An analysis of movements of the wood mouse *Apodemus sylvaticus* in its home range

Simon Benhamou

CNRS, Laboratoire de Neurosciences Fonctionnelles, 13402 Marseille Cédex 9, France

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Abstract

The aim of this study was to quantify the movements of the wood mouse *Apodemus sylvaticus* in its home range. The movements were recorded using a new tracking method: it consisted of tracking a visually tagged wood mouse by a telescope from an observation tower and automatically recording the successive positions of this telescope (corresponding to the successive positions of the wood mouse in the field). Statistical analysis of 51 recorded movements, involving 10 wood mice, was carried out. The characteristics of the general movement patterns fitted a first order correlated random walk model. Furthermore, the detailed structure of paths was quantified. An analysis of variance showed that an individual factor was involved in metric and temporal movement characteristics but not in the statistical structure of the paths. Lastly, examination of all the movements of 6 wood mice, with for which at least 4 different paths were recorded, revealed their space use patterns within their home ranges.

Key words: Wood mouse; Movement; Space use pattern; Tracking

Introduction

Foraging behaviour largely determines how animals use available space. Precise spatio–temporal analysis of movement patterns in the field therefore constitutes a fundamental approach to the study of this behaviour: in a given sedentary species, this analysis provides characteristic parameters on strategies used by individuals foraging in their home ranges. Although spacing patterns have been studied extensively in mammals and birds (review in Brown & Orians, 1970; Waser & Wiley, 1980), only a few field studies, such as those by Cody (1971, 1974) and Smith (1974a,b) on
birds and Siniff and Jessen (1969) and Macdonald (1980) on mammals, have concentrated on spatio-temporal analysis of movement patterns in the field. The present study aimed to conduct an analysis of this kind on the wood mouse *Apodemus sylvaticus*.

A close-cropped lawn sprinkled with shrubs was used as study area (see methods). In a previous study carried out in a similar field, wood mice were observed to move in their home ranges by piloting from one shrub to another (Jamon & Benhamou, 1989). The present study was designed to precisely quantify the wood mouse’s movement characteristics in order:

(1) to determine whether the general movement patterns of wood mice from one shrub to another would fit the first order correlated random walk model developed by Bovet & Benhamou (1988). This model was already shown to be useful for theoretical studies of some space use and orientation mechanisms (Benhamou & Bovet, 1989; Benhamou, 1989; Benhamou et al, 1990; Bovet & Benhamou, 1990). Here it was attempted to determine whether this model might be useful for analysing actual movements of wood mice in their home ranges.

(2) to analyse the detailed structure of the movements of the wood mice between shrubs, in which only the parts of movement located in the lawn were considered.

(3) to determine which movement characteristics of the wood mice are individually controlled and which are not.

(4) to analysis the characteristics of the space use patterns exhibited by the wood mice within their home ranges.

From the practical point of view, it was necessary to record the wood mouse’s movements with a satisfactory level of precision. Recording punctual tracks of small mammals, such as the footprints of toe clipped animals or marked faeces, or locating radioactive labelled animals (review in Sanderson, 1966 and in Twigg, 1975a,b) does not provide sufficiently precise data about the animals’ paths. Recording continuous tracks left by dyed animals (Jones, 1978; Duplantier et al., 1984; Lemen & Freeman, 1985) is tricky to use in the field to record an individual’s path over large distances, and affords only static information. Although radio-tracking has been used to locate small rodents in the field (Rawson & Hartline, 1964; Madison, 1977; Mineau & Madison, 1977; Wolton, 1983, 1985), the practicability of this method is limited because of the weight of transmitters and the imprecision of the recordings when working far enough from the animal to not disturb it. Consequently, a new tracking method was developed to precisely record wood mice’s movements in the field.

