

## Flooding ecology of voles, mice and shrews: the importance of geomorphological and vegetational heterogeneity in river floodplains

Sander WIJNHOVEN, Gerard VAN DER VELDE,  
Rob S. E. W. LEUVEN and Antonius J. M. SMITS

Wijnhoven S., Van Der Velde G., Leuven R. S. E. W. and Smits A. J. M. 2005. Flooding ecology of voles, mice and shrews: the importance of geomorphological and vegetational heterogeneity in river floodplains. *Acta Theriologica* 50: 453–472.

Since voles, mice and shrews are important animals in food chains of river floodplains, there is a need for data on their spatial and temporal distribution in periodically flooded areas. During a live trapping study between two successive floods in an embanked river floodplain, the 'Afferdensche en Deestsche Waarden (ADW)', six species were frequently observed, viz, *Microtus arvalis* (Pallas, 1778), *Clethrionomys glareolus* (Schreber, 1780), *Sorex araneus* (Linnaeus, 1758), *Crocidura russula* (Hermann, 1780), *Micromys minutus* (Pallas, 1771) and *Apodemus sylvaticus* (Linnaeus, 1758). Ungrazed rough herbaceous vegetation appeared to be rich in numbers and species, whereas no spoors of small mammals were observed in large parts of the ADW floodplain (eg bare substrates and maize fields). Vegetation structure seemed to be very important in guiding the recolonisation process after flood events. Throughout the year the highest numbers of small mammals were captured on and near the non-flooded elevated parts functioning as refugia during inundation. Poor habitat connectivity, sparseness of non-flooded recolonisation sources and small numbers of survivors led to slow recolonisation. The time between two successive floods (eight months) was not long enough for entire recolonisation of ADW. Small mammal densities at more than 30 m from the non-flooded areas were always lower than in non-flooded areas.

Centre for Water and Society, Faculty of Science, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands, e-mail: S.Wijnhoven@science.ru.nl (SW, AJMS); Department of Animal Ecology and Ecophysiology, Institute for Wetland and Water Research, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands (GVDV); Department of Environmental Science, Institute for Wetland and Water Research, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands (RSEWL); Water Management and Sustainability, Faculty of Social Sciences, Erasmus University Rotterdam, The Netherlands (AJMS)

*Key words:* small mammals, river floodplains, recolonisation, densities, connectivity, live trapping

### Introduction

The floodplains of pristine rivers harbour a great diversity of habitats (Andersen *et al.* 2000, Ward *et al.* 2001, Van der Velde *et al.* 2004). The hydromorphodynamic nature of these floodplains, with their flood pulses, alternating erosion and

sedimentation processes and vegetation processes like colonisation, succession and rejuvenation, creates a broad spectrum of habitats for animals (Junk *et al.* 1989).

It is assumed that small mammals play an important role in the food chain (Erlinge *et al.* 1983), also in floodplain ecosystems (Hendriks *et al.* 1995, Kooistra *et al.* 2005, Leuven *et al.* 2005). However, flooding events here influence the seasonal population development cycles of small mammals, as generally found in temperate zones. Flooding means that large parts of the floodplain are cleared of individuals, after which populations redevelop and the floodplain is recolonised. Knowledge of recolonisation and data on the occurrence, habitat preferences and spatial and temporal distribution of voles, mice and shrews in floodplains are limited. This is especially true in embanked floodplains, where the impact of flooding seems to be more severe than in natural floodplains.

Several small mammal ecotopes can be distinguished in floodplains, based on vegetation structure and habitat characteristics, functioning as suitable, marginal, or unsuitable habitats for the various species. The development of small mammal densities is assumed to reflect habitat suitability of the ecotopes for each species (Hansson 1997). In floodplains, the process of recolonisation is also important, because individuals are forced to survive in refugia on the non-flooded parts during floods. Short periods of inundation can possibly be survived by certain species in vegetation above the water level. In periodically inundated floodplains, individuals may be present in the so-called marginal habitats for substantially longer periods of time than in areas without flooding. The densities in marginal habitats are expected to remain low in comparison with those in suitable habitats on non-flooded parts (Wolff 1998). Marginal habitats may therefore play an important role in population dynamics in floodplains (Stelter *et al.* 1997).

In the vicinity of the non-flooded areas, the suitable habitats are expected to be recolonised first when floodwaters recede. The numbers of small mammals in these suitable habitats remain stable or increase during the period after recolonisation. Marginal habitats may also be recolonised relatively soon after the floodwater has receded, but numbers remain low or even drop after colonisation by the first individuals. These areas may function as transition habitats or stepping-stones for dispersal. How long it takes before the first individuals of a species can be found in the flooded parts after receding of the floodwater is dependent of the species-specific recolonisation rate, the quality of the non-flooded areas (refugia) and the connectivity of habitats with source populations in the refugia. As the time till the arrival of the first individuals is dependent of several aspects, this is not always a good measure of habitat suitability.

The goal of our study was to analyse which environmental variables determine the spatial and temporal distribution of small mammals (ie, voles, mice and shrews) in an embanked river floodplain. The research questions were:

(a) Which habitat characteristics are related to the occurrence of small mammal species?

(b) What does the density pattern development of small mammals between two successive annual floods look like?

(c) Do habitat suitability and connectivity affect the recolonisation of floodplains by small mammals after a flooding event?

(d) Are recolonisation patterns of small mammals species-specific?

### Study area

The 'Afferdensche en Deestsche Waarden' (ADW) is a floodplain with an area of 280 ha, embanked by means of summer and winter dikes (Fig. 1). It is situated 20 km west of the city of Nijmegen along the river Waal, the main distributary of the Rhine river in the Netherlands. The area is the subject of an ecological rehabilitation programme in which safety precautions against high river discharges are combined with the conversion of agricultural land into natural floodplain ecotopes. A programme of floodplain and summer dike lowering, clay excavation, construction of a side channel and removal of buildings and roads started during 1995, and will last until 2007 (Zandberg 1999). The present study at ADW included areas with and without agricultural activities,

