

Movements of small mammals in the heterogeneous landscape

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Abstract

Distances and directions of *Apodemus agrarius* and *Clethrionomus glareolus* movements were studied using snap traps and colored bait. The longest distances traversed exceeded **1500** m. Some directions of movement were significantly more common. High variability in the number of captures along traplines suggests distinct movement routes. Small mammals appear to base their movement on the landscape and not on individual biotopes.

Introduction

Movements of animals are important in landscape ecology because flows and transfers between spatial components are of special significance and 'the process of redistribution of organisms, materials, and/or energy is thus an essential feature of landscape ecology' (Risser *et al.* **1983**). Knowledge of the actual distances, directions, and routes of movement is necessary to understand the links between various biotopes within larger ecological systems and hence the functioning of the ecological landscape.

Most studies of movements of small mammals have been devoted either to activity within home ranges or migration as a factor involved in population regulation. The common method of studying movement has been live-trapping which limits movements of animals (*e.g.* Sheppe **1967**; Andrzejewski and Babinska-Werka **1986**). In spite of increasing interest in stability of populations of small mammals in the landscape there is inadequate information on the actual distances, directions and

routes of movements (Middleton and Merriam **1981, 1983**; Fahrig and Merriam **1985**; Henderson *et al.* **1985**; Hansson **1987**). There is evidence that the distances traversed by small mammals may be much greater than is commonly believed (Andrzejewski and Babinska-Werka **1986**; Liro and Szacki **1987**; Clark *et al.* **1988**).

The aim of this study was to determine distances and directions of movements of small mammals in heterogeneous landscape.

Study area and methods

The study was conducted in suburban Warsaw in a fine-grained mosaic of different biotopes, bound on two sides by closely-positioned buildings. The landscapes was dominated by meadows, barren land covered by ruderal plants, vegetable and fruit cultivation, gardens, and cultivated land with belts of forests. There was also a park with oak-hornbeam (area **100** ha) (Natolin Park) and pine-oak forest (area **900** ha) (Kabacki Forest) (Fig. **1**).

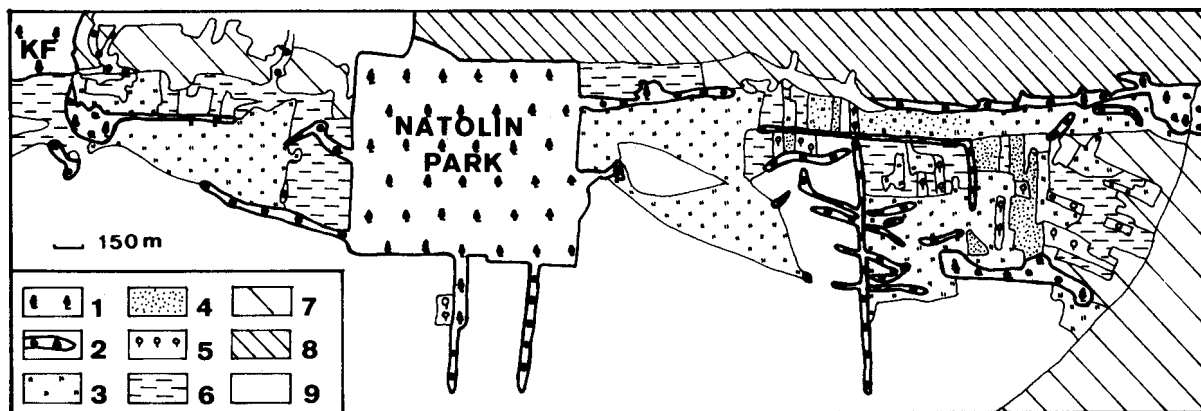


Fig. 1. A map of the study area. 1 – woody areas; 2 – linear forests; 3 – meadows; 4 – ruderal vegetation; 5 – orchards; 6 – vegetable and fruit cultivation; 7 – single-family homes; 8 – closely-positioned buildings; 9 – fields; KF – Kabacki Forest.