**Methods**

*Principle of the recording method*

The recording method was adapted (and considerably improved) from a method used by Jamon & Benhamou (1989). It consisted of tracking each wood mouse from an observation tower with a telescope placed on a tripod and recording the successive angular positions of the ball-and-socket joint in the horizontal (δ) and vertical planes (θ). Corresponding positions of the animal can be determined by trigonometry, on
condition that it moves on a flat area. Each position of the wood mouse on the field
\((X, Y)\) then corresponded to a recorded position of the joint:
\[X = OM \cdot \cos \theta \quad \text{and} \quad Y = OM \cdot \sin \theta,\]
with \(OM = OT \cdot \tan \theta\)
where \(OT\) is the observation height (at which the telescope is positioned) and \(OM\) is
the distance from which the animal is observed. Thus, an animal's path can be
perfectly reconstructed from the successively recorded positions of the joint. A similar
recording principle was used by Tyack (1981) to determine the position of whales
using a theodolite from the top of a cliff.

**Visual tagging of the wood mouse**

As established by Brown (1956a), Baumler (1975), Greenwood (1978), and Wolton
(1983), the wood mouse is a nocturnal rodent. Direct observations were conducted at
night using Buchler's (1976) technique: the animal was tagged with a small bulb (0.4
ml) containing cyalume (1/4 reagent, 3/4 solvent), a chemiluminescent product that
allows observations for 4 hours at distances over 100 m. To facilitate changing of
bulbs, the male part of a press-stud was sewed (under anesthesia) onto the neck of
the wood mouse and the female part was glued onto the bulb. The sewing held for
about 15 days. It was then possible to sew another press-stud on the animal. The bulb
was filled with cyalume and afterwards set on the animal, just before its movements
were recorded. The bulb weighed about 1 g (< 5% of the body weight). Each bulb was
used only once. The cyalume technique did not disturb the behaviour of the animal,
as previously noted by Buchler (1976), Jamon & Bovet (1987) and Jamon & Benhamou
(1989). The telescope (15 \(\times\) 50) used to track the tagged wood mouse was equipped
with a radio-luminescent reticle, so that one could focus on the animal during its
nocturnal movements.

**Recording technique**

The telescope was set on the joint and placed on a steady tripod at the top of an
observation tower, strongly guyed to the soil, at an observation height of 10.84 m.
Successive positions of the joint corresponding to the tracked wood mouse's succes-
sive positions in the field were recorded by two precision potentiometers fixed to the
joint (Fig. 1a): the angle \(\theta\) was measured by the vertical potentiometer and the angle \(\delta\)
was measured by the horizontal potentiometer. The mechanical multiplication (by 6)
of the vertical movements of the joint considerably improved the precision of the
vertical angular measurement which is of major importance because of the "perspec-
tive effect", while the mechanical demultiplication of the horizontal movements (by
0.875) ensure to avoid the blind area of the potentiometer (between 355 and 360
degrees).

The angular values of \(\theta\) and \(\delta\), as measured by the potentiometers, were digitalized
by a 17-bit analological-numerical converter. The time factor was given in seconds by an
electronic clock. The data were stored in the central memory of a microcomputer.
Every time the wood mouse was centered with the telescope, its spatio-temporal
position was coded, using a switch (Fig. 1b). The electronic working of the system was
under the general control of a computer program. After each recording session, the
data were conveyed from the central memory for storage on the magnetic tape of a cassette recorder. The whole system was supplied in the field by three 12 V batteries. The maximum electronic error (1 bit) corresponded to a radius of approximately 25 cm around the actual position of an animal observed from a distance of 100 m. Accuracy depended on other factors, such as the sighting, so that the actual error was about 1 m at a distance of 100 m.

Fig. 1. Scheme of the tracking (a) and recording (b) system. T: telescope; R: radio-luminescent reticle; W1, W2, W3, W4: notched wheels with 96, 16, 21, 24 teeths, respectively; VP, HP: vertical and horizontal potentiometers; VB, HB: vertical and horizontal notched belts (transmission W1-W2, W3-W4, respectively); S: switch controlling the recording system; ANC: analogical-numerical converter; EC: electronic clock; VIA: versatile interface adapter; MC: micro-computer; CR: cassette recorder.
Study area and timing

The field work was conducted, from July to December 1984, at the Biological Station of Tour du Valat, in the Camargue (Southern France). The field was a flat horizontal close-cropped lawn sprinkled with shrubs (*Phillyrea angustifolia*; density: 85 shrubs/ha). This lawn was delimited by meadows and cultivated fields to 180 m in width (N-S) and 300 m in length (E-W).