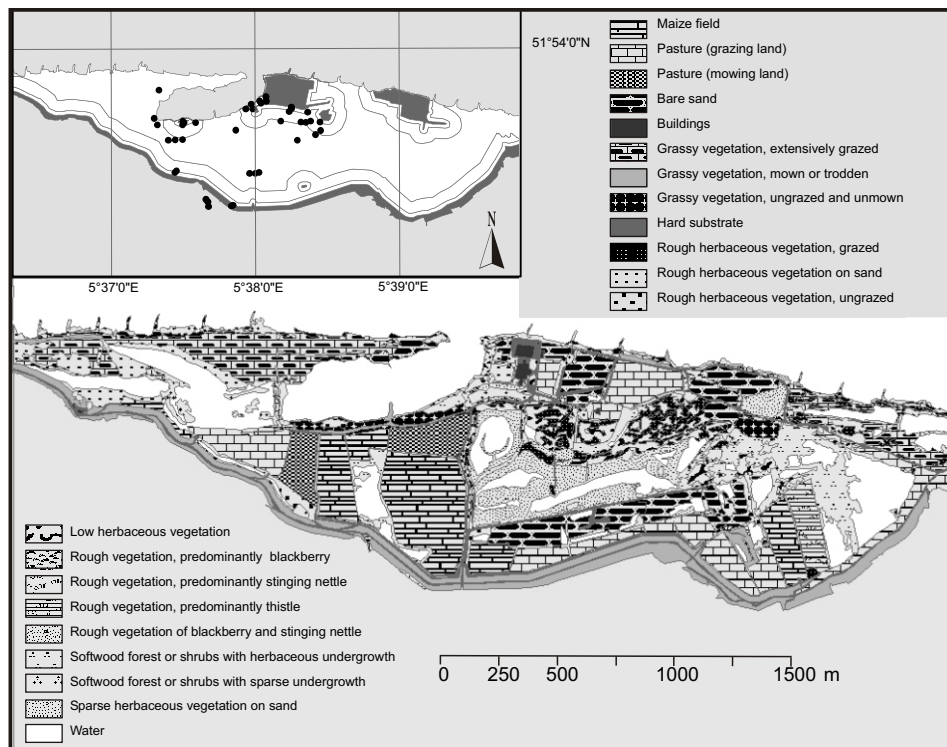


Fig. 1. (a) Positioning of the ADW floodplain, in which the monitoring locations are indicated by dots. Non-flooded areas are shown in grey, and the parallel lines indicate the borders of the other three distance zones (viz 0–30 m, 30–120 m, and more than 120 m from non-flooded areas). (b) Classification of the ADW floodplain into small mammal ecotopes.

the latter favouring natural development of the vegetation and offering a wide range of habitats. The floodplain area between the summer and winter dikes (about two-thirds of the total floodplain) is periodically flooded during times of high water discharges of the river. Flooding of the diked part (in general once or twice a year) occurs between November and May. Once the water transgresses the summer dike, the entire floodplain is inundated within two or three days, except for two areas with somewhat higher elevation, housing remnants of brick factories, two smaller areas of just a few square metres, and the winter dike (Fig. 1a). Within this short time, the water in the floodplain raises, to more than two metres above ground level at most locations. Water mainly leaves the floodplain by seepage towards the river channel, which means that inundations last much longer than the high water discharge period itself. Once inundated, it usually takes several weeks before the floodplain is dried up again; inundations of two or three months are not unusual.

The ADW floodplain was classified into four zones based on the distance to non-flooded areas (Fig. 1a) as follows: (a) non-flooded areas, (b) 0–30 m from non-flooded areas, (c) 30–120 m from non-flooded areas and (d) more than 120 m from non-flooded areas, this being the largest area. The distances were chosen such that similar numbers of monitoring sites were present in each zone.

## Material and methods

### Flooding patterns during 2001–2002

Investigations were carried out during the period between two successive flooding events, one in March 2001 and one in February 2002. The flooding of ADW in the spring of 2001 started on 16 March, and the first inundated areas started to dry up on 6 April. The first metres adjoining the non-flooded areas had dried up by 18 April, while the entire floodplain had fallen dry on 5 May. In the winter of 2002, the water level in the river reached the summer dike level on 29 January, and a second time on 15 February. This caused an inundation of about 65% of the floodplain, followed by a complete flooding on 24 February.

### Vegetation monitoring and live trapping of small mammals

A total of 40 plots (10 × 5 m) were selected, reflecting the wide range of vegetation structures present at various distances from non-flooded areas. These plots were used to monitor vegetation developments, using the method developed by Braun-Blanquet *et al.* (1932) to describe plant species composition and vegetation cover and height.

Four live trap sessions were held during May, July, October and December to monitor small mammal distribution patterns in ADW. Recorded small mammal densities are often derived from trapping studies (using pitfalls, live traps or snap traps) and are based on estimated trapping ranges, which depend on the animals' action diameters, daily movement distances or home ranges. Measuring home range sizes or animal movements is most accurately achieved using radio tracking, beta lights or fluorescent powders, but such studies commonly include a limited number of individuals, and results can be influenced by the observation technique (Boyce and Boyce 1988a, Jorgensen 2002). Trapping studies are usually executed in trapping lines or grids. The advantage of grids is that fewer calculations and assumptions are necessary to calculate densities of small mammals. A disadvantage of this approach is, however, that fewer trapping localities can be examined, as grids require more traps and effort per locality. Since we wanted to study the entire floodplain, and include as many relevant structures as possible at various distances from the elevated areas, we decided to use traps in lines, taking the disadvantages of a less accurate estimation of real densities for granted. Trap lines consisting of 10 Longworth live traps spaced at 5 m intervals were installed through each of the 40 plots and checked every 4 hours for 72 hours, after a two-day prebaiting period. The traps were baited with apple, carrot and tinned meat, and stuffed with tissue paper and hay. Trapped animals were individually marked by means of fur clipping, so they could be recognized at recapture (Gurnell and Flowerdew 1990), and released.

The research plots were positioned using a GARMIN GPS 12 Personal Navigator, and the coordinates were plotted on a digital aerial photograph of the research area made available by the

Geometric Services of the Directorate-General of Public Works and Water Management. The distances from trap lines to non-flooded areas and the surface areas of the homogeneous vegetation units were estimated using ArcView GIS for Windows (version 3.1).

