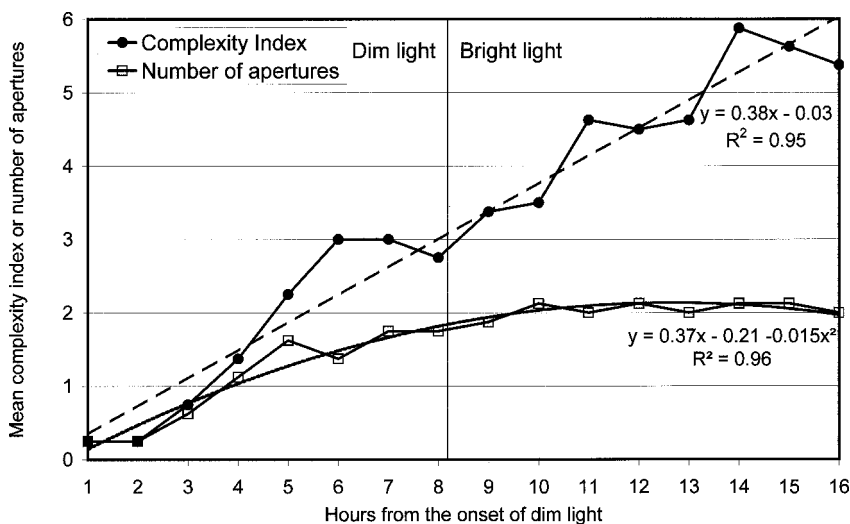


Fig. 4. Modification of mean complexity and number of apertures of mother-daughter burrows from experiment 2 (F-D,  $N = 8$ ) during 16 h on day 0 (4 h after the beginning of the experiment). The first 8 h are under dim light, the following ones are under bright light. The complexity increased linearly whereas the number of apertures reached a maximum of 2.

between mother and daughter, one female removing the earth thrown by the other one.

The complexity of a burrow increased in a linear way (Spearman, one-tailed,  $N = 16$ ,  $r = 0.97$ ,  $p < 0.001$ , Fig. 4) whereas the number of apertures reached a maximum of 2.05 (SD = 1.11) 10 h after the onset of dim light.

### 3. Modification in time of the burrow complexity

On day 1, whereas all F-D dyads had built a burrow, three D-D dyads (27%) were still without one. In experiments 1, four solitary males (33%) had no burrow after 24 hours while 21 of solitary females (95%) had one. As we expected, the F-D burrows were more complex than those of D-D dyads ( $U$ -test, one-tailed,  $N_1 \times N_2 = 110$ ,  $U = 25$ ,  $p = 0.017$ , Fig. 5). These comparisons indicate that the greater burrow complexity in F-D may result from the association of the young with an experienced digger. However, F-D burrows, but also D-D burrows, had more chambers than solitary females' ones (1.5 (SD = 0.6) vs 1.1 (SD = 0.3),  $U$ -test, one-tailed,  $N_1 \times N_2 = 210$

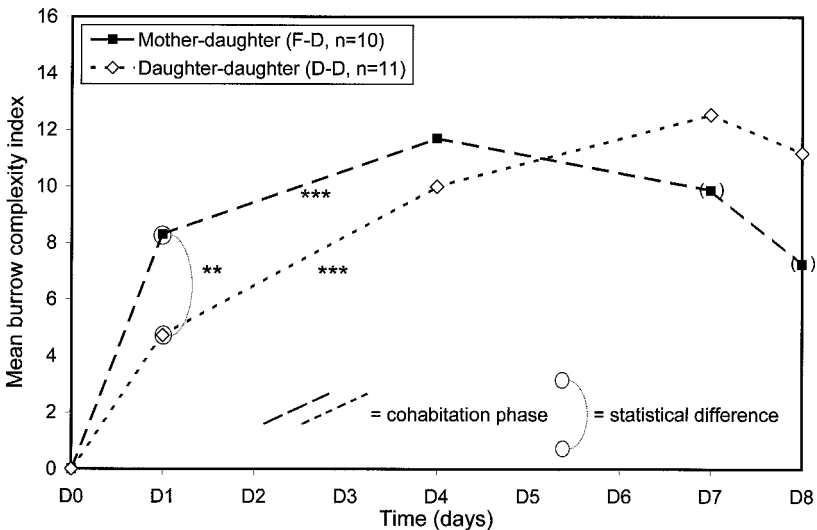


Fig. 5. Modification of mean burrow complexity (see Fig. 2) of mother-daughter (F-D) and daughter-daughter (D-D) dyads during eight days in experiment 2. As in Fig. 2, the cohabitation is in dotted lines. Wilcoxon and Mann-Whitney  $U$  tests were used (\*\*:  $p < 0.025$ ; \*\*\*:  $p < 0.010$ ).

and 168,  $U = 62$  and  $60$ ,  $p = 0.007$  and  $0.034$ ). The number of chambers in a burrow is thus related to the number of occupants.

