

Movement patterns of male common voles (*Microtus arvalis*) in a network of Y junctions: role of distant visual cues and scent marks

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Abstract: Common voles (*Microtus arvalis*) use networks of runways around their burrows, which are dug in meadows. Their orientation among such networks could be based on rigid "egocentred" routes (possibly through the use of olfactory "trails") or on more general, "allocentred" spatial representations (with distant visual cues). In this 5-day study, male voles should reach food in the centre of a maze of three-way (Y) junctions offering similar local views but surrounded by distant visual cues. I tested whether the animals navigated using olfactory trails, implying one main direct foraging route, or allocentred representations, allowing flexibility among equivalent routes. Males quickly marked their environment, preferentially at the periphery, where they moved the most. However, during most direct trips between the nest and the food, they used one of the central shortest routes, which included the least scent-marked zones. Moreover, the voles preferred different shortest routes to go to the food and return from it, showing a bias in favour of the side where the distant goal (food or nest) was situated. This suggests that male common voles base their choices on the general direction of their goal rather than on trails. Finally, there was no major difference in initial exploration between a clean and a scent-marked maze.

Résumé : Les Campagnols des champs (*Microtus arvalis*) utilisent des réseaux de sentes autour de leurs terriers creusés dans des prairies. Leur orientation au sein de tels réseaux pourrait être basée sur des routes égocentrées rigides (éventuellement via des « pistes » olfactives) ou sur des représentations spatiales allocentrées plus générales (avec des repères visuels à distance). Dans cette étude de 5 jours, des campagnols mâles devaient atteindre leur nourriture au centre d'un labyrinthe de jonctions à trois voies (en Y), offrant des vues locales similaires mais entouré de repères visuels à distance. J'ai tenté de déterminer si les animaux allaient s'orienter selon des pistes olfactives, en suivant une route directe principale vers leur nourriture, ou selon une représentation allocentrée, permettant une flexibilité entre des routes équivalentes. Les mâles ont rapidement marqué leur environnement, particulièrement à la périphérie, où ils se déplaçaient le plus souvent. Toutefois, lors de la plupart des parcours directs entre leur nid et leur nourriture, ils ont emprunté l'un des chemins centraux les plus courts, là où se trouvaient les zones les moins marquées. De plus, ils ont choisi, parmi les trajets les plus courts, des chemins différents pour aller à leur nourriture et pour en revenir, avec une préférence pour le côté de leur but lointain (nourriture ou nid). Cela semble indiquer que les campagnols des champs mâles basent leur choix sur la direction générale de leur but plutôt que sur des pistes. Enfin, il n'y a pas eu de différences majeures entre l'exploration d'un labyrinthe propre et celle d'un labyrinthe marqué d'odeurs.

Introduction

Common voles (*Microtus arvalis*) often live in pastures with short vegetation, in contrast to closely related species like *Microtus agrestis*, which need dense, wet plant cover (Dienske 1979). In this environment, networks of runways radiate from their burrows (Pelikán 1982; Blumenberg 1986). These networks link the entrances of a single burrow but also those of different burrows. They are probably used for foraging as well as for the transfer of individuals between burrows, which is common (Blumenberg 1986). They can also be used for dispersal, which involves almost no mortality, an advantage that is perhaps due to their presence, as

was suggested by Boyce and Boyce (1988a). In *Microtus pennsylvanicus* and *Microtus ochrogaster*, a runway can be used by up to 10 voles in 24 h (Harper and Batzli 1996). In other small rodent species, it is reported that even strangers and heterospecifics use the same runways (Pearson 1960; Lidicker 1980). This assemblage of features is probably essential for foraging and emigration of common voles, especially during peaks of population density, which are responsible for agricultural plagues (Frank 1953; Delattre et al. 1996). A better understanding of the orientation mechanisms of this species is therefore crucial if we are to increase our pest-control efficiency.

The complexity and large size of the runway networks presuppose efficient spatial-information processing by the voles, which is not documented for *M. arvalis*. According to theory (for a review see Thinus-Blanc 1996), animals could use path integration (through egocentred internal cues) to find their way back after having followed a rather simple route. More complex animal orientation implies that local views are first memorized and then linked by elemental

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movements or paths. To accomplish this, animals could use egocentred routes based on sequentially ordered stimulus responses, which could be visual and (or) olfactory cues, or could develop more general, allocentred spatial representations of visually connected places (= geocentric maps), which involve not rigid routes but precise localization of places. Such a level of spatial processing probably involves the summation of mental vectors, i.e., linking a distant visual landmark to a far-away goal permits the individual to reach the goal without seeing it and also to approach from different directions.

While the majority of studies investigate mainly the processing of visual information, in rodents one can expect olfaction to play a determining role, as has been shown in wood mice and rats, which can follow foraging trails by means of scent marks, at least as a complement to other orientation mechanisms (Jamon 1994; Galef and Buckley 1996; Lavenex and Schenk 1998). In this study I first tested whether voles used mainly visual or olfactory information for orientation in a regular maze in which they had to reach food in a central location at a distance from the nest. The maze is designed to simulate natural networks of runways or galleries in a burrow, i.e., it contains mainly three-way (Y) junctions, which only offer dichotomous choices, well adapted to rodents' learning ability (Poucet et al. 1990; Airoidi and de Werra 1993; Dobly and Rozenfeld 2000). Based on optimal-foraging theory, I first predicted that isolated voles would be able to quickly use at least one of the shortest routes leading directly to the food rather than follow the periphery of the maze until they saw or smelled the food. Using direct routes is shorter but demands complex spatial cognition, as the maze offers similar local views. However, as it is surrounded by distant visual cues, like natural runways in meadows, I expected the animals to navigate using allocentred representations. In that case they would be able to show flexibility in their use of routes by following various equivalent shortest pathways. In contrast, if they established an olfactory trail, they would mainly mark and use one of the shortest routes available.

Common voles were ideal for this study, as they live in established networks of trails, built in open fields and probably scent-marked. Although both sexes are capable of long-distance dispersal (Boyce and Boyce 1988a, 1988b), I worked with males for several reasons. They mark more than females (A. Dobly, unpublished data) and they have larger home ranges (Reichstein 1960), therefore their spatial ability should be greater than that of females, as in another promiscuous vole, *Microtus pennsylvanicus* (Kavaliers et al. 1998). Moreover, in the laboratory, in a median of 99.5% of observations made under light conditions, isolated females stayed in their burrows (A. Dobly, unpublished data).

Finally, in this work I also studied the main characteristics of the initial exploration of the maze by a naive individual, comparing exploration in a clean maze and a scent-marked maze. As adults do not avoid male odours (de Jonge 1980) and as fresh tracks indicate the reassuring recent presence of a conspecific, I hypothesized that the voles would enter the maze more quickly when scent marks were present. I expected the naive males to reach the food more quickly in the maze with trails that led to the main point of interest in the maze (food) than in a clean maze without trails.