### Regression analyses

To identify the habitat preferences of small mammal species, the small mammal numbers were related to environmental variables using the Canoco for Windows package (version 4) (Ter Braak and Smilauer 1998). As the trapping numbers appeared to be very low in spring, the data of the monitoring session in May were not included. Since distances to non-flooded areas, recolonisation rates and connectivity are assumed to be major factors in explaining the small mammal distribution patterns in floodplains, only the non-flooded parts and areas situated within 30 m of non-flooded parts were included in this analysis. The number of combinations of environmental parameters with trapping results equals 42 (viz 14 monitoring sites  $\times$  3 monitoring moments). Van Apeldoorn *et al.* (1992) studied *Clethrionomys glareolus* (Schreber, 1780) and found that in areas where food is not the limiting factor, habitat suitability for small mammal species is mainly determined by structure variables, rather than by the species composition of the vegetation. We also focused our analysis especially on vegetation structure or plant species groups representing a particular structure, to make interpretation of the trapping results for the total floodplain possible. The environmental parameters incorporated were vegetation cover (%), vegetation height (cm), management (pastures; habitat creation areas; waste land; other (paths and roads)), shape of vegetation unit (rectangular shaped; line shaped; other (patchy)), vegetation type (stinging nettle; blackberry; blackberry and stinging nettle; rough herbaceous vegetation; shrubs; other (grass dominated), soil humidity (dry soil; humid soil; marshy land; other (water)), mowing regime (mowing land; other (unmowed)), grazing regime (grazing land; other (ungrazed)), positioning related to inundation (inland areas, periodically flooded areas, other (high water free areas)), soil texture (sandy soil; loamy soil; clayey soil; other (hard substrate)). Also the trapping period (week number of the year) was included in the analyses as a measure for seasonality and available time for population development. The classes mentioned as 'other' were not separately taken into the analyses, to minimize co-linearity. When a species is negatively related to the incorporated classes of an environmental variable this means that the species is especially related to the class 'other'. As the gradient length for the dataset was found to be smaller than three (by means of a Detrended Correspondence Analysis (DCA)), a Redundancy Analysis (RDA) was conducted (ordination of small mammal species with an optimal environmental basis). The data were log-transformed before analysis to prevent that a few high values influence the ordination, as species abundances often display a highly skewed distribution. As  $\log(0)$  is undefined we used the transformation model  $Y' = \log(Y+1)$  (Ter Braak and Smilauer 1998).

### Calculation of densities

The ADW was classified in 21 easy to observe homogeneous vegetation units based on those environmental variables incorporated in the RDA. The 21 structure classes are referred to below as small mammal ecotopes (Fig. 1b). The presence of species in the trap lines within small mammal ecotopes on elevated areas and in the 0–30 metres zone was decisive for our attempts to verify the hypothesis of suitability of the ecotopes. If a species was present during each trapping period after the first observation in a trap line, the trap line was assumed to be in a suitable ecotope. If it was only occasionally present, the trap line was assumed to be in a marginal habitat. If a species was only present in a trap line located on an elevated part in December (the final trapping session), while there were neighbouring ecotopes that were assumed to be suitable, the trap line was assumed to be in a marginal habitat. For those classes in which no trap lines were present, the most important environment variables as determined from the RDA plot were decisive for the suitability of that small mammal ecotope class. We verified our expectations by observations in the field (spoor inventory; including burrowing activities and feeding trails).

The numbers of each species observed at the 40 monitoring sites were converted into average numbers per standard trap line per distance zone (consisting of a total of 30 traps, with 10 traps in each of the three suitability (suitable, marginal, unsuitable) classes; 72 hours of trapping, checking

every 4 hours). These values are referred to below as the relative densities per distance zone. However, these relative densities are not completely independent of the suitability of the available habitats, since relative densities are influenced not only by distances but also by connectivity (the quality of the intervening habitats).

For comparison of the density development between zones, the species-dependent trapping range of a trap line must be considered, for which it is necessary to know the home range size. The general definition of home range in small mammal studies is 'the area traversed by the individual in its normal activities of food gathering, mating and caring for young' (Kikkawa 1964). This means that it can be assumed that an animal will encounter an unoccupied trap in its home range within the three trapping days. Our own observations showed that after a three-day trapping period, the number of newly trapped individuals was approaching zero. A weakness of the method is the fact that the trapping efficiency for some trap-shy individuals may be reduced, even though their home range overlap the trap line. There will also be individuals living at larger distances from the trap line that occasionally sally outside their home ranges and encounter an unoccupied trap. Also dispersing individuals passing by can be included in the trap numbers. This is inherent to the use of live traps (even when they are positioned in grids) but deliver some uncertainty to the density estimations. However, it is expected that this uncertainty is comparable for the various monitoring sites. A wide range of species-specific mean home range sizes has been recorded in West- and North-European studies, as is shown in the Appendix. Besides the method of sampling and calculating, the home range size depends on factors like habitat quality, developmental stage of individual animals, season, population density and geographical region (Randolph 1977, Pusenius and Schmidt 2002).

The calculated home range size also depends on the method of calculation (Gurnell and Flowerdew 1990). The species-dependent trapping ranges we used were calculated from the mean home range sizes derived from the literature. A circular home range shape was assumed, although also elliptic shapes (Andrzejewski and Babińska-Werka 1986) and elongated shapes with preferred directions have been suggested (Randolph 1977). Elliptic or linear home ranges might have been more realistic for the linear structures in the study area, especially for territorial species, but the assumption of circular home ranges seems reasonable for most biotopes. Possible overestimations or underestimations of densities were expected to be similar in the various zones of the area, justifying comparison of these zones.

As the ecological niche of *Microtus agrestis* (Linnaeus, 1761) in England and Scandinavia is similar to that of *Microtus arvalis* (Pallas, 1778) in other West-European countries (Myllymäki 1977b), studies of the former were used to estimate the mean home range size of *M. arvalis* at 400 m<sup>2</sup> (Table 1). The smallest mean home range size is that of *Crocidura russula* (Hermann, 1780), measuring 125 m<sup>2</sup>, while the largest is that of *Apodemus sylvaticus* (Linnaeus, 1758), at 2500 m<sup>2</sup>. This means that the trapping range equalled  $50d + \pi(d/2)^2$  square metres (Fig. 2), in which  $d$  is the action diameter of the expected mean circular home ranges in metres. The suggested trap range of the trap line was largest for *A. sylvaticus* (5320 m<sup>2</sup>) and smallest for *C. russula* (760 m<sup>2</sup>). Thus, equal relative densities of these two species would mean that the real densities would be about 7 times

Table 1. Action diameters and home range sizes of the various species as estimated from literature data (Appendix).

Species	Home range (m <sup>2</sup> )	Action diameter (m)	Trap range of trap line (m <sup>2</sup> )
Common vole <i>Microtus arvalis</i>	400	22.6	1530
Bank vole <i>Clethrionomys glareolus</i>	1000	35.7	2780
Common shrew <i>Sorex araneus</i>	600	27.6	1980
White-toothed shrew <i>Crocidura russula</i>	125	12.6	760
Harvest mouse <i>Micromys minutus</i>	400	22.6	1530
Wood mouse <i>Apodemus sylvaticus</i>	2500	56.4	5320



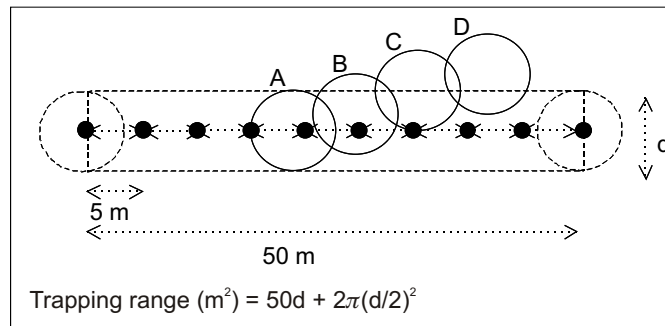


Fig. 2. Calculation of the trapping range. A trap line was 50 m long and consisted of 10 traps at 5 m intervals.  $d$  – diameter of a circular home range. The species-specific trapping range is the area lying within a distance of half a diameter from the trap line, assuming circular home ranges. All individuals for which the centres of their home range lie within a distance of half a diameter from the trap line will encounter a trap (A and B). Although these individuals can forage outside this expected trapping range (B), this is compensated for by the fact that other individuals can forage within the trapping range without encountering a trap (D).

higher for *C. russula* than for *A. sylvaticus*. The trapping range and the available surface area of each habitat suitability class allowed us to estimate the total number of individuals in the floodplain for each species. Calculated total numbers divided by the total surface area of each zone (Fig. 1a) allowed us to compare species densities between zones.