In both groups, as in experiment 1, the complexity of the burrows increased significantly between day 1 and day 4 (Wilcoxon test, one-tailed,  $N = 10$  and  $11$ ,  $p < 0.015$  and  $0.005$ ). On day 4, there was no more difference in the complexity of F-D and D-D burrows ( $U$ -test, one-tailed,  $N_1 \times N_2 = 110$ ,  $U = 40$ ,  $p = 0.30$ ).

On day 7, however, in F-D dyads only, the complexity markedly decreased but the number of chambers remained constant. This reduction resulted from the merging or collapsing of some galleries, probably because of the limited size of the terrarium.

#### 4. Changes in body weight

All females lost weight during the experiment, the difference being significant in mothers and in both sisters (Wilcoxon test, one-tailed,  $N = 8$  and  $11$ ,  $p < 0.01$  and  $0.025$ ) but not in the daughters living with their mothers.

#### *Discussion*

During the initial phase of burrowing, mothers and daughters were as active at night as at daytime and the complexity of their burrows increased in a linear way while the number of apertures became constant after ten hours. They then essentially modify the internal structure. In the rather small and almost two-dimensional space of our terrarium, once an elementary burrow has been dug, any lengthening of a gallery increases the probability that it runs into another already existing one, with an increase in complexity. We can therefore hypothesise that the complexity increment for the building of a given length of gallery (*i.e.* a given energy expense by the animals) increases during the burrow's development. The linear modification of complexity should thus involve that the females diminish their effort in time.

Although females were seen digging at the same moment or alternatively, nothing in the behaviour of most females nor in the modification of their common burrow supports our hypothesis of co-operative or even co-ordinated burrowing in female common voles. On the other hand, in our first experiment, dyads of friendly females built two chambers in both burrows. In comparison with male burrows, we may conclude that the more complex structure of female burrows results from their reshaping in relation with the social nesting of the dwellers.

The present experiment also shows that after 24-hour digging, F-D dyads had built more complex burrows than D-D dyads. In a previous study on burrowing in both wild and laboratory rats, Boice (1977) found no such difference between burrows dug by adult or young. However the analysis was rather rough and subtle differences might therefore have been gone unnoticed. At least two hypotheses may explain our result: (a) an older female is simply more efficient in building a burrow than a young one or (b) a naive daughter may have learned to dig more efficiently from her experienced mother. After four days burrowing, the difference in the burrow complexity between F-D and D-D dyads disappeared. This fact suggests that, as in *Peromyscus polionotus* (Wolfe & Esher, 1977), inexperienced young may rapidly improve their performance simply by practice.

## General discussion

A characteristic feature of the burrows of common voles in the field is that their openings, instead of being covered by a mound like those of the water vole (*Arvicola terrestris*) or the mole (*Talpa europaea*), are surrounded by several pathways running to foraging sites. The present study shows that during burrowing, common voles do accumulate excavated soil in front of their burrow but that, by repeatedly moving from their burrow to their food sources, they spread out this soil and form pathways similar to those observed in the field.

Our comparative study shows that, in all groups and whatever the social context, as soon as a vole discovered a burrowing area it reacted by some digging. Wolfe & Esher (1977) suggested that, in the old-field mouse, very early digging on the surface should be regarded rather as an exploratory or/and foraging behaviour than as a first step in the construction of a nesting place. We may conclude that digging may have different aspects in relation to the physical and social environment of a vole. In relation with its social context, digging appears as a classic burrowing pattern in new established friendly female groups whereas it has an aggressive aspect between intolerant males, leading to their spacing.

Our first experiment on the social behaviour of dyadic females is an indication that the territorial female groups, which have been described by ecologists, are not necessarily constituted by related females only.

We supposed that grouped females co-operate in building their common burrow. Co-operative burrowing in rodents has not been widely studied. Wolfe & Esher (1977), working on couples with new born old-field mice (*Peromyscus polionotus*) showed that 'male and female co-operated in the construction of the tunnel by digging alternately'. Co-ordination between individuals working jointly in excavating a tunnel was observed in rats (Flannelly & Lore, 1977) and in *Octodon degus* (Ebensperger & Bozinovic, 2000). In our second experiment on genetically related females, nothing in their behaviour may support the hypothesis of burrowing co-operation in female common voles. We may conclude that the greater complexity of the burrows built by cohabitating adult females (F + F) in the first experiment was the consequence of reshaping the existing burrows in response to social nesting.