Wood mice caught by Sherman live traps were individually marked by ear-tagging. Trapping began in July using a 200 by 160 m trapping grid and recording began in August. Only sedentary wood mice were studied. Sedentariness was established when a wood mouse was trapped for at least one week in a definite area (Andrzejewski & Wierzbowska, 1961; Bovet, 1963).

During the recording session, only a few traps were used. They were checked in the morning. One wood mouse was selected from the trapped wood mice. Because it is more important in movement analysis to have numerous data available on the same animal than to have only some data for a large number of animals, priority was always given to the wood mouse whose movements had been recorded most often. The selected wood mouse was kept in its trap until night. A cyalume bulb was then tagged onto its neck, and it was released at the same place where it was trapped. The procedure then consisted of tracking the wood mouse until 4 hours had elapsed (lifetime of cyalume). Recordings were made during moonless nights, for 15 successive days of a lunar month, to ensure good conditions for detecting the tracked wood mouse.

Data processing

Recorded data were first transferred from magnetic tape to the micro-computer, and afterwards, to a powerful computer by means of a communication interface (RS232). A computer program was then used to decode the recordings, i.e. to reconstitute the paths as sequences of points (X, Y, t).

With each recording, path length (L), travel time (T), time spent in shrubs (TS), percentage of time spent in shrubs (%TS = 100 · TS/T) and mean speed of movements between shrubs (V = L/(T-TS)) were computed.

As explained above, two analysis levels of wood mouse's paths were used, because of the heterogeneity of the environment:
- Level 1: analysis of the general movement patterns of wood mice from one shrub to another. It was tested if these patterns, represented by the locations of the successively visited shrubs, could fit the first order correlated random walk model. Movements between successively visited shrubs were therefore approximated by straight line segments, which are referred to as steps, according to the terminology given in Bovet & Benhamou (1988). The model assumed that changes of direction between successive steps are randomly drawn in a wrapped normal distribution with a null mean and a standard deviation σ. Then the sinuosity of the paths can be computed as $S = \sigma / \sqrt{m(P)}$, where m(P) is the mean step length, under the condition that σ is less than 1.2 rad (Bovet & Benhamou, 1988). Step number (N), mean step length (m(P)), corresponding percentage of path length (%L = 100 · N · m(P)/L), and standard deviation (σ) and mean vector length (r, which expresses the concentration of angular
values around the angular mean; Mardia, 1972; Batschelet, 1981) of the distributions of changes of direction were computed.

Level 2: analysis of the detailed structure of the paths between the shrubs, in which only the parts of the movements located on the lawn were considered. These movements were arbitrarily discretized by the tracking apparatus during the recording. They were analysed by computing the distribution of changes of direction obtained after rediscretization with different constant step lengths, according to the method given by Bovet & Benhamou (1988). However, no attempt to use the first order correlated random walk model was made at this second level analysis, because movements in the lawn were obviously shrub oriented, which constituted an external constraint which is not taken into account in the model.

Note that it is possible to use the standard deviation (σ) of an angular distribution instead of the mean vector length (r) when the dispersion of angular values is not too large (r > 0.5, corresponding to σ < 1.2 rad for a wrapped normal distribution); it was always the case for the second level analysis, but not for the first level analysis (see below).

Finally, by examining all the movements of the wood mice, movement characteristics which are individually controlled were identified by analyses of variance, and the space use patterns were determined from the time spent by the wood mice in the shrubs.

Results

The analysis was carried out on 51 recordings of 10 wood mice, including six males (C, F, G, H, I, and J) and four females (A, B, D, and E). Three examples of paths are given in Fig. 2. Wood mice spent on average 56% of their time in shrubs. The modal (i.e. most usual) speed of movement ranged from 0.5 to 2 m/s, that is therefore much greater than the mean speed between shrubs (V) which was about 10 m/min (Table 1). This difference was due to irregular slow movements the wood mice performed in the lawn.

First level analysis

Movements from one shrub to another constitute the general framework of the wood mice’s movements. The schematization of movements by straight line segments between successively visited shrubs accounts for 67% in average of the total path lengths (Table 1).