## Results

### Species diversity and habitat suitability

The classification of the ADW floodplain into small mammal ecotopes (Fig. 1b) based on the most important environmental variables as shown in Fig. 3, shows that the southern and south-western parts of the floodplain were characterised by large rectangular homogeneous units. These rectangular homogeneous units are bordered by linear structures like verges and ditches, which is typical for agricultural landscapes. The small mammal ecotopes in the eastern and northwestern parts showed a patchier pattern, which is typical for habitat rehabilitation areas. The patchiness of this area has become more obvious since habitat rehabilitation preparations started a few years ago, and is being promoted by extensive grazing by cattle or horses.

The trapping program resulted in a total 572 captures of 271 individuals representing seven species [*M. arvalis*, *M. agrestis*, *C. glareolus*, *Sorex araneus* (Linnaeus, 1758), *C. russula*, *Micromys minutus* (Pallas, 1771) and *A. sylvaticus*]. During the whole monitoring, 11 animals died in a trap. As only 4 individuals of *M. agrestis* were captured during the research period, this species was excluded from the analyses. The numbers of species trapped during July, October and December related to environmental parameters in a Redundancy Analysis (RDA)

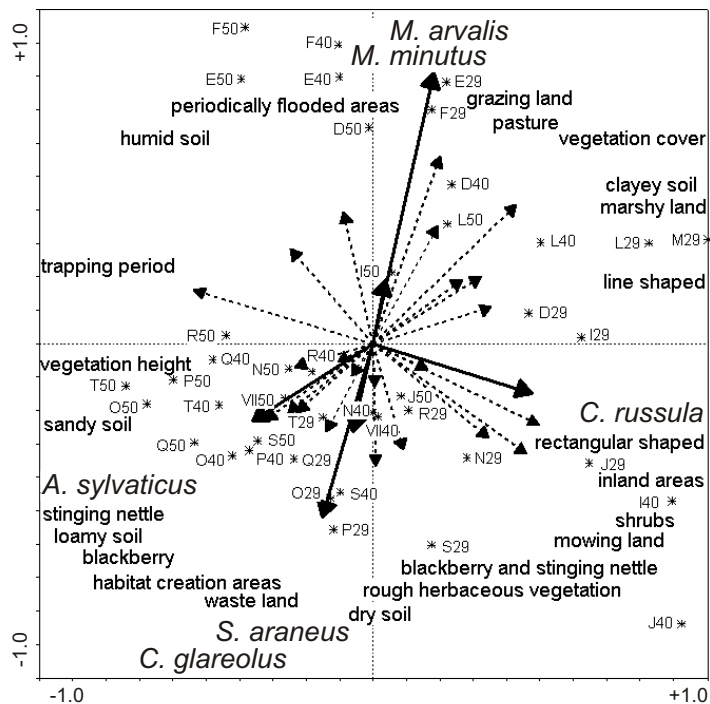


Fig. 3. Redundancy Analyses (RDA) of trapping results of small mammal species related to environmental variables. The plot shows the results of the analysis for the July, October and December monitoring data from the non-flooded areas and the areas located at 0–30 m from non-flooded areas. The ordination with an optimal environmental basis is shown. Ordination axes are aggregates of environmental variables that best explain the species data. The length of a species vector corresponds to the strength of regression to the environmental variables. The positioning of the individual monitoring sites at the three monitoring moments are shown as well (the letter indicates the monitoring site, the number shows the monitoring date in weeks after the drying up of the floodplain). The monitoring sites are described by the following environmental variables: vegetation cover (%), vegetation height (cm), trapping period (week number of the year) management (pastures; habitat creation areas; waste land; other (paths and roads)), shape of vegetation unit (rectangular shaped; line shaped; other (patchy)), vegetation type (stinging nettle; blackberry; blackberry and stinging nettle; rough herbaceous vegetation; shrubs; other (grass dominated)), soil humidity (dry soil; humid soil; marshy land; other (water)), mowing regime (mowing land; other (unmowed)), grazing regime (grazing land; other (ungrazed)), positioning related to inundation (inland areas, periodically flooded areas, other (high water free areas)), soil texture (sandy soil; loamy soil; clayey soil; other (hard substrate)).

are shown in Fig. 3. The distribution patterns of the most commonly trapped species, *M. arvalis* and *C. glareolus*, were best explained by the variables measured. As had also been found in other studies, *M. arvalis* was associated with grazed grasslands with a high vegetation cover. The pastures at ADW seemed to provide more suitable habitats than the meadows and grasslands of the habitat creation areas. The distribution patterns of *C. glareolus* were more closely related



to vegetation height than to coverage. This species tended to prefer vegetation dominated by blackberry *Rubus caesius* and stinging nettle *Urtica dioica*, as this ensures a certain vegetation height and probably opportunities for climbing. These vegetation types are often described as wasteland. *C. glareolus* was not found in pastures or large rectangular shaped homogeneous vegetation units. The relations between the distribution pattern and the ecological parameters were less significant for *S. araneus*, and *A. sylvaticus*, due to the smaller numbers trapped. These species showed the strongest positive regression with rough vegetation types like those dominated by *U. dioica* alone, by *U. dioica* and *R. caesius*, and wasteland. Both species appeared to be more common in taller vegetation, and they seemed to have a preference for dry substrates. The two species seemed to avoid pastures and natural grasslands. The opposite pattern was seen for *M. minutus*. Trapping period, which included only three monitoring moments, did not show a positive relation with one of the species, indicating that other factors (seasonality) did already reduce the increase of the populations before a new flooding event. No species seemed to be specifically linked to the habitat restoration areas. *C. russula* was found to be especially related to shrubs and line shaped structures along mowing land.