Materials and methods

Subjects

I used 16 adult males bred in the laboratory through fewer than five generations from wild parents captured in southern Belgium. They were reared in polycarbonate cages (36 × 25 × 15 cm) containing 2 cm deep commercial wood shavings, soft paper as nesting material, and a 20 × 4 cm polyvinyl chloride tube as a refuge. Water and dry pellets for rats, mice, and hamsters were available ad libitum. Once a week, voles received oat flakes to habituate them to this food, which would be used during the experiments. They were 8.3 months old (SD = 3.5 months) and each was used only once. Rearing and experiments were performed at room temperature (18–21°C) and humidity (50–70%) under a photoperiod of 16 h light : 8 h dark. Light was provided by four 120-W bulbs that were on from 01:30 to 17:30. For dim conditions one 60-W yellow bulb was used. The animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

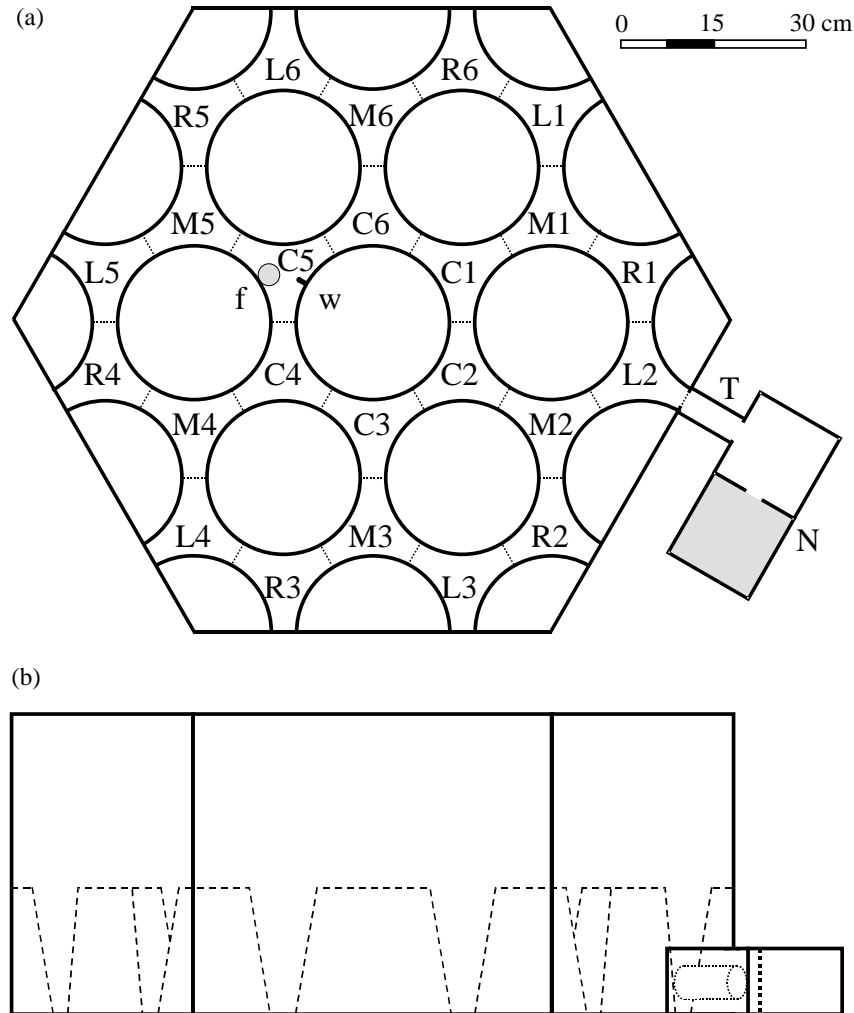
Experimental enclosure

The enclosure was a regular hexagon with walls (each 60 × 50 cm) and floor of aluminium (Fig. 1). Nineteen brown polypropylene flowerpots (21 cm high, 26 and 19 cm in diameter at the top and bottom, respectively, 7.5 L, Soparco) were glued upside down on the enclosure floor. Each had six symmetrical indentations (1.7 × 1.7 cm) around the top, therefore all bifurcations looked the same in front view. One pot was in the centre of the enclosure and six pots were in a circle on the diagonals of the hexagon; one half of another six pots, cut vertically, was at the middle of each wall, and one-third of each of the last six pots, cut vertically, was in each corner. As voles cannot climb the pots, the floor space between the pots formed a network of 4 cm wide passages with a total length of 7.5 m. By taking into account the dead ends facing the partitions, this network contained only three-way (Y) junctions ($N = 24$). Each junction was termed a zone (125 cm²). The zones were numbered according to their location in six clockwise sectors and labelled according to their position relative to the middle of the maze: six central (C1–C6), six median (M1–M6), and 12 peripheral (L1–L6 and R1–R6 for those to the left and right of the median zone of the corresponding sector, respectively). When I refer to all the zones in one category, I call them centre, median zones, and periphery. Zone C5 contained a small jar with oat flakes and the nozzle from a water bottle that was inside the central flowerpot. I chose oat flakes rather than dry pellets because their small size compelled voles to go out regularly to eat and ensured that they were not detected by the video-tracking system (see below). Oat flakes were permanently available, as the jar was refilled every morning. The water contained methylene blue (1 g/L, Hoechst; Rozenfeld et al. 1987) to stain the vole's urine for easier identification. However, other secretions were also visible on the aluminium (A. Dobly, unpublished data). One day before the experiment, the future resident of the enclosure (see below) had already drunk methylene blue water in its isolation cage. The nesting box was constructed of aluminium walls and floor; it contained two square chambers (15 × 15 × 8 cm) connected by a central opening (5 cm in diameter) and covered by a pane of glass. The distal chamber was darkened by a red filter and contained 5 cm long pieces of wool ($N = 60$). The nesting box was connected to the main enclosure by a glass tube (10 × 4 cm).

The enclosure was on the floor of a room with white walls. The voles could see some external cues such as the wire or support for the camera, which was directly above the centre of the enclosure. The light sources were at a height of 3 m behind a 3 × 2 m hanging white sheet (to the right in Fig. 1).

The inconvenience of thigmotaxis, which causes voles to follow the walls during their movements (an edge effect), was greatly

Fig. 1. Top view (a) and front view (b) of the aluminium enclosure used as a maze. Upside-down flowerpots (indicated by circles and part circles in a and trapeziums in b) form a network of 24 three-way (Y) junctions. These Y junctions are numbered in six clockwise sectors and labelled according to their position (C, central; M, median; L and R, left and right when coming from the corresponding median zone (zones L and R are defined as peripheral)); "f" is a small jar with oat flakes; "w" is a nozzle with water; "T" is a glass tube; "N" is a nesting box covered by a pane of glass (the shading represents a red filter).



diminished in this setup, as the voles were always in contact with the side of at least one object. The size of my setup was adapted to common voles, which spend about 96% of their trips less than 2 m from a burrow entrance (Boyce and Boyce 1988b). I tried to minimize the stress in my setup in order to facilitate observation of the spatial capacities of voles and to avoid nonrunner voles as observed by Teskey et al. (1998), who put the animal inside a tube in the middle of a radial maze.