Statistical analysis of the distribution of changes of direction between successive steps was carried out on 43 recordings where the number of changes of direction was equal to or greater than 5. Using Kuiper’s test (1960; also see Stephens, 1965; Mardia, 1972; Batschelet, 1981), it was found that the distribution of changes of direction did not significantly differ at p = 0.10 from a wrapped normal distribution with null mean and with a concentration (given by r) equal to that of the observed distribution, with 38 out of 43 paths. Furthermore, using the test of Jupp & Mardia (1980; also see Batschelet, 1981), only 2 paths were found to show significant correlation at p = 0.05 between the successive changes of direction, whereas 37 paths did not show any such
correlation at $p = 0.10$. Therefore, it does not seem possible to reject the hypothesis that the changes of direction are randomly drawn in a wrapped normal distribution centered on 0, that is compatible with the first order correlated random walk model. However, the dispersion of angular values was too large ($\sigma < 0.5$, i.e. $\sigma > 1.2$ rad) in 66% of all recordings for us to be able to compute their sinuosity. In the cases where this was possible ($\sigma < 1.2$ rad), the sinuosity of the paths was computed to be between 0.22 and 0.44 rad/m$^{1/2}$.

How, then, did the wood mice choose the next shrub? Because the distribution of changes of direction did not differ significantly from a wrapped normal distribution with a null mean, it can first be said that the shrub chosen by a mouse to make its next step was more or less in the direction of the last step. However, no significant correlation existed at $p = 0.10$ with 41 out of 43 paths between the size of the chosen shrub and the distance to it. It cannot therefore be said that the wood mice preferentially chose the successively visited shrubs on the basis of their apparent size.

**Second level analysis**

Since the schematization of movements by straight line segments between successively visited shrubs accounts for 67% in average of the total path lengths, the
difference between the actual structure of the paths taken on the lawn and a straight line therefore corresponded on average to 33% of these total path lengths. The movements in the lawn were rediscretized with five different step lengths R (from 1 to 5 m) in order to analyse the distribution of changes of direction (see Bovet & Benhamou, 1988). This showed that the standard deviations \( \sigma_R \) of these distributions observed after rediscretization increased more slowly than the square root of the rediscretization step length R, contrary to what happen with first order correlated random walks, whereas the angular means remained close to 0. This was expected, because movements between shrubs were goal oriented. However, the values of \( \sigma_R \) did not decrease with R as is the case with strictly goal oriented movements, indicating the existence of a random search component.

The characteristics of the distributions of changes of direction were analysed after rediscretization with a step length R = 2 m. The value of the standard deviations \( \sigma_2 \) are given in Table 1. Statistical analysis of the distribution of changes of direction was carried out with 45 out of the 51 recordings where the number of changes of direction was equal to or greater than 5. The angular mean did not differ significantly from 0 at \( p = 0.05 \) (from the confidence interval chart given in Batschelet, 1981) with 43 out of

### TABLE 1

Mean values (and SD) of the main movement characteristics.