Table 2 shows the habitat suitability of the ecotope classes distinguished at ADW, based on the trapping results. Although buildings can provide good habitats for several species, they were not taken into account. Many small mammals were found especially in ungrazed rough herbaceous vegetation, which provided a suitable habitat for five of the six species, and represented a marginal biotope for *A. sylvaticus*. Large parts of the floodplain, viz those with sparse herbaceous vegetation on sand, bare sand, maize fields and hard substrates, did

Table 2. Suitability of ecotope classes for the various small mammal species. The distribution of small mammal ecotopes is shown in Fig. 1a. 1 – rough herbaceous vegetation, ungrazed; 2 – rough herbaceous vegetation, grazed; 3 – low herbaceous vegetation; 4 – rough herbaceous vegetation on sand; 5 – sparse herbaceous vegetation on sand; 6 – bare sand; 7 – softwood forest or shrubs with herbaceous undergrowth; 8 – softwood forest or shrubs with sparse undergrowth; 9 – rough vegetation of blackberry and stinging nettle; 10 – rough vegetation, predominantly blackberry; 11 – rough vegetation, predominantly stinging nettle; 12 – rough vegetation, predominantly thistle; 13 – grassy vegetation, ungrazed and unmown; 14 – grassy vegetation, extensively grazed; 15 – grassy vegetation, mown or trodden; 16 – pasture (mowing land); 17 – pasture (grazing land); 18 – maize field; 19 – hard substrate; 20 – buildings, not included and 21 – water, not included.

Species	Suitable classes	Marginal classes	Unsuitable classes
<i>Microtus arvalis</i>	1, 2, 13	3, 14, 15, 16, 17	4, 5, 6, 7, 8, 9, 10, 11, 12, 18, 19
<i>Clethrionomys glareolus</i>	1, 9	7, 10	2, 3, 4, 5, 6, 8, 11, 12, 13, 14, 15, 16, 17, 18, 19
<i>Sorex araneus</i>	1	2, 4, 7, 9, 10	3, 5, 6, 8, 11, 12, 13, 14, 15, 16, 17, 18, 19
<i>Crocidura russula</i>	1, 2, 14	9, 13, 15	3, 4, 5, 6, 7, 8, 10, 11, 12, 16, 17, 18, 19
<i>Micromys minutus</i>	1, 4	2, 9, 10, 13	3, 5, 6, 7, 8, 11, 12, 14, 15, 16, 17, 18, 19
<i>Apodemus sylvaticus</i>	8, 9, 10	1, 2, 7, 11, 12	3, 4, 5, 6, 13, 14, 15, 16, 17, 18, 19

not harbour any small mammals at all. These unsuitable biotopes form potential (partial) barriers to recolonisation, especially if they were large rectangular homogeneous units.

**Small mammal densities**

Trapping numbers in May appeared to be very low. Irrespective of habitat quality, relative densities of *M. arvalis* showed an increase in all distance zones from May till October, followed by a decrease at the start of winter (Fig. 4). Relative densities were highest in the 0–30 m zone. Unlike those of *M. arvalis*, the relative densities of *C. glareolus* were fairly stable throughout the year for the

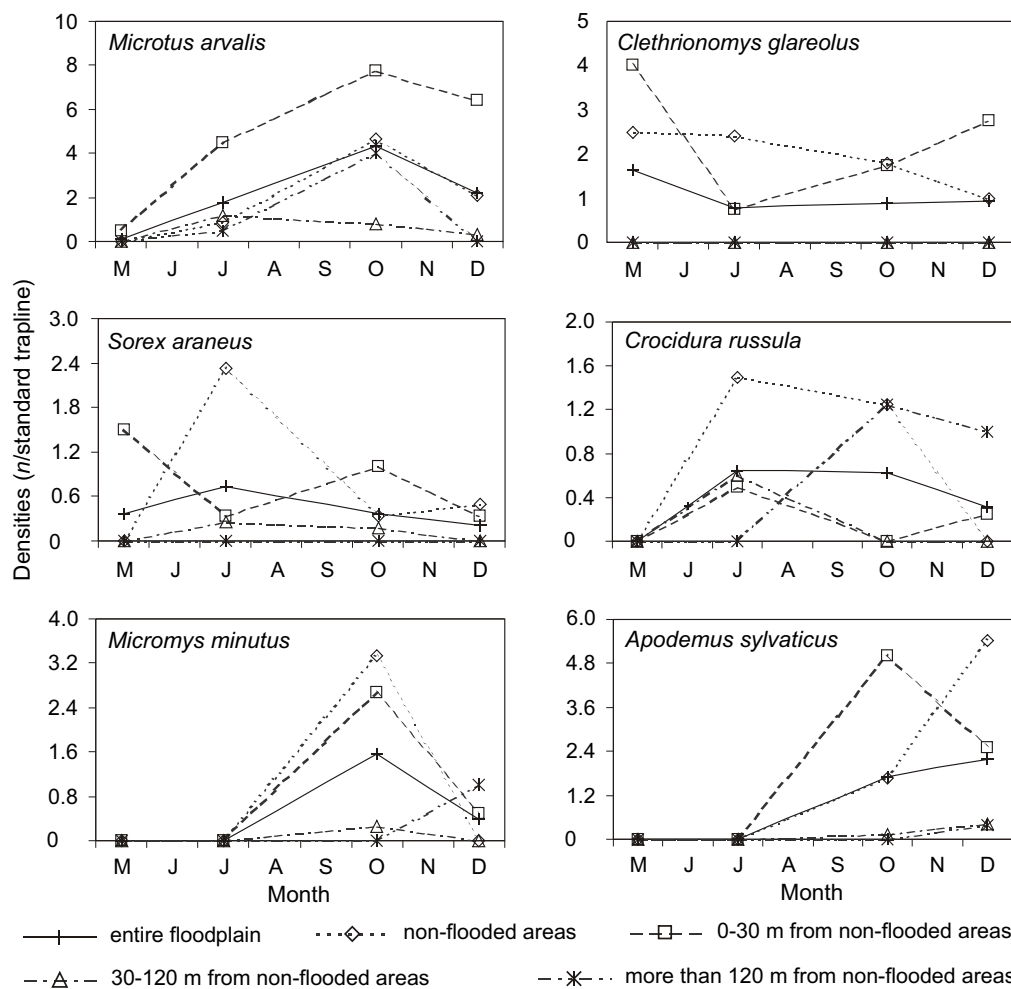


Fig. 4. Graphs showing estimated relative densities throughout the year in each distance zone in the ADW floodplain for the various species.

whole floodplain. No individuals of *C. glareolus* were observed in areas situated more than 30 m from non-flooded parts. *S. araneus* showed a slight tendency to increase its relative densities from spring to summer, followed by a decrease, but the densities seem to be low. No individuals of this species were observed at more than 120 m from non-flooded parts. *C. russula* also showed relatively low densities throughout the year, with an increase from almost zero in spring to peak densities from summer to autumn (depending on the distance from non-flooded parts), followed by a decrease at the start of winter. This species was found all over the floodplain at the end of the year. *M. minutus* and *A. sylvaticus* were both not trapped until autumn. The relative densities of *A. sylvaticus* in the total floodplain were still increasing towards winter, when *M. minutus* densities were