Experimental procedure

The movements of a male inside the maze were observed over 5 days ($N = 9$ replicates). All manipulations were carried out at 12:00. On day 0, a small aluminium plate closed the connection between the tube and the maze. A naive male was gently transferred from his refuge tube to the nesting box and after 10 min the small plate was removed. As soon as he put his four legs inside the glass tube, the recording began and continued for 3 h. Then, each day until day 4, a 3-h recording was started at 12:00 wherever the animal was. At the end of the last recording, the male and his nesting material were removed from the setup and a naive male, unrelated and unknown to the resident male, was put inside the closed nesting box for 10 min ($N = 7$). He had then free access to the

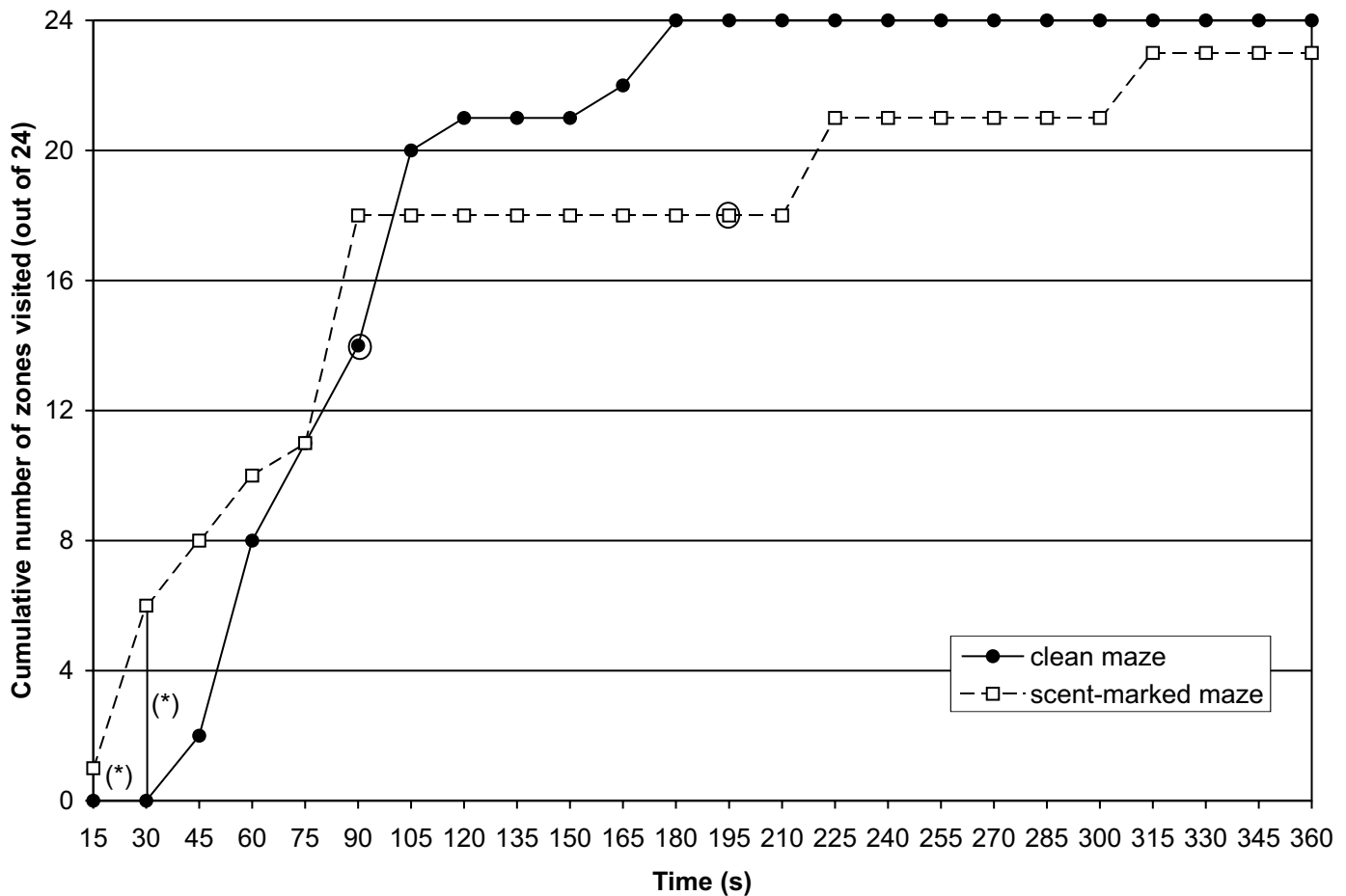
scent-marked maze for 34 min. The area in square millimetres of the marks (whether blue or not) made by the resident was then recorded along every border between two zones of the maze ($N = 30$) on a 1×4 cm band (400 mm^2) through transparent paper bearing millimetre squares.

Data recording and analysis

The recordings were carried out with video-tracking software (Ethovision, Noldus). A colour CCD camera (Elmo with Tamron 3.5–8 lens) was suspended from the ceiling over the enclosure at a height of 305 cm and connected to a computer provided with a video-digitizer card. The position of the vole was determined every 340 ms, for a total of 31 765 samples in 3 h. For the naive male on day 4, the recording included 6000 samples, which were compared with the first 6000 samples obtained from the resident on day 0.

Each movement from the nesting box until the first return to the nesting box was defined as a trip. A visit to a given zone refers to a single occasion when the vole was present in this zone. When a vole rapidly crossed a zone without being actually detected in it by the tracking system, I still considered that a visit. I defined a stop in a zone as a visit to that zone which lasted for at least 15 s. In addition to the parameters calculated by means of the tracking

Fig. 2. Median cumulative numbers of different zones visited by common voles (*Microtus arvalis*) during the first 6 min of exploration of a clean and a scent-marked maze. Circled data points denote the mean position of the food zone (C5) in the sequence of 24 zones and the approximate median time of the first visit to C5. Tendencies were detected in only two cases (Mann–Whitney U test, $N = 16$, $P < 0.10$).



system, I myself analysed each digitized trip on day 1 that included at least one visit to the food zone (C5). I determined the sequence of zones visited and zones with stops. For days 0–4, for each trip I also analysed the choice made by the voles at the first bifurcation encountered after leaving the nesting box (zone M2 vs. zone R1, termed the left and right zones, respectively).

As successive trips made by one vole on a given day were not considered to be independent, when necessary I used the mean number per animal for all trips in a day. I used two-tailed non-parametric statistics. To compare differences between two days or two zones, I used Wilcoxon's matched-pairs signed-ranks test. I used a Mann–Whitney U test to compare exploration in a clean and a scent-marked maze and Friedman's two-way ANOVA for the change over several days or for ranking the numbers of visits or quantities of scent marks in zones.

Results

First exploration of a clean maze

Very soon after the tube was opened, the males went in the maze. They explored it in all directions and quickly visited all zones (Fig. 2). When they entered the food zone (C5) for the first time, they did not stop. The first long stop (>2 min) occurred in the nesting box after a median of 30 min (range 12–74 min), while the first long rest (>10 min) occurred after 48 min (range 33–96 min). During the 3-h ob-

servations, the nine males entered the maze 27 (15–99) times and the centre 48 (22–113) times. On average, 58% of the total exploration time was spent at the periphery, 11% in the median zones, and 31% in the centre (in fact 24% of the time was spent in C5, which was the zone with the longest visit time). Only in three other zones (L2, L3, and R3) was a visit longer than the average, 4.2% (9.6, 8.6, and 7.6%, respectively). During the 3-h observation, the left zone at the first choice after leaving the nesting box was entered more times than the right zone (M2 vs. R1; Wilcoxon's test, $N = 9$, $P = 0.008$).