<table>
<thead>
<tr>
<th>WM</th>
<th>RN</th>
<th>L</th>
<th>T</th>
<th>%TS</th>
<th>V</th>
<th>%L</th>
<th>r</th>
<th>( \sigma_2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2</td>
<td>195.0</td>
<td>93.8</td>
<td>49.0</td>
<td>6.6</td>
<td>59.0</td>
<td>0.36</td>
<td>0.56</td>
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<tr>
<td></td>
<td></td>
<td>(91.9)</td>
<td>(22.1)</td>
<td>(55.1)</td>
<td>(4.2)</td>
<td>(35.4)</td>
<td>(0.26)</td>
<td>(0.19)</td>
</tr>
<tr>
<td>B</td>
<td>2</td>
<td>422.5</td>
<td>195.0</td>
<td>40.0</td>
<td>3.9</td>
<td>53.5</td>
<td>0.28</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(150.6)</td>
<td>(13.9)</td>
<td>(4.2)</td>
<td>(1.3)</td>
<td>(13.4)</td>
<td>(0.01)</td>
<td>(0.11)</td>
</tr>
<tr>
<td>C</td>
<td>4</td>
<td>967.5</td>
<td>175.1</td>
<td>23.3</td>
<td>7.7</td>
<td>57.0</td>
<td>0.27</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(143.6)</td>
<td>(40.8)</td>
<td>(14.0)</td>
<td>(1.3)</td>
<td>(6.9)</td>
<td>(0.08)</td>
<td>(0.13)</td>
</tr>
<tr>
<td>D</td>
<td>14</td>
<td>711.5</td>
<td>82.9</td>
<td>55.4</td>
<td>9.0</td>
<td>71.9</td>
<td>0.45</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(150.4)</td>
<td>(51.6)</td>
<td>(21.0)</td>
<td>(6.9)</td>
<td>(17.6)</td>
<td>(0.17)</td>
<td>(0.23)</td>
</tr>
<tr>
<td>E</td>
<td>2</td>
<td>196.0</td>
<td>27.2</td>
<td>46.0</td>
<td>13.8</td>
<td>69.5</td>
<td>0.52</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(26.9)</td>
<td>(8.9)</td>
<td>(14.1)</td>
<td>(0.8)</td>
<td>(3.5)</td>
<td>(0.43)</td>
<td>(0.11)</td>
</tr>
<tr>
<td>F</td>
<td>2</td>
<td>558.5</td>
<td>137.2</td>
<td>26.5</td>
<td>8.1</td>
<td>75.5</td>
<td>0.48</td>
<td>0.57</td>
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<td></td>
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<td>(318.9)</td>
<td>(71.7)</td>
<td>(10.6)</td>
<td>(8.1)</td>
<td>(5.7)</td>
<td>(0.08)</td>
<td>(0.00)</td>
</tr>
<tr>
<td>G</td>
<td>6</td>
<td>182.7</td>
<td>85.4</td>
<td>54.2</td>
<td>5.7</td>
<td>59.2</td>
<td>0.31</td>
<td>0.74</td>
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<tr>
<td></td>
<td></td>
<td>(139.0)</td>
<td>(68.3)</td>
<td>(16.7)</td>
<td>(2.7)</td>
<td>(17.7)</td>
<td>(0.26)</td>
<td>(0.24)</td>
</tr>
<tr>
<td>H</td>
<td>7</td>
<td>337.7</td>
<td>145.7</td>
<td>61.6</td>
<td>7.7</td>
<td>71.6</td>
<td>0.41</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(247.2)</td>
<td>(59.0)</td>
<td>(19.3)</td>
<td>(5.1)</td>
<td>(14.2)</td>
<td>(0.26)</td>
<td>(0.14)</td>
</tr>
<tr>
<td>I</td>
<td>6</td>
<td>99.7</td>
<td>40.2</td>
<td>84.3</td>
<td>19.6</td>
<td>69.2</td>
<td>0.56</td>
<td>0.47</td>
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<td></td>
<td></td>
<td>(34.4)</td>
<td>(19.4)</td>
<td>(9.4)</td>
<td>(5.7)</td>
<td>(4.7)</td>
<td>(0.19)</td>
<td>(0.14)</td>
</tr>
<tr>
<td>J</td>
<td>6</td>
<td>137.5</td>
<td>78.7</td>
<td>67.8</td>
<td>15.8</td>
<td>65.7</td>
<td>0.38</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(80.7)</td>
<td>(60.3)</td>
<td>(25.7)</td>
<td>(14.9)</td>
<td>(7.3)</td>
<td>(0.15)</td>
<td>(0.22)</td>
</tr>
</tbody>
</table>

WM: wood mouse; RN: number of paths recorded; L: path length (m); T: travel time (mn); %TS: percent of time spent in shrubs; V: mean speed in the lawn (m/min); %L: percent of path length represented by general movement patterns; r: mean vector length of the distribution of changes of direction for general movement patterns; \( \sigma_2 \): standard deviation of the distribution of changes of direction for movements in the lawn (rad) after rediscretization with a step length R = 2 m.
45 paths, but the normal distribution assumption was rejected at $p = 0.05$ with 28 paths, although the distribution shapes were symmetrical and unimodal. Standard deviations ranged from 0.26 to 1.15 rad, which points to the existence of a major random component. Furthermore the assumption that no correlation existed between successive changes of direction was rejected at $p = 0.05$ with 11 paths, which is not as high as might be expected with strictly goal oriented movements: indeed, such oriented movements lead to an alternation of right and left turns (whatever the rediscretization step length) which appears as an important correlation between successive changes of direction. This also points to the existence of a random search component in the path taken in the lawn.