Small mammals were trapped during seven-day sessions in the autumn of 1986 and during five day sessions in April, June and at the end of September and beginning of October, 1987. In 1986 snap traps were placed along 4500 and 2500 m lines and in 1987 along 8 lines of 1000 m each. Traps were placed in sets of three at stations, located at 50 m intervals along each line. In addition to this, colored bait made from flour, margarine and finely cut colored plastic or woollen fibres (Holisova 1968) was placed in different biotopes within the study area four days before the beginning of trapping, and supplemented as required. Different colors of bait were used in each biotope within the study area. Weight, sex and reproductive condition were recorded for each animal and the contents of stomachs and intestines were examined microscopically to determine the presence and color of the bait fibers.

Results

Occurrence of small mammals in different biotopes

The field mouse (*Apodemus agrarius*) was the most common species (726 captures) in the study area. This species was recorded in all biotopes, with the exception of dry meadows under intensive cultivation. Other common species were the bank vole (*Clethrionomys glareolus*) (266) and the wood

mouse (*Apodemus flavicollis*) (82). Bank voles were associated with woody or bushy plants, wood mice with forests. The highest densities of all mammals were recorded in patches of thick ruderal plants and linear forests (Table 1). Of all the animals containing colored bait, the most numerous were those who had consumed the bait in the linear forested areas. The greatest species diversity was found in forest biotopes (oak-hornbeam forest and pine-oak forest) (Table 1).

Small mammals were caught unequally on all lines of traps. The actual distribution of catches along the lines was significantly different from a uniform distribution (χ^2 test, $p < .01$ or $p < .02$), regardless of whether a given line ran through only one biotope or more than one biotope.

Distances and directions of small mammals movements

During the study, colored fibers were found in 361 individuals, 31% of all of the animals caught. The distribution of the distances moved by the two most numerous species is presented in Table 2. For both species the longest routes exceeded 1000 m; there was little tendency for the numbers of *Apodemus* to diminish with distance covered. In the spring and summer very few small rodents were trapped. Thus, we have few data regarding distances moved during these seasons. Even so, individual cases of move-

Table 1. The occurrence of small mammals in different biotopes, A.ag., *Apodemus agrarius*, C.gl., *Clethrionomys glareolus*, A.fl., *Apodemus flavicollis*. S is the number of other species; H – Shannon-Wiener index of species diversity. D – density. Data for fall 1986 and 1987 combined.

	Number of traps in a habitat	Total numbers of captures			S	D	H
		A.ag.	C.gl.	A.fl.			
Degraded oak-hornbeam forests	104	185	97	64	2	.58	1.2
Pine-oak forest	21	31	49	12	0	.62	1.0
Linear afforestations	84	253	48	0	5	.73	.7
Moist meadows with reeds and bushes	20	50	2	0	2	.55	.5
Meadows	26	62	0	0	3	.56	.3
Ruderal vegetation	12	42	0	0	5	.82	.6
Orchards, fruit and flowers cultivations	14	59	3	0	0	.67	.2
Areas with buildings	10	2	0	0	2	.1	–

Table 2. Distances of small mammal movements in the study area.

Distances	Number of individuals	
	A. agrarius	C. glareolus
< 100	51	9
101–250	28	7
251–400	23	5
401–550	19	6
551–700	13	3
701–850	13	2
851–1000	23	3
> 1000	27	9
Total	197	44

ments over 250 m were recorded; *e.g.*, for field mice in April, 1 out of 3 individuals, in June 2 out of 9 individuals; for bank voles, 2 out of 3 in April and 3 out of 5 in June. There was no difference, in either species, in weight, sex or reproductive condition among individuals moving more than 300 m and the rest of the population.