Routes taken after 1 day of access to the maze

On day 1, each vole performed a median of 6 (2–18) trips in the maze, for a total of 74 trips, which was fewer than on day 0 (Wilcoxon's test, $N = 9$, $P = 0.008$). I classified the trips into four types according to their shape, their length, and the presence or absence of visits to the food zone (Fig. 3 and Table 1): A, short trips lasting less than 90 s and with fewer than 12 zones visited, with no visit to C5; B, long trips with no visit to C5; C, trips crossing C5 but without stopping in it; D, trips with at least one feeding stop lasting >15 s in C5. I compared the crossing and feeding trips, which all included at least one visit to the food.

Fig. 3. Four main types of pathways inside the maze taken by the voles on day 1. They started from the solid square in the nesting box (N) and returned to the nesting box. The open squares represent the positions of the voles every 340 ms. The arrows show the direction taken. The duration of the trip in seconds is shown in each case. (a) Short trip. (b) Long trip without a visit to the food zone. (c) Trip in which the food zone was crossed without stopping in it. (d) Feeding trip.

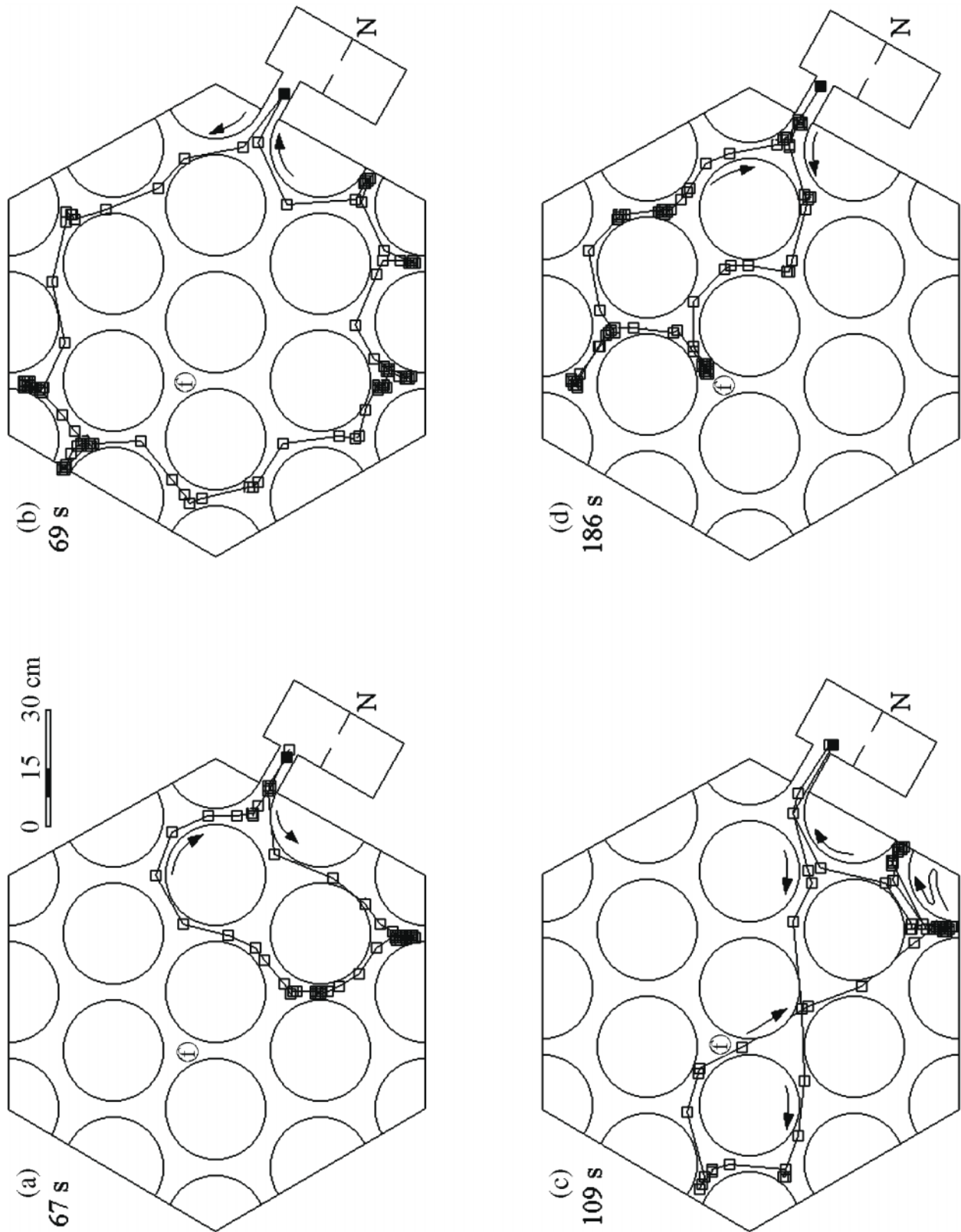


Table 1. Characteristics of trips of different types observed over 3 h for nine common voles (*Microtus arvalis*) having access to the maze for 1 day.

Classification of trips			Zones visited				
Type of trips	Visits to C5	No. of trips	Total	Per trip		Before C5	
				Median	Range	Median	Range
Short	No visit	15	108 (6)	9	1–11	—	—
Long	No visit	12	288 (15)	20	13–63	—	—
Crossing	Only crossing	19	772 (40)	29	11–155	13	5–39
Feeding	Stop(s) >15 s	28	760 (39)	21	13–73	5	5–21
Total		74	1928	19	1–155		

Note: Values in parentheses are percentages.

Table 2. Median time spent and median distance covered in the maze by eight male voles during 3-h observations on 5 days.

	Day 0		Day 1		Day 2		Day 3		Day 4	
	Median	Range	Median	Range	Median	Range	Median	Range	Median	Range
Time spent in maze (%)	30	18–59	20	8–48	19	9–67	25	6–39	15	11–46
Distance covered (m)	166*	99–488	42*	10–122	39	18–175	33	12–182	32	14–105

*According to Friedman's two-way ANOVA, $N = 8$, $df = 4$, $P = 0.001$.

During the feeding trips, the initial choice at the first bifurcation (L2) was biased in favour of the left zone (M2), whereas both ways were chosen almost equally during the crossing trips (Wilcoxon's test, $N = 9$, $P = 0.018$ and $P = 0.910$). For the return, there was no difference between zones M2 and R1 for both types of trip (Wilcoxon's test, $N = 9$, $P > 0.39$).

In the feeding trips but not the crossing trips, fewer zones were visited in going from the nesting box to the food than in returning from the food to the nesting box (Wilcoxon's test, $N = 9$, $P = 0.018$). The small number of zones visited before stopping in C5 showed that animals went directly to the food (last column in Table 1). In only one instance did a vole take the same route to go to the food from its nest and return to the nest.