In social groups, we may expect that all members participate in building or in reshaping their common burrow but without any apparent co-ordination. Communal burrowing activity may be particularly important when members of social groups are forced to emigrate as during agricultural activities. It may also explain that common voles rapidly colonise an available habitat (Frank, 1953; Delattre *et al.*, 1996).

Our data on the loss of body mass in young females dwelling without their mothers and on the structure of their burrows support two of the classical hypotheses on the advantages from living in groups put forward by several authors. Firstly, the physical benefit (Cotton & Griffiths, 1967; Madison, 1984) that young may gain from living with experienced adult females through a reduction in the cost of thermoregulation and a better water conservation. This advantage may also explain the fact that, in experiment 1, friendly unrelated adults did not lose weight during cohabitation whereas mothers did so in experiment 2. Secondly, the social learning (Laland & Plotkin, 1992) that may improve the burrowing of the young in reducing the energy requirements of building a burrow.

Unlike females, male common voles are very intolerant to each other. In our experimental enclosure, the strategy of a competitive male was to repeatedly invade the burrow of a less competitive male and to put the owner to flight. This strategy, however, had a high energy cost since both males lost weight. In such a social context, most males with low competitive ability would probably emigrate.

In conclusion, although our vertical terrarium is not comparable to natural surroundings, its design enabled us to gather some original data on the behaviour of common voles when discovering a new habitat, on the digging of their burrow and on their reactions to the invasion by a neighbour. These findings, in turn, shed some light on the spacing mechanisms in this species.

## References

- Blumenberg, D. (1986). Telemetrische und endoskopische Untersuchungen zur Soziologie, zur Aktivität und zum Massenwechsel der Feldmaus, *Microtus arvalis* (Pall.). — *Z. Angew. Zool.* 73, p. 301-344.
- Boice, R. (1977). Burrows of wild and albino rats: Effects of domestication, outdoor raising, age, experience, and maternal state. — *J. Comp. Physiol. Psychol.* 91, p. 649-661.
- Bowen, D.W. & Brooks, R.J. (1978). Social organisation of confined male collared lemmings (*Dicrostonyx groenlandicus* Traill.). — *Anim. Behav.* 26, p. 1126-1135.
- Boyce, C.C.K. & Boyce, J.L. (1988a). Population biology of *Microtus arvalis*. I. Lifetime reproductive success of solitary and grouped breeding females. — *J. Anim. Ecol.* 57, p. 711-722.
- — & — (1988b). Population biology of *Microtus arvalis*. III. Regulation of numbers and breeding dispersion of females. — *J. Anim. Ecol.* 57, p. 737-754.
- Chelkowska, H. (1978). Variations in number and social factors in a population of field voles. — *Acta Theriol.* 23, p. 213-238.
- Clarke, J.R. (1956). The aggressive behaviour of the vole. — *Behaviour* 9, p. 1-23.
- Colvin, D.V. (1973). Agonistic behaviour in males of five species of voles *Microtus*. — *Anim. Behav.* 21, p. 471-480.
- Cotton, M.J. & Griffiths, D.A. (1967). Observations on temperature conditions in vole nests. — *J. Zool. Lond.* 153, p. 541-568.
- de Jonge, G. (1983). Aggression and group formation in the voles *Microtus agrestis*, *M. arvalis* and *Clethrionomys glareolus* in relation to intra- and interspecific competition. — *Behaviour* 84, p. 1-73.
- Delattre P., Giraudoux, P., Baudry, J., Quéré, J.-P. & Fichet, E. (1996). Effect of landscape structure on common vole (*Microtus arvalis*) distribution and abundance at several space scales. — *Landscape Ecol.* 11, p. 279-288.
- Drickamer, L.C., Vandenberg, J.G. & Colby, D.R. (1973). Predictors of dominance in the male golden hamster (*Mesocricetus auratus*). — *Anim. Behav.* 21, p. 557-563.
- Ebensperger, L.A. & Bozinovic, F. (2000). Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? — *Behav. Ecol. Sociobiol.* 47, p. 365-369.
- Flannelly, K. & Lore, R. (1977). Observations of the subterranean activity of domesticated and wild rats (*Rattus norvegicus*): A descriptive study. — *Psychol. Record* 2, p. 315-329.
- Frank, F. (1953). Zur Entstehung übernormaler populationsdichten im Massenwechsel der Feldmaus *Microtus arvalis* (Pallas). — *Zool. Jb., Abt. Syst.* 81, p. 610-624.
- — (1954). Beiträge zur Biologie der Feldmaus, *Microtus arvalis* (Pallas). Teil I: Gehegeversuche. — *Zool. Jb., Abt. Syst.* 82, p. 354-404.