The movements over 300 m (N = 131) were also analyzed with respect to direction (mainly based on data for the field mouse, 108 passages) between

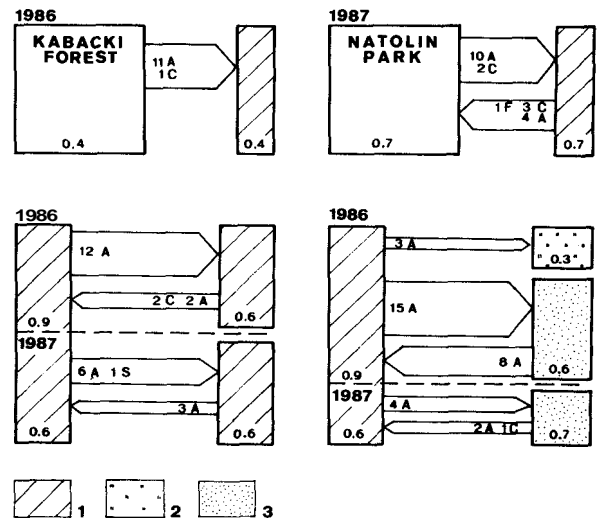


Fig. 2. Directions of small mammal movements. 1 – linear forests; 2 – meadows; 3 – ruderal vegetation. A – *A. agrarius*; C – *C. glareolus*; F – *A. flavicollis*; S – *A. sylvaticus*. The width of arrows is proportional to the number of passages. Numbers inside arrows represent number of passages. Numbers inside rectangles representing habitats indicate density of small mammal communities.

individual biotopes (Fig. 2). In large, relatively natural areas (*i.e.* Natolin Park and Kabacki Forest) more field mice moved out of than into the

habitat. Some directions of movements were dominate over others in other parts of the study area, too, but in most cases movements of field mice were multidirectional. In many cases directions of movements were not consistent with the density gradient (*i.e.* more animals moved from less dense into more dense habitats than in the opposite direction). The number of bank vole passages was too small for analysis. It was only noted that numbers of animals leaving and entering Natolin Park were similar. Figure 2 illustrates directions of small mammal movements during autumn of 1986 and 1987. The number of animal movements in other seasons was too small for analysis but their directions were similar.

Barriers, such as gravel roads and concrete ditches, were no obstacle to the movements of rodents. On the other hand, a belt of single-family homes and a ploughed field presented barriers to movement; not a single case of passage through these obstacles was noted.

Discussion

In a heterogenous landscape the probability of local extinction and recolonization depends on the degree of isolation of individual patches (*e.g.* den Boer 1981; Fahrig and Merriam 1985). The distances that animals can move, and thus the degree of their isolation, is an important factor in the maintenance of populations in isolated patches. Knowledge of movement distances and the possibility of movement of animals between different elements of the mosaic of habitats is also important for an understanding of the stability of the ecological landscape as a whole. Thus, consideration of the heterogeneity of the landscape should take into account distances of movements of the resident animals (Adler 1987).

We found the movement distances of field mice and bank-voles to be much greater than was previously assumed. Most of the previous data on the distances covered by small mammals were obtained through the live-trapping which restricts the movements of small mammals (*e.g.* Sheppe 1967; Andrzejewski and Babińska-Werka 1986). Obvi-

ously, there are also some disadvantages in our method. As a rule we have information on only two points of animal movements: the bait station and the trap where animals were killed (animals visiting more than one bait station were rare). We did not know how animals behaved between the two points. Live-trapping allows for subsequent captures and thus for studying movement patterns between points of subsequent captures. The main disadvantage of the latter method is that animals can get accustomed to traps and they can be caught almost immediately after release. Thus, they spend most of the time in traps and their use of space is not natural (Andrzejewski and Babińska-Werka 1986). Even if traps are set for short periods, they surely change small mammals mobility. Obviously, snap traps do not inhibit movements in that way.

Moreover, as a rule live traps are placed within limited areas so that long-distance movements cannot be recorded. However, there is evidence that small mammals are able to cover distances greater than the diameter of their home range (Brown 1966; Tegelstrom and Hansson 1987). A number of authors mention lengthy 'sallies outside the home range' (Stickel 1968; Furrer 1973). Homing experiments also demonstrate that small mammals are capable of moving considerable distances with an effective speed of at least a few hundred m/h (*e.g.* Jamon and Bovet 1987). Other methods have been used, such as colored bait, tracking or radio-telemetry, which often show greater movement distances than does live-trapping (Sheppe 1967; Randolph 1973; Innes and Skipworth 1983; Andrzejewski and Babińska-Werka 1986; Liro and Szacki 1987; Bergstrom 1988).