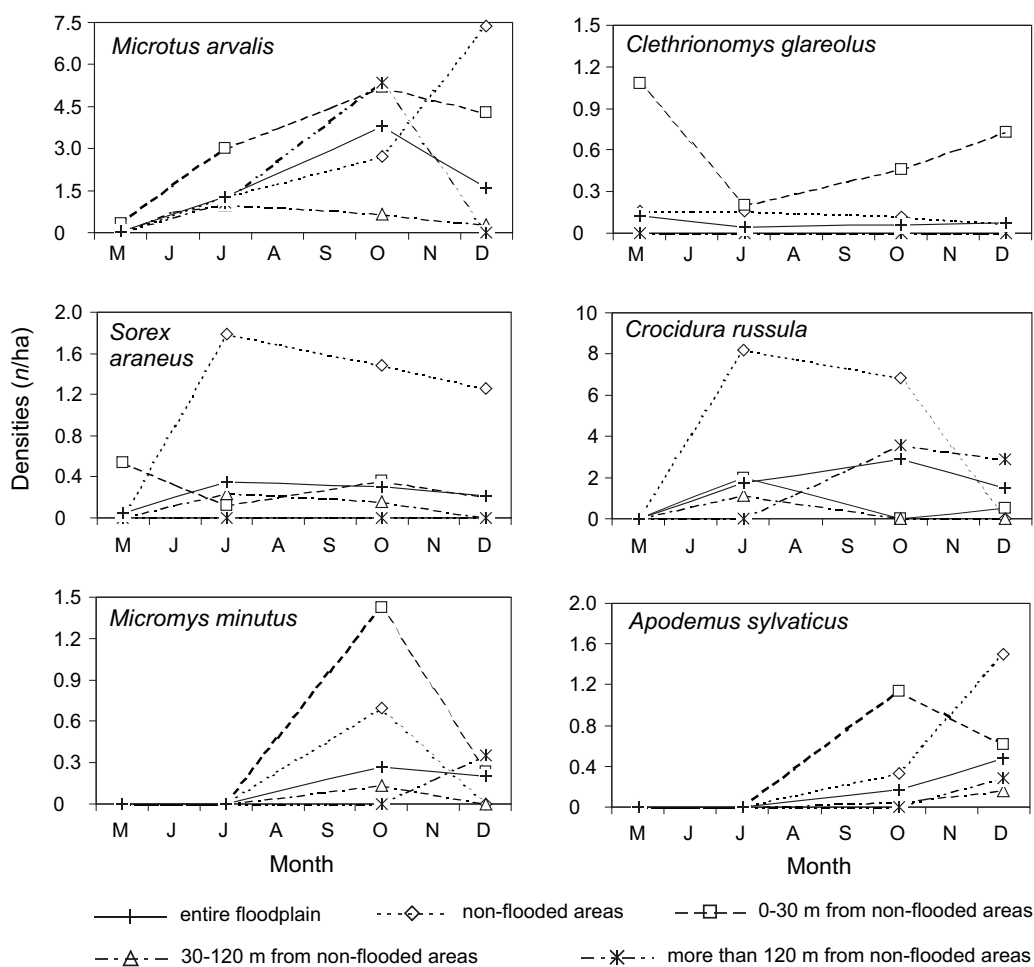


Fig. 5. Estimated population development in densities per distance zone in the ADW floodplain.

decreasing, except for the areas located at the greatest distance from non-flooded parts. Both species were present throughout the floodplain in December.

Calculated peak autumn densities of *M. arvalis* of about 4 individuals per hectare were found in the entire ADW floodplain, but densities in particular zones sometimes rose to more than 7 individuals per hectare by December (Fig. 5). The densities of *C. glareolus* were highest in the zone located 0–30 m from the non-flooded areas, where densities of more than 0.7 individuals per hectare were found in May and December. Densities of *C. glareolus* in the non-flooded parts remained relatively low. Only in the non-flooded areas were *S. araneus* densities higher than 1 per hectare. The rest of the floodplain harboured fairly constant numbers of between 0 and 0.5 individuals per hectare. The densities of *C. russula* were estimated to peak at about 8 individuals per hectare in July in the non-flooded parts. *M. minutus* was only observed in October and December, showing a clear dispersal pattern from non-flooded and adjoining parts towards the more distant areas at the end of the year, but estimated total densities were again low. *A. sylvaticus* was also observed only at the end of the year, showing an increase in total densities in December.

## Discussion

### Habitat characteristics

Important habitat characteristics for the presence of small mammal species are found to be structure-related parameters, instead of plant species composition (Van Apeldoorn *et al.* 1992). We found that the presence of *C. glareolus* was related to wasteland, often with tall vegetation types. Such biotopes probably provide sufficient shelter and climbing opportunities (Geuse *et al.* 1985). Stinging nettle or the combination of blackberry and stinging nettle dominated this vegetation. *M. arvalis* is associated with herbaceous grasslands with dense vegetation cover, probably providing adequate shelter, which was more commonly present in the periodically flooded parts of the floodplain. Like *M. arvalis*, *M. minutus* also seemed to be more closely associated with the agricultural parts of the area, while the other species were more abundant in rough vegetation, not present in large connected areas, but especially found in smaller patches and wasteland areas.

### Impact of flooding

A relation between the abundance of certain small mammal species and the trapping period, as has been observed in several other studies (Erlinge *et al.* 1983, Crespin *et al.* 2002) was not found, due to the low number of monitoring moments included in the analyses (Fig. 3). Reproduction of small mammals generally starts in spring or early summer, leading to an increase in numbers and densities. Peak densities are normally reached in autumn, after which a decrease in numbers can

be observed, as reproduction stops, but predation and other mortality continue (Churchfield 1980, Hansson 1997). This general pattern depends on predator presence, food availability and climatic factors, which means that winter breeding or peak densities in spring may be found under particular conditions (Boyce and Boyce 1988b, Hanski *et al.* 2001). However, we did not find that the presence of species was negatively related to the periodically flooded areas, which means that the impact of flooding is not so severe that small mammals do not return to these areas. Recolonisation of the periodically flooded parts was indeed observed.

Trapping numbers in May appeared to be extremely low. This indicates that after floods, the numbers in flooded parts are reduced to zero or almost zero for all species. It is known that small mammals in lower parts of the floodplain run a great risk of drowning (Andersen *et al.* 2000). Even if they reach non-flooded areas, mortality remains high, due to hypothermia (Pachinger and Haferkorn 1998), stress and exhaustion or predation. The predation risk in such a new environment will be high just after arrival, as the environment is unfamiliar and often unsuitable, and several predators (eg, crows, herons and gulls) are waiting for the arrival of this easy to catch prey. Flooding is most common during winter, increasing mortality due to low temperatures. Recolonisation of the largest area of the floodplain must occur from the small populations surviving in refugia on the elevated parts.