In only 10 feeding trips performed by seven voles (36%), the voles made a detour and (or) stopped at the periphery before eating in C5. In the other 18 feeding trips made by eight voles (64%), the voles went directly to the food; 14 trips followed one of the three shortest routes, which comprised five zones, and lasted 5 s (1–16 s) (Fig. 4a). The preferred shortest route was through zones M2 and C2 (Wilcoxon's test, $N = 8$, $P = 0.018$; Fig. 4a). In 12 feeding trips made by six voles (43%), the voles were in the food zone before returning to the nesting box without stopping or half-turning. In 11 of these direct returns, the voles used one of the shortest routes but now showed a preference for the route that included R1, which was not significant because only six voles were seen coming back from the food (Fig. 4b; but see below for the analysis over 4 days).

The stops did not occur in random zones. Except for C5, which represented 35% of all stops (44 out of 124), voles stopped mainly at the periphery (60%). Only 2 trips out of 47 (4%) contained an even number of zones visited. This was probably due to the configuration of the maze.

Time dynamics of movements

One male died before day 2, leaving eight subjects for days 2, 3, and 4. The distance covered and the number of

visits were greater on day 0 than on the following days (Friedman's two-way ANOVA, $N = 8$, $df = 4$, $P = 0.001$ and $P = 0.005$; Table 2). However, time spent in the maze did not significantly diminish after day 0 (Friedman's two-way ANOVA, $N = 8$, $df = 4$, $P = 0.095$). Thus, the speed of the vole was higher on day 0 than on the following days (Friedman's two-way ANOVA, $N = 8$, $df = 4$, $P = 0.001$). This was due to more frequent and (or) longer stops from day 1 onwards. It is worth mentioning that time spent in the food zone did not diminish after day 0; on the contrary, on day 4 it reached a maximum of 42% (SD = 8.5%) of the total time spent in the maze. The voles also spent some time gnawing at the base of the partition at the dead end of different peripheral zones.

During the whole experiment, apart from the entrance to the maze (zone L2), the most frequently visited zones were, in decreasing order, the link between the food and the periphery (M5), the left choice at the entrance (M2), and the food zone (Friedman's two-way ANOVA, $N = 9$ and 8, $df = 23$, $P = 0.001$; Fig. 5). The left zone (M2) from the first bifurcation was visited significantly more often than the right zone (R1). Similarly, despite their greater distance from the nesting box, a part of the left peripheral route to the food (zones R3, L4, and M4) was more visited than its equivalent to the right (zones L1, R6, and M6). From day 1 to day 4, the five-zone routes from the nesting box to the food zone went through zone M2 twice as often as through zone R1 (Wilcoxon's test, $N = 8$, $P = 0.018$; Fig. 4c). However, the reverse was true for the five-zone return routes to the nesting box from the food zone after feeding: the voles ran by zone C6 twice as often as by zone C4 (Wilcoxon's test, $N = 8$, $P = 0.027$; Fig. 4d).

Network of scent-marked tracks

After 24 h, all passages were already marked by a central trail with footprints on both sides. The marks were not completely blue but also included whitish trails of a different origin. Many large blue urine spots were present at the dead ends of peripheral zones. The marks (on all borders between

Fig. 4. Schematic representation of the numbers (in circles) of all direct routes taken by the nine voles during 3 h on day 1 to go from the nesting box (N) to the food (f) and return (a) and return (b). The sums of all five-zone routes taken to the food (c) and from the food (d) from day 1 to day 4 are shown. The solid circles represent significantly biased preferences (Wilcoxon's test, $N = 9$ and 8 , $P < 0.038$).

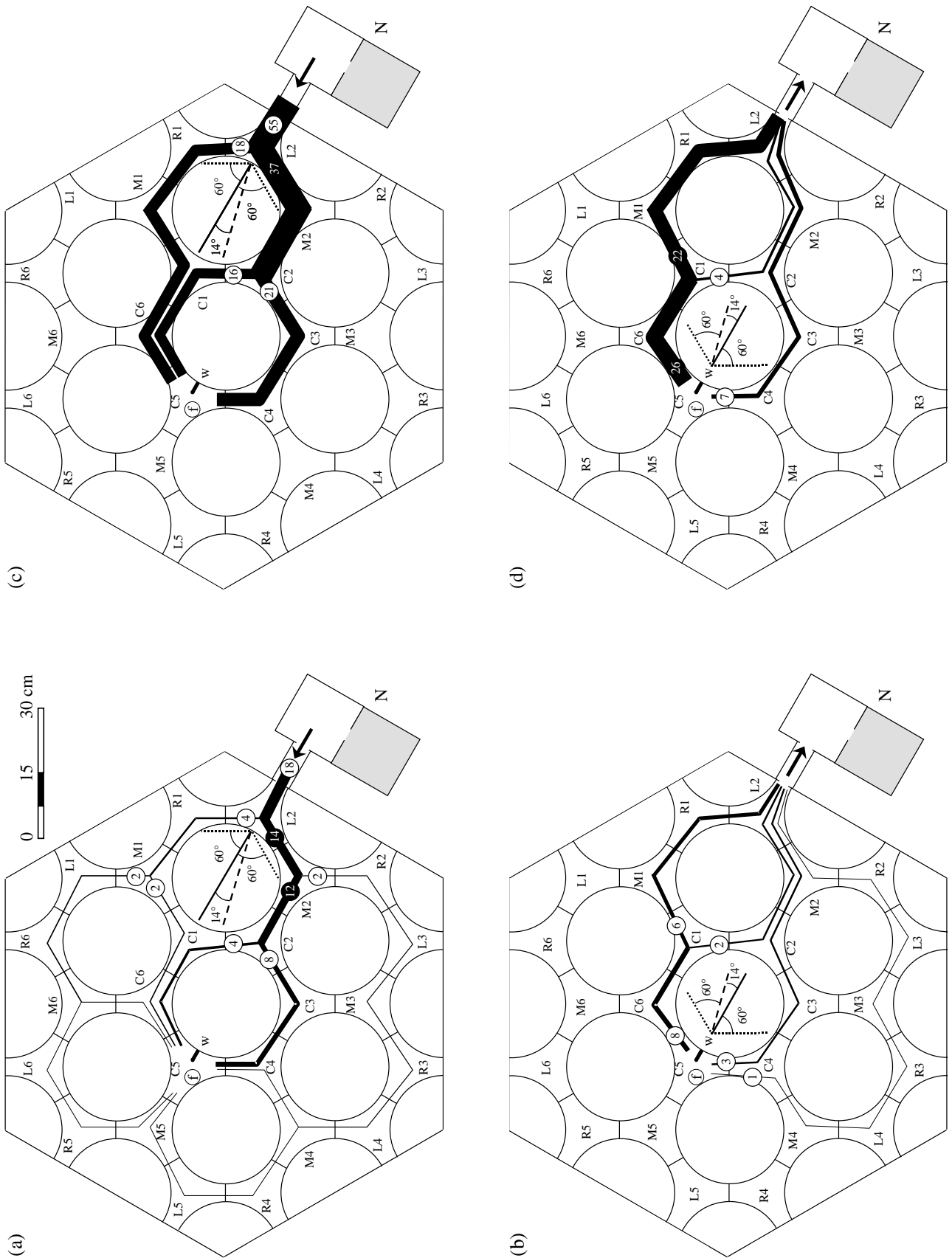
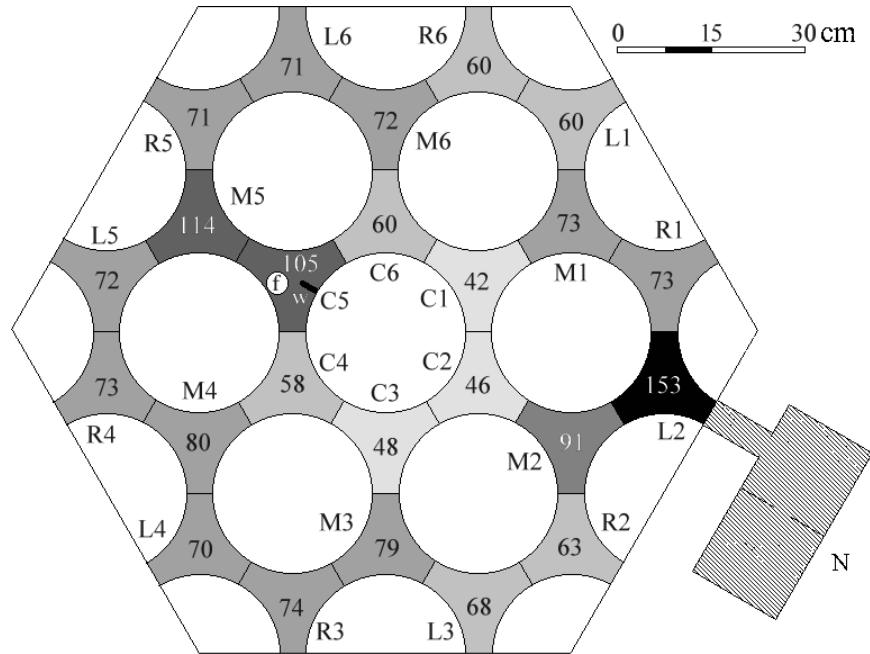