Long distance wandering was found not only for field mice, but also for the presumed less mobile (*e.g.*, Brown 1966) bank voles. For both species no significant differences were found between individuals moving long distances and the rest of the population, with respect to sex, weight and reproductive condition. This lack of difference, combined with the fact that a relatively high percentage of the individuals moved more than 300 m, indicates that movements of several hundred meters are common, at least in a heterogeneous environment. Because of low population densities of small

mammals in seasons other than autumn it was difficult to evaluate seasonal changes in movement. The few data from April and June, however, suggest that mobility of the animals was not associated solely with autumn dispersal. The high percentage of animals moving more than 300 m and mobility of different categories of individuals suggest that actual isolated patches of habitat did not exist in the study area and that there might be gene flow between patches. Results of some studies of electrophoretic variation of small mammals enzymes conducted in environmental mosaics (*e.g.* Merriam 1988) suggest high genetic identity among individuals from different patches. We think that the model of a metapopulation consisting of subpopulations inhabiting isolated patches of an environment, suffering local extinctions and then recolonizing habitat islands does not apply to fine-grained mosaics. The landscape under study was inhabited by large populations and animals were able to move freely among individual patches.

Relatively large and natural areas such as Kabacki Forest and Natolin Park seem to be source habitats ('donor' habitats according to Hansson 1977). However, in many cases directions of movements were not consistent with the density gradient. Therefore, it was impossible to distinguish 'typical' dispersal sinks where animals end up. In most population studies it was assumed that rodents were attached to small home ranges in relatively homogeneous habitats (but see Merriam 1990). Every movement outside that home range was assumed to be dispersal and in fact most of those movements ended in low density, suboptimal habitats. In the case of fine-grained mosaics and high mobility of animals every single home range might incorporate many habitat types of different quality. Thus, many small mammal movements might be not connected to dispersal and animals could travel back and forth between habitats. We think that in our study not all animals leaving 'source' areas were doing that to end up in dispersal sinks but just to visit some parts of areas normally used during their life. High density and high species diversity in small linear forests suggest that those habitats might serve as corridors between habitats.

Our data show that small mammals can move

long distances and pass through different biotopes. These movements, however, do not seem to be accidental. The significant differences in number of captures among individual stations along the trap lines and the domination of certain directions over others suggest that there are rather distinct routes of movement.

Individual patches differed with respect to density and number of species of small mammals. The unequal attractiveness of individual biotopes can also be seen from a comparison of the density of small mammals in various parts of the study area. Species abundant in some biotopes were not present elsewhere, for example the bank vole was absent from meadows. However, analysis of the direction of movement of this species shows that in the course of translocation some individuals also had to cross meadows. They were not caught there either because they did not encounter the traps or because of low trappability when moving through unsuitable biotopes. In 'homing' experiments North American field-voles (Robinson and Falls 1965) were not caught between the release point and their home range. Thus it is possible that the behavior of small mammals moving through a 'foreign' habitat is different than that when in their natural biotope. It is also possible that the probability of capture is not the same in the different biotopes. Thus, our understanding of space use can be significantly biased both by the uneven distribution of this probability and the biology of animal movement. One should take into account this methodological bias when considering the use of individual patches and corridors by animals.

Bank voles do not normally live in meadows, but their use of this biotope as movement routes supports the conclusion that many small mammals are animals of the landscape and not of individual biotopes (*e.g.* Hansson 1977, 1979; Middleton and Merriam 1983; Vandruuff and Rowse 1986) and that not only the preferred patches but also the matrix surrounding them are important for the stability of populations of animals. Mobility of animals and the use of the matrix surrounding patches for movements indicate that preferred patches may be less isolated than it is often assumed. Therefore, we agree with those authors who question application

of island biogeography theory (MacArthur and Wilson 1967) to habitat islands (e.g. Middleton and Merriam 1983; Merriam 1988).

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