**Movement variability analysis**

The results of analysis of the variability of given movement characteristics allowed us to test the hypothesis that the values of these characteristics obtained with individual wood mice are drawn from parent populations with the same expected value.

Taking each wood mouse as an independent data group, an analysis of variance showed the existence of an “individual wood mouse” factor contributing to the metric and temporal movement characteristics: indeed the homogeneity hypothesis was rejected at $p = 0.05$ for $L$, $T$, %TS, and $V$. On the other hand, this factor could not be shown at $p = 0.10$ in the case of characteristics depending on the statistical structure of paths: %L, $r$ and $a^2$ (Table 2).

**Space use pattern**

The home ranges of the six wood mice on which at least four recordings were obtained were represented by the elliptical home range model at the 0.95 probability level (Jennrich & Turner, 1969; Mazurkiewicz, 1969, 1970; see also Benhamou & Jamon, 1988), from the times spent by these wood mice in the shrubs (Table 3).

**TABLE 2**

Variance analysis of the main movement characteristics.

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>T</th>
<th>%TS</th>
<th>V</th>
<th>%L</th>
<th>$r$</th>
<th>$a^2$</th>
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<tbody>
<tr>
<td>F</td>
<td>11.75</td>
<td>4.07</td>
<td>3.40</td>
<td>2.23</td>
<td>1.00</td>
<td>0.83</td>
<td>1.13</td>
</tr>
<tr>
<td>df</td>
<td>9-41</td>
<td>9-41</td>
<td>9-41</td>
<td>9-41</td>
<td>9-41</td>
<td>9-33</td>
<td>9-35</td>
</tr>
<tr>
<td>p</td>
<td>&lt; 0.0005</td>
<td>&lt; 0.001</td>
<td>&lt; 0.005</td>
<td>&lt; 0.05</td>
<td>&gt; 0.10</td>
<td>&gt; 0.10</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>F</td>
<td>20.10</td>
<td>4.69</td>
<td>5.30</td>
<td>3.25</td>
<td>1.29</td>
<td>1.24</td>
<td>1.51</td>
</tr>
<tr>
<td>df</td>
<td>5-37</td>
<td>5-37</td>
<td>5-37</td>
<td>5-37</td>
<td>5-37</td>
<td>5-29</td>
<td>5-31</td>
</tr>
<tr>
<td>p</td>
<td>&lt; 0.0005</td>
<td>&lt; 0.001</td>
<td>&lt; 0.005</td>
<td>&lt; 0.025</td>
<td>&gt; 0.10</td>
<td>&gt; 0.10</td>
<td>&gt; 0.10</td>
</tr>
</tbody>
</table>

Upper part gives variance analysis results on the 10 wood mice, whereas lower part deals only with the 6 wood mice on which at least four recordings were obtained (see Table 1). F: variance ratio; df: degrees of freedom; p: probability level.
Fig. 3. Home ranges and paths of wood mice C, D, G, H, I, and J. Home range limits are drawn by the elliptical home range model at the 0.95 probability level. The size of the represented field is 240 m by 180 m.

It can be seen that this representation of home ranges is accurate enough, even if the bivariate normal distribution of animals' position in space assumed by the elliptical home range model was not confirmed, in particular because of the considerable heterogeneity of the environment (Fig. 3).

The home range areas were between 1700 and 14000 m², with a mean of 6500 m². They were similar in size to those obtained in the same environment by trapping.
TABLE 3
Home range characteristics as estimated by the elliptical home range model at the 0.95 probability level.