Fig. 5. Means of the cumulative numbers of observed visits made by eight male voles in different zones during the 3-h sessions from day 0 to day 4. Darker areas denote more visits (40–159 visits in 15-visit steps). The nesting box (N, hatched area) was not taken into account. The zones are identified inside each flowerpot; “f” is the food and “w” is the water.



two zones) observed on day 4 were correlated with the number of transitions between zones observed on day 1 (Spearman's correlation, $N = 30$, $r_s = 0.70$, $P = 0.000$). This confirms the voles' preference for the peripheral zones, as the peripheral borders (between zones L–R, L–M, and R–M) were, on average, more marked than the radial (C–M) and central (C–C) borders (Friedman's two-way ANOVA, $N = 8$, $df = 2$, $P = 0.002$).

However, a possible preference for the left peripheral route to the food was confirmed to some extent. Indeed, only the R3–L4 border was more marked than the L1–R6 border (Wilcoxon's test, $N = 8$, $P = 0.025$). Of the borders between the median and central zones, M5–C5 and M4–C4 were the most marked (Friedman's two-way ANOVA, $N = 8$, $df = 5$, $P = 0.001$; Fig. 6). Thus, M4–C4 was more marked than M6–C6. Finally, the shortest routes to the food included the less marked zone borders (C1–C2 and C1–M1).

Comparison of explorations of a clean and a scent-marked maze

The main statistical analysis is shown in Table 3. The entire maze was visited as quickly when it was clean as when it was scent-marked (Fig. 2), but both zones from the first bifurcation (M2 and R1) were visited more quickly in a marked maze. During the first trip, in a clean maze zone M2 was more visited than zone R1, whereas there was no difference in the marked maze (Mann–Whitney U test, $N = 16$, $P = 0.015$ and $P = 0.68$). The first trip was more extensive in a clean maze than in a marked one, but the pattern of movements (i.e., the relative frequency of visits as a percentage) showed that zones M2 and C5 were proportionally more visited in a clean maze than in a marked one. This was not the case for zone R1.

For all trips during the 34-min observations, no preference

was shown at the first choice between zones M2 and R1 (Mann–Whitney U test, $N = 16$, $P > 0.42$). Under both conditions, the peripheral zones (divided by 2 to represent the same surface as the median or central zones) were, on average, explored for longer than the central ones (Friedman's two-way ANOVA, $N = 9$ and 7, $df = 2$, $P < 0.000$ and $P < 0.002$). However, in a clean maze, the voles spent more time close to the wall (periphery), whereas in a marked maze, they spent as much time in the median zones as at the periphery. Indeed, in a clean maze, the median zones were visited for a short time, like the central ones, whereas in a marked maze the median zones were visited often, as were the peripheral ones.

There was no other major difference. Voles moved as much in a clean maze as in a scent-marked maze (Table 3). Under both conditions, the zones visited for longer were, in decreasing order: L2, C5, R3, L6, and R2 (which totalled 41% of the exploration time).

Discussion

In this study, the activity dynamics of male voles during their initial exploration of a maze were first determined, as well as the pattern of trips made during subsequent days. As one may expect, the initial trip in the maze was dedicated to exploration and not to feeding. This exploration was characterized by high-speed movements and should have helped the voles to visually integrate the spatial invariance and the distant visual landmarks as well as to mark the new environment.

In my setup, the voles preferred to move and stop at the periphery, even during their initial exploration of an entirely scent-marked network. This can be explained by their preference for using travel routes with overhead cover or darker

Fig. 6. Quantity of scent marks observed after 4 days at the borders between the zones defined in Fig. 1. The zone designations are shown beside each set of three converging lines, which indicate the centre of a zone. Darker areas denote more scent marks, on average (from 0.1 to 21% of the total recorded surface, in 3% steps). The nesting box (N) and dead ends were not recorded; the dead ends, shown as black areas; were marked with many urine spots; "f" is the food and "w" is the water.

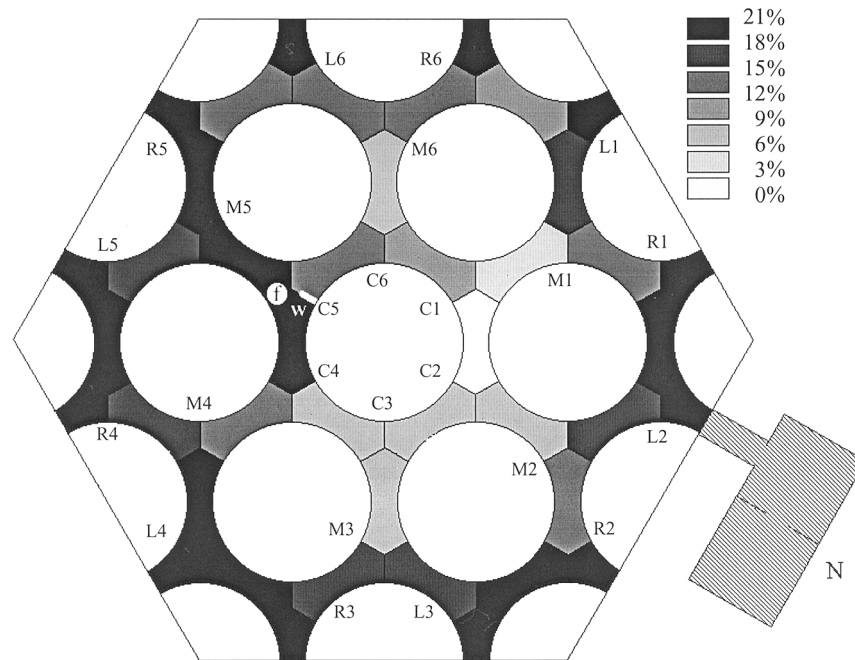


Table 3. Comparison of initial explorations by a naive male vole in a clean and a scent-marked maze.