- Gerkema, M.P. & Verhulst, S. (1990). Warning against an unseen predator: a functional aspect of synchronous feeding in the common vole, *Microtus arvalis*. — *Anim. Behav.* 40, p. 1169-1178.
- Goszczynska, W. & Goszczynski, J. (1977). Effect of the burrowing activities of the common vole and the mole on the soil and vegetation of the biocenose of cultivated fields. — *Acta Theriol.* 22, p. 181-190.
- Grant, E.C. & Mackintosh, J.H. (1963). A comparison of the social postures of some common laboratory rodents. — *Behaviour* 21, p. 246-259.
- Jobsen, J.A. (1988). Plagues of *Microtus arvalis* in grassland areas in the Netherlands. — *EPPO Bull. (Oxford)* 18, p. 271-276.
- Laland, K.N. & Plotkin, H.C. (1992). Further experimental analysis of the social learning and transmission of foraging information amongst Norway rats. — *Behav. Processes* 27, p. 53-64.
- Liro, A. (1974). Renewal of burrows by the Common Vole as the indicator of its numbers. — *Acta Theriol.* 19, p. 259-272.
- Mackin-Rogalska, R. (1979). Elements of the spatial organisation of a Common Vole population. — *Acta Theriol.* 24, p. 171-199.
- —, Adamczewska-Andrzejewska, K. & Nabaglo, L. (1986). Common vole numbers in relation to the utilization of burrow systems. — *Acta Theriol.* 31, p. 17-44.
- Madison, D.M. (1984). Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. — In: *Winter Ecology of Small Mammals* (J.F. Merritt, ed.), Carnegie Museum Natural History, Special publication 10, p. 267-274.
- Meadows, P.S. (1991). The environmental impact of burrows and burrowing animals—conclusions and a model. — *Symp. zool. Soc. Lond.* 63, p. 327-338.
- Reichstein, H. (1960). Untersuchungen zum Aktionsraum und zum Revierverhalten der Feldmaus (*Microtus arvalis*, Pall.). — *Z. Säugetierkd.* 25, p. 150-169.
- Rozenfeld, F.M. & Denoël, A. (1994). Chemical signals involved in spacing behavior of breeding female bank voles (*Clethrionomys glareolus* Schreber 1780, Microtidae, Rodentia). — *J. Chem. Ecol.* 20, p. 803-813.
- Wolfe, J.L. & Esher, R.J. (1977). Burrowing behaviour of old-field mice (*Peromyscus polionotus*): A Laboratory investigation. — *Biol. Behav.* 2, p. 343-351.

## Résumé

Les femelles du campagnol des champs vivent en groupes dans de grands terriers alors que les mâles sont probablement solitaires et volages. A haute densité de population, alors que les terriers deviennent un facteur limitant, certaines femelles sont forcées d'émigrer de leur groupe. Afin d'examiner si ces émigrantes peuvent partager un nouveau terrier commun avec des voisines non apparentées, nous avons analysé au laboratoire le fouissage et les comportements sociaux de dyades de femelles sauvages non apparentées avant et après leur cohabitation. Elles ont été comparées à des dyades de mâles sauvages.

Aucune différence sexuelle dans le mode de fouissage n'a été observée chez des campagnols solitaires mais les femelles ont construit un terrier plus vite que les mâles. Chez les deux sexes, les premières rencontres se sont passées dans un des terriers et ont été agressives; les intrus y ont utilisé du fouissage lors d'approches offensives. Alors que les mâles ont montré une hiérarchie et ont nidifié séparément, les femelles sont rapidement devenues

amicales et ont nidifié ensemble. Elles ont réorganisé leurs terriers en réponse à leur nidification sociale et ceux-ci sont devenus plus complexes que ceux de femelles solitaires ou de mâles intolérants. Nous pouvons conclure que, chez le campagnol des champs, au moins des femelles non apparentées et pas en reproduction peuvent contribuer à la formation de groupes sociaux.

Afin d'examiner si, au sein d'un groupe matriarcal, les femelles peuvent coopérer avec leurs propres filles pour construire un nouveau terrier commun, nous avons analysé le fouissage chez des dyades constituées soit d'une mère expérimentée sauvage avec une de ses filles naïves soit de deux filles familières naïves. Aucun comportement de coopération n'a pu être détecté mais l'expérience dans le fouissage a accéléré la construction. Les résultats suggèrent fortement qu'en peu de temps, les jeunes femelles peuvent améliorer leur fouissage.

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