<table>
<thead>
<tr>
<th>WM</th>
<th>RN</th>
<th>TL</th>
<th>TT</th>
<th>TTS</th>
<th>XC</th>
<th>YC</th>
<th>HRA</th>
<th>R1</th>
<th>R2</th>
<th>OR</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>4</td>
<td>3870</td>
<td>700.1</td>
<td>180.5</td>
<td>-51</td>
<td>-5</td>
<td>13801</td>
<td>98</td>
<td>45</td>
<td>53</td>
</tr>
<tr>
<td>D</td>
<td>14</td>
<td>2989</td>
<td>1161.1</td>
<td>649.8</td>
<td>-11</td>
<td>-38</td>
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WM: wood mouse; RN: number of paths recorded; TL, TT and TTS: total length (m), total time (min) and total time spent in shrubs (min) in all paths taken by each wood mouse; XC and YC: coordinates of activity centers (m); HRA: home range area (m²); R1 and R2: major and minor semi-axis lengths (m); OR: orientation of the major axis in relation to the W-E direction (deg)
Furthermore, a significant correlation was found to exist at $p = 0.02$ between the mean path length of each wood mouse and the size of its home range area. A similar result was previously obtained by Brown (1956b) by trapping and by Wolton (1985) by radio-tracking, which suggested that the home range area might reflect the mean amount of movement.

If one looks at all the paths of each wood mouse, it can be seen that several portions overlap. This might indicate that wood mice move more or less along a network of pathways. The structure of this network may be favoured by the heterogeneity of the environment, the shrubs corresponding to the junctions of the network. Furthermore, the figure showing all the 51 paths together (Fig. 4) points that these networks had common portions.

**Discussion**

The hypothesis that mammals move on a network of pathways or scent-marked trails has been put forward in connection with numerous species (Pearson, 1959; O'Farrel, 1965; Adams & Davis, 1967; Frame, 1975; Peters & Mech, 1975; Peters, 1979; Rathbun, 1979; Pulliainen, 1982; Thompson, 1982), but has not always been clearly demonstrated. The space use pattern exhibited by wood mice in this study is compatible with this hypothesis. It is not clear, however, whether wood mice actually move on a network of scentmarked pathways or move by visual piloting from one shrub to another, as suggested by Barry & Francq (1980) and Drickamer & Stuart (1984).

The general movement patterns of the wood mice from one shrub to another were associated with the exploitation of shrubs, as indicated by the high proportion of time spent (56% on average) by the animals therein. Shrubs are indeed favourable places for wood mice, providing both various sources of energy (seeds, arthropods, etc.) and protection against predators. On the other hand, movements in the lawn between the shrubs corresponded on average to 33% of these total path lengths. The mean speed of movements on the lawn was 10 m/mn, whereas the usual speed ranged from 0.5 to 2 m/s. Consequently, the wood mice did not travel on the lawn as fast as possible from one shrub to another. They spent on average 44% of their time in the lawn. All these findings indicate that these movements taken in the lawn were associated with an exploitation of the lawn. Furthermore, the general organization of the movements exhibited by the wood mice in this study, where they were released within their home ranges was quite different from that exhibited in the same environment when they were released at the periphery of their home ranges using the same procedure for release and tracking: in the latter case, the wood mice did not explore their home ranges, but oriented their movements to a significant extent towards their activity centres (Jamon & Benhamou, 1989).

Statistical analysis of distributions of changes of direction observed in general movement patterns from one shrub to another showed that their characteristics fit the basic assumptions of the first order correlated random walk model fairly well: indeed, in most cases, it was statistically possible to show that changes of direction appeared randomly drawn in a wrapped normal distribution centered on 0. Because of the great dispersion of most of the distributions, however, I was able to compute the sinuosity of only some paths. This might be due to the heterogeneity of the environment which
led the wood mice to walk great distances between successively visited shrubs, i.e. 9 m on average. Wood mice therefore need to make large turns in order to restrict their movements within their home ranges (6500 m² in average). On the other hand, although movements in the lawn were shrub directed, they contained a large residual random search component, probably due to the exploitation of the lawn.

The results of movement variability analysis showed that the metric and temporal characteristics of the wood mice’s movements, but not the characteristics depending on the statistical path structure, were sensitive to an “individual factor”. This confirms the hypothesis put forward in Bovet & Benhamou (1988) that the random component of paths might constitute a general adaptation of movement behaviour to the stochasticity of the environment: unlike metric and temporal movement characteristics, this component did not depend on an individual factor but was imposed by the environment.

Various habitats have been colonized by the wood mouse. This study showed how the movements can be influenced by a “semidesertic” environment (i.e. an open area sprinkled with shrubs). The movement and space use patterns exhibited by the wood mice in this study are similar to those of other rodents species living in this type of environment. They are probably different, however, from patterns exhibited by wood mice living in a more homogenous environment.
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References