	Clean maze (<i>N</i> = 9)		Scent-marked maze (<i>N</i> = 7)
First trip (even very brief with rapid return)			
Zone chosen at the first bifurcation	6 M2 / 9 voles	ns	5 M2 / 7 voles
First extended trip with at least five zones visited			
Zone chosen at the first bifurcation	7 M2 / 9 voles	(*)	2 M2 / 7 voles
Time before both M2 and R1 were visited (s)	69 (45–482)	**	39 (9–80)
Time elapsed before contact with food (s)	94.5 (36.7–662.3)	ns	276.4 (27.9–2040.0)
Percentage of visits to R1	2.0 (0.0–7.7)	***	14.3 (2.7–20.0)
Number of visits to M2	2 (2–4)	***	1 (0–2)
First stop was in C5	7 voles / 9	**	1 vole / 7
Number of zones visited	39 (17–60)	**	11 (5–37)
All trips (during 34 min)			
Time of exploration (%)	58.5 (31.1–74.9)	ns	53.6 (14.3–78.1)
Distance covered (m)	97.0 (54.5–214.2)	ns	89.2 (42.6–153.1)
Number of visited zones	468 (188–1074)	ns	410 (232–765)

Note: M2 and R1 are the zones to the left and right of the nesting box and C5 is the food zone (see Fig. 1). Values in parentheses are ranges. A Mann–Whitney *U* test was used (*N* = 16; *, *P* < 0.05; **, *P* < 0.025; ***, *P* < 0.01); (*) indicates a tendency (*P* = 0.057); ns, not significant).

areas to forage, as documented for *Microtus townsendii* (Harestad and Shackleton 1990). The periphery meets these requirements better than the centre because of the proximity of the high partition, which shields one of the vole's sides. For subsequent days, the attempts to dig a hole in the corners, possibly in order to exit the maze, as was indicated by some gnawing, offer a second possible explanation.

However, common voles do not seem to follow a partition in order to find their way in a maze, in contrast to mice studied in the absence of distant landmarks, which was not the case in my experiment (Alyan and Jander 1994). As the goal

(food and water) was not visible from the starting point, the voles had to process spatial representations rather than being visually attracted by the goal, as was reported for cats and chicks (Poucet et al. 1983; Regolin et al. 1994). During most feeding trips, the voles preferred to follow direct pathways rather than peripheral routes. These direct routes were more exposed to potential aerial predators, whose overhead flight causes a strong antipredator response in common voles (even to a kestrel model; Gerkema and Verhulst 1990). However, taking a direct route minimized travel time and energy expenditure for foraging and, as I expected, was probably

made easier by the permanent contact with a flowerpot, which to a certain extent sufficed for the thigmotactic vole.

The results of this study highlight the spatial abilities of the common voles, which were able to assess the general direction of a distant goal. During direct trips to the food, the voles preferred not only the shortest routes but also, of these, the route to their left. This preference can be explained, as it corresponded to the general direction towards the goal (food). Indeed, at the first bifurcation (L2), the food, though out of sight, was positioned 14° to the left of the body axis when the vole was coming from the nesting box, whereas the two available routes were 60° to either the left or the right (Fig. 4). Like cats, for example (Poucet et al. 1983), voles chose the route on the side of the goal. Moreover, when returning from the food to the nest, they used a different shortest route from that used to go to the food. Symmetrical routes were taken to go and come back because in both cases the goal direction was biased to the left of the vole when facing its distant goal (Fig. 4). This inversion of routes used to go and come back could explain why the scent marks were not biased to the right or the left at the nesting-box exit.

This flexibility, as well as the fact that the shortest pathways comprised several of the less marked zones, indicate that the formation of a scent-marked trail along the shortest foraging routes, as an itinerary indicator, did not prevail as the orientation mechanism. Rather, it seems that the voles knew the general direction between the food and the nesting box, probably by using distant visual cues (or auditory cues from the PC), because in my maze, close front views looked all the same and were thus confounding. Distant information is indeed perceived by red-backed voles (*Clethrionomys glareolus*) and allows them to detect remote wooded habitats (Gillis and Nams 1998). Moreover, in golden hamsters (*Mesocricetus auratus*) and mice, distal visual landmarks are preferred for navigational reference rather than path integration and guided orientation by means of close cues (Etienne et al. 1990; Alyan and Jander 1994). I cannot exclude the possibility that some olfactory information is used, but it was probably not the main means of orientation within my setup, as the inverted approaches and returns from the food to the nest prove.

Even during the first 3 h of exploration as well as throughout the experiment, the voles went into the zone to the left of the first bifurcation more frequently than into the zone to the right (zones M2 and R1 in Fig. 1). I showed that this was probably due not to bias during feeding trips but most likely to the fact that, unlike R1, M2 is a bifurcation and could thus be reached from one more zone than R1.

Observation of the scent marks left during 4 days of the voles' presence reveals first that there were at least two types of marks: tracks along the routes and spots at the dead ends. The tracks did not consist solely of urine, as was indicated by the faint blue colour, but could have contained preputial-gland secretions (Brinck and Hoffmeyer 1984). They can also be composed of secretions from the plantar and (or) anal glands, which have been studied in other rodents (Paclt 1952; Griffiths and Kendall 1980; F.M. Rozenfeld and D. Avermaet, unpublished data). The scent marks could have been due to the repeated passage of the voles, possibly representing a passive act. The quantity of marks was correlated with the main areas of movements and stops of the voles,

i.e., the periphery and the food. The significant marking of the dead ends, which corresponded to the borders of the available area, was probably not linked to orientation but rather to boundary delimitation (Wolff and Johnson 1979). As males are intolerant of strange males, such marks could provide information for a visitor (Ralls 1971).

Males were quicker when visiting the two zones next to the first bifurcation in a marked but unknown area than in a clean unknown maze. It is probable that the naive voles in a marked maze, rather than choosing and exploring one of the two ways out of the nesting box, first investigated the beginning of both "trails" made by the resident. The males in a marked maze visited the median zones as much as the peripheral ones, which was not the case in a clean maze; they thus seemed less reluctant to enter the maze than males confronted with a clean area. This diminution of neophobia could be explained by the presence of fresh olfactory cues from a conspecific, which could make the new area less foreign, as it was already colonized. Indeed, rat pups prefer to explore and feed in areas with residual olfactory cues from females, even nulliparous ones that are not their kin (Galef and Heiber 1976). Moreover, Jamon (1994) stated that wood mice were reassured by conspecific olfactory trails, which showed the relative safety of this route from predators.

Contrary to what I expected, the existing scent marks did not lead the naive male towards the food. Two explanations can be put forward: there were no effective trails and (or) the priority for the males was to explore and not to look for food. Indeed, firstly, as already pointed out, the routes towards the food were less marked than other zones. Secondly, even in a clean maze, during the initial exploration the males did not stop when they found the food for the first time.