As the populations grow, the animals will disperse over the non-populated parts. The moment at which this dispersal starts differs among species. When flooding occurs in spring, the increase in small mammal numbers may be delayed due to a shortage of suitable habitats. In addition, food availability, for both herbivorous and insectivorous species, will also be influenced by the flooding event.

If the influence of floods on small mammal distribution is only temporary, relative densities, which are supposed to be independent of habitat quality as this is standardised, might be expected to be similar in the various zones shortly after inundation. Since relative densities, except for *M. minutus* and *C. russula*, were lower in areas more than 30 m from the recolonisation source populations (Fig. 4), this means either that recolonisation through suitable habitats is a slow process, or that these areas are less accessible due to partial or temporal recolonisation barriers. This indicates that the floodplain was not completely recolonised over a period of 8 months between the two successive floods. However, just after the initial flood has subsided, higher relative densities of *M. arvalis*, *C. glareolus* and *S. araneus* were observed in the zone between 0 and 30 m from the non-flooded areas than on the elevated parts. This may have been the result of differences in food availability and quality. The presence of young leaves emerging after inundation could have been important for the herbivorous vole species. The insectivorous *S. araneus* is probably especially attracted by the great abundance of macro-invertebrates in the debris at the flood mark, and by the presence after flooding of relative inactive earthworms (Zorn *et al.* 2005), which are their main

food (Rudge 1968, Pernetta 1976). *C. glareolus* was in ADW never observed at distances of more than 30 m from the non-flooded areas.

The trapping results may not directly reflect their densities, especially for those species for which the trappability depends on the season. We assume that the numbers of *S. araneus* recorded at ADW are especially underestimated in May, as this species shows reduced surface activity in winter and early spring (Churchfield 1980). The trappability of *M. minutus* was probably also reduced until autumn. This species is known to forage especially in the aboveground vegetation, and will only be trapped when vegetation is falling over, and seeds, their preferred food items, have dropped onto the ground. Failure to trap a species does not mean that this species is absent, but may also reflect very low densities. Like *M. minutus*, *C. russula* was not trapped in May. This was probably because *C. russula* is known to hibernate in buildings (Lange *et al.* 1994), where we did not trap. The densities of *A. sylvaticus* appeared to be low until autumn, which has been found in other studies as well (Montgomery 1989), and populations were still growing in December, especially on the elevated parts and their surroundings, showing the recolonisation source of the population. Peak densities in winter and winter breeding have been recorded for this species as well (Southern 1965, Smyth 1966).

#### Habitat suitability

For all species, suitable habitats seemed to cover only small areas within the ADW floodplain. As unsuitable ecotopes can be potential partial or temporal barriers to recolonisation, the present vegetation structures may impact the recolonisation process. However, linear biotopes suitable for small mammals can enhance connectivity in the landscape by providing corridors, and patchiness can provide stepping-stones. It is only for the Microtidae, in this case especially *M. arvalis*, that large parts of the ADW floodplain seem to function at least as marginal habitats, as the species is also found in the low grassland-related ecotopes (Myllymäki 1977b). An exception is *A. sylvaticus*, which can be found in the ecotope types with little coverage or undergrowth (Geuse *et al.* 1985). Other species are associated with denser and rougher vegetation. These species either need a certain amount of coverage (*C. russula* and *M. minutus*) or have a need for climbing opportunities (*C. glareolus*) or rough vegetation (*C. glareolus* and *S. araneus*) (Geuse *et al.* 1985; Van Apeldoorn *et al.* 1992). These scarce ecotopes were present only in a patchy pattern of small pieces in the habitat restoration parts of our area, predominantly along ditches and roadside verges, as well as along the edges of pastures in the agricultural part of the floodplain.

Except in December, the densities of *M. arvalis* were lower on the elevated non-flooded parts than in the lower parts (Fig. 5). This indicates that the suitable habitat for this species, that is various types of grassy vegetation, was more abundant in the lower parts. Other species, especially *S. araneus* and *C. russula*, showed the opposite pattern. The densities of these shrews were highest on the



non-flooded parts, indicating that more suitable habitat (rough herbaceous vegetation types) was present there. According to the species densities graph, the suitable habitat for *C. glareolus*, which is dominated by blackberry and stinging nettle, was more common in the 0–30 m zone than on the elevated parts.

#### Small mammal densities and their implications

The occurrence, and especially the densities, of small mammals are season- and habitat-dependent, and also vary per geographical region. Pristine and non-regulated rivers have vast flooding zones where water levels in flooding zones do not rise that much as water levels in floodplains of embanked rivers during floods. This because the embanked floodplains are often narrow and sometimes even excavated, which give them a bath-tube shape. The natural variation in elevations in pristine rivers normally creates a whole range of non-flooded biotopes. Water levels rise more gradually, and have lower peaks, leaving fauna more opportunities to escape. It has been shown in an American study that small mammal species do not leave the lower parts of floodplains before a flood (Andersen *et al.* 2000). The small mammal densities recorded in the present study seem to be much lower than those recorded in the literature for inland areas (Appendix). This could be explained by the impact of flooding, the low recolonisation rate, and the poor connectivity, but can also be a result of our trapping methodology, and on home range based calculations of densities. However, much lower densities at distances more than 30 m from the recolonisation sources than on the non-flooded parts are observed in most of the ADW area. This is a strong indication that densities within the area have the potential to be much higher when flooding events are absent. As we did not intensively monitor in grids or use radio-tags to observe the dispersal of individuals, we cannot conclude that species are absent in those areas where we did not trap them. However, it is clear that densities were low in 2001 in large parts of the ADW floodplain.

Frequency, duration and timing of floods are thought to influence recolonisation, due to the impact on small mammal populations, habitat structures and food availability. Therefore it has been suggested that monitoring in different years can provide valuable information. The present study has shown that in the ADW, a semi-natural Dutch floodplain, with a periodical flooding regime, the time between two successive floods seems to be not nearly long enough for recolonisation of the entire floodplain. Although the area is relatively small, resulting in short recolonisation distances of no more than a few hundred metres, densities in the lower parts of the floodplain were always lower than on the elevated parts. We found that the quantity and quality of elevated areas in floodplains and the connectivity of habitat structures were important factors determining the recolonisation process, with quality and connectivity values proving to be species-dependent.