This work shows that, after a period of exploration, common voles are able to find their way in a limited but intricate environment with similar local views but with distant visual cues. Though scent marks were present, it was not linked principally to orientation. In such an environment, common voles do not need to follow scent-marked trails to reach a goal at a distance from them. Whereas this ability is probably present in this species, it is supplemented by other sources of information, probably visual in this case.

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References

- Airoldi, J.-P., and de Werra, D. 1993. The burrow system of the fossorial form of the water vole (*Arvicola terrestris scherman* Shaw) (Mammalia, Rodentia): an approach using graph theoretical methods and simulation models. *Mammalia*, **57**: 423–433.
- Alyan, S., and Jander, R. 1994. Short-range homing in house mouse, *Mus musculus*: stages in the learning of directions. *Anim. Behav.* **48**: 285–298.

- Blumenberg, D. 1986. Telemetrische und endoskopische Untersuchungen zur Soziologie, zur Aktivität und zum Massenwechsel der Feldmaus, *Microtus arvalis* (Pall.). *Z. Angew. Zool.* **73**: 337–344.
- Boyce, C.C.K., and Boyce, J.L., III. 1988a. Population biology of *Microtus arvalis*. II. Natal and breeding dispersal of females. *J. Anim. Ecol.* **57**: 723–736.
- Boyce, C.C.K., and Boyce, J.L., III. 1988b. Population biology of *Microtus arvalis*. III. Regulation of numbers and breeding dispersion of females. *J. Anim. Ecol.* **57**: 737–754.
- Brinck, C., and Hoffmeyer, I. 1984. Marking urine and preputial gland secretion of male bank voles (*Clethrionomys glareolus* L.): chemical analyses and behavioural tests. *J. Chem. Ecol.* **10**: 1295–1307.
- de Jonge, G. 1980. Response to con- and heterospecific male odours by the voles *Microtus agrestis*, *M. arvalis* and *Clethrionomys glareolus* with respect to the competition for space. *Behaviour*, **73**: 277–303.
- Delattre, P., Giraudoux, P., Baudry, J., Quéré, J.-P., and Fichet, E. 1996. Effect of landscape structure on common vole (*Microtus arvalis*) distribution and abundance at several space scales. *Landscape Ecol.* **11**: 279–288.
- Dienske, H. 1979. The importance of social interactions and habitat in competition between *Microtus agrestis* and *Microtus arvalis*. *Behaviour*, **71**: 1–126.
- Dobly, A., and Rozenfeld, F.M. 2000. Burrowing by common voles (*Microtus arvalis*) in various social environments. *Behaviour*, **137**: 1443–1462.
- Etienne, A.S., Maurer, R., Saucy, F., and Teroni, E. 1986. Short-distance homing in the golden hamster after a passive outward journey. *Anim. Behav.* **34**: 696–715.
- Etienne, A.S., Teroni, E., Hurni, C., and Portenier, V. 1990. The effect of a single light cues on homing behaviour of the golden hamster. *Anim. Behav.* **39**: 17–41.
- Frank, F. 1953. Zur Entstehung übernormaler Populationsdichten im Massenwechsel der Feldmaus *Microtus arvalis* (Pallas). *Zool. Jahrb. Abt. Syst.* **81**: 610–624.
- Galef, B.G., and Buckley, L.L. 1996. Use of foraging trails by Norway rats. *Anim. Behav.* **51**: 765–771.
- Galef, B.G., and Heiber, L. 1976. Role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *J. Comp. Physiol. Psychol.* **90**: 727–739.
- Gerkema, M.P., and Verhulst, S. 1990. Warning against an unseen predator: a functional aspect of synchronous feeding in the common vole, *Microtus arvalis*. *Anim. Behav.* **40**: 1169–1178.
- Gillis, E.A., and Nams, V.O. 1998. How red-backed voles find habitat patches. *Can. J. Zool.* **76**: 791–794.
- Griffiths, J., and Kendall, M.D. 1980. Structure of the plantar sweat glands of the bank vole *Clethrionomys glareolus*. *J. Zool.* (1965–1984), **191**: 1–10.
- Harestad, A.S., and Shackleton, D.M. 1990. Cover and use of travel routes by female Townsend's voles in a laboratory arena. *Biol. Behav.* **15**: 196–204.
- Harper, S.J., and Batzli, G.O. 1996. Monitoring use of runways by voles with passive integrated transponders. *J. Mammal.* **77**: 364–369.
- Jamon, M. 1994. An analysis of trail-following behaviour in the wood mouse, *Apodemus sylvaticus*. *Anim. Behav.* **47**: 1127–1134.
- Kavaliers, M., Ossenkopp, K.-P., Galea, L.A.M., and Kolb, B. 1998. Sex differences in spatial learning and prefrontal and parietal cortical dendritic morphology in the meadow vole, *Microtus pennsylvanicus*. *Brain Res.* **810**: 41–47.
- Lavenex, P., and Schenk, F. 1998. Olfactory traces and spatial learning in rats. *Anim. Behav.* **56**: 1129–1136.
- Lidicker, W.Z., Jr. 1980. The social biology of the California vole. *Biologist*, **62**: 46–55.
- Paclt, J. 1952. Scent glands in the bank vole. *Experientia (Basel)*, **8**: 464.
- Pearson, O.P. 1960. Habits of *Microtus californicus* revealed by automatic photographic recorders. *Ecol. Monogr.* **30**: 231–250.
- Pelikán, J. 1982. *Microtus arvalis* on mown and unmown meadow. *Acta Sci. Nat. Brno*, **16**: 1–36.
- Poucet, B., Thinus-Blanc, C., and Chapuis, N. 1983. Route-planning in cats related to the visibility of the goal. *Anim. Behav.* **31**: 594–599.
- Poucet, B., Bolson, B., and Herrmann, T. 1990. Spatial behaviour of normal and septal rats on alternate route maze problems. *Q. J. Exp. Psychol. B*, **42**: 369–384.
- Ralls, K. 1971. Mammalian scent marking. *Science (Washington, D.C.)*, **171**: 443–449.
- Regolin, L., Vallortigara G., and Zanforlin, M. 1994. Perceptual and motivational aspects of detour in young chicks. *Anim. Behav.* **47**: 123–131.
- Reichstein, H. 1960. Untersuchungen zum Aktionsraum und zum Revierverhalten der Feldmaus (*Microtus arvalis*, Pall.). *Z. Säugetierkd.* **25**: 150–169.
- Rozenfeld, F.M., Le Boulangé, E., and Rasmont, R. 1987. Urine marking by male bank voles (*Clethrionomys glareolus* Schreber, 1780, Microtidae, Rodentia) in relation to their social rank. *Can. J. Zool.* **65**: 2594–2601.
- Teskey, G.C., Ossenkopp, K.-P., Kavaliers, M., Innis, N.K., and Boon, F.H. 1998. Individual differences in radial maze performance and locomotor activity in the meadow vole, *Microtus pennsylvanicus*. *Physiol. Behav.* **65**: 555–561.
- Thinus-Blanc, C. 1996. Animal spatial cognition: behavioral and neural approaches. World Scientific Publishing, Singapore.
- Wolff, J.O., and Johnson, M.F. 1979. Scent marking in taiga voles, *Microtus xanthognathus*. *J. Mammal.* **60**: 400–404.