## Conclusions

In spite of small distances between non-flooded and flooded suitable habitats, it took more than 8 months for small mammals to recolonise suitable habitats in an embanked floodplain. Two of the six common species were never observed farther than 120 metres from non-flooded recolonisation sources. Densities of small mammals at more than 30 metres from elevated areas were always lower than those in the non-flooded parts. The recolonisation process appeared to be slow due to the poor habitat connectivity, the limited number of recolonisation sources, and the small number of survivors from which populations must recover. Suitable habitats for the small mammals included especially rough herbaceous vegetation, which was mostly present in small areas of wasteland. Five of the six investigated species (*M. arvalis*, *C. glareolus*, *S. araneus*, *C. russula* and *M. minutus*) were found there frequently. There were no spoor of small mammals observed in large areas with sparse herbaceous vegetation or maize fields. Vegetation structure parameters like coverage and height appear to be decisive for the small mammal composition. Active dispersers like *A. sylvaticus*, *M. minutus* and *C. russula* were observed throughout the floodplain after 8 months, but their densities were lower there than in the elevated areas, or were still increasing, indicating incomplete recolonisation. The recolonisation of the floodplain by *S. araneus* and *C. glareolus* appeared to be hampered, as suitable habitats at larger distances from sources of recolonisation were not inhabited after 8 months. The recolonisation by *M. arvalis*, driven by population expansion into adjoining habitats, was too slow to result in similar densities throughout the Afferdensche en Deestsche Waarden floodplain.

Acknowledgements: We would like to thank S. Finote, M. Oostendorp, M.-J. Verbruggen, C. Doukoure, A. Lequien and S. Tonk for their valuable help during the collection of the field data. Thanks are also due to G. Geerling for his help with the GIS, to E. Schellekens and the Alterra research institute for lending us the live traps, and especially to P. de Bie for his advice on live trapping small mammals. We would also like to thank our colleagues at the Vrije Universiteit Amsterdam (M. Zorn, H. Eijsackers and C. van Gestel) for their comments on the research planning, J. Klerkx for his linguistic comments, the State Forestry Services (SBB) for their permission to do research in the ADW floodplain, and dr D. C. Andersen and two anonymous referees for their useful comments on the manuscript. This research was a part of the NWO-SSEO and NWO-LOICZ programme and is CWE publication nr. 389.

## References

- Agrell J., Erlinge S., Nelson J. and Sandell M. 1992. Body weight and population dynamics: cyclic demography in a noncyclic population of the field vole (*Microtus agrestis*). *Canadian Journal of Zoology* 70: 494–501.
- Alibhai S. K. and Gipps J. H. W. 1985. The population dynamics of bank voles. *Symposia of the Zoological Society of London* 55: 277–313.
- Andersen D. C., Wilson K. R., Miller M. S. and Falck M. 2000. Movement patterns of riparian small mammals during predictable floodplain inundation. *Journal of Mammalogy* 81: 1087–1099.
- Andrzejewski R. and Babińska-Werka J. 1986. Bank vole populations: Are their densities really high and individual home range small? *Acta Theriologica* 31: 409–422.

- Bergstedt B. 1966. Home ranges and movements of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linnaeus) in southern Sweden. *Oikos* 17: 150–157.
- Boyce C. C. K. and Boyce III J. L. 1988a. Population biology of *Microtus arvalis*. II. Natal and breeding dispersal of females. *Journal of Animal Ecology* 57: 723–736.
- Boyce C. C. K. and Boyce III J. L. 1988b. Population biology of *Microtus arvalis*. III. Regulation of numbers and breeding dispersion of females. *Journal of Animal Ecology* 57: 737–754.
- Braun-Blanquet J., Fuller G. D. and Shoemaker Conard H. 1932. Plant sociology; the study of plant communities, 1st ed., McGraw-Hill Book Company, Inc., London: 1–439.
- Bujalska G. 1970. Reproduction stabilizing elements in an island population of *Clethrionomys glareolus* (Schreber 1780). *Acta Theriologica* 15: 381–412.
- Churchfield S. 1980. Population dynamics and the seasonal fluctuations in numbers of the common shrew in Britain. *Acta Theriologica* 25: 415–424.
- Crawley M. C. 1969. Movements and home ranges of *Clethrionomys glareolus* (Schreber) and *Apodemus sylvaticus* L. in North-east England. *Oikos* 20: 310–319.
- Crespin L., Verhagen R., Stenseth N. C., Yoccoz N. G., Prévot-Julliard A.-C. and Lebreton J.-D. 2002. Survival in fluctuating bank vole populations: seasonal and yearly variations. *Oikos* 98: 467–479.
- Dickman C. R. 1975. Estimation of population density in the Common shrew, *Sorex araneus*, from a conifer plantation. *Notes From The Mammal Society* 41: 550–552.
- Erlinge S., Göransson G., Hansson L., Högstedt G., Liberg O., Nilsson I. N., Nilsson T., Von Schantz T. and Sylvén M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* 40: 36–52.
- Favre L., Balloux F., Goudet J. and Perrin N. 1997. Female-biased dispersal in the monogamous mammal *Crocodyrus russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London; Series B* 264: 127–132.
- Geuse P., Bauchau V. and Le Boulengé E. 1985. Distribution and population dynamics of bank voles and wood mice in a patchy woodland habitat in central Belgium. *Acta Zoologica Fennica* 173: 65–68.
- Gliwicz J. 1989. Individuals and populations of the bank vole in optimal, suboptimal and insular habitats. *Journal of Animal Ecology* 58: 237–247.
- Gurnell J. and Flowerdew J. R. 1990. Live trapping small mammals. A practical guide. 2nd Edition. An occasional publication of The Mammal Society: no. 3, London, UK: 1–39.
- Hanski I., Henttonen H., Korpimäki E., Oksanen L. and Turchin P. 2001. Small-rodent dynamics and predation. *Ecology* 82: 1505–1520.
- Hansson L. 1997. Population growth and habitat distribution in cyclic small rodents: to expand or to change? *Oecologia* 112: 345–350.
- Hendriks A. J., Ma W.-C., Brouns J. J., De Ruiter-Dijkman E. M. and Gast R. 1995. Modelling and monitoring organochlorine and heavy metal accumulation in soils, earthworms, and shrews in Rhine-delta floodplains. *Archives of Environmental Contamination and Toxicology* 29: 115–127.
- Jorgensen E. E. 2002. Small mammals: consequences of stochastic data variation for modeling indicators of habitat suitability for a well-studied resource. *Ecological Indicators* 1: 313–321.
- Junk W. J., Bayley P. B. and Sparks R. E. 1989. The flood pulse concept in river-floodplain systems. [In: *Proceedings of the International Large River Symposium*. D. P. Dodge, ed]. *Canadian Special Publication of Fisheries & Aquatic Sciences* 106: 110–127.
- Kikkawa J. 1964. Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *Journal of Animal Ecology* 33: 259–299.
- Kooistra L., Huijbregts M. A. J., Ragas A. M. J., Wehrens R. and Leuven R. S. E. W. 2005. Spatial variability and uncertainty in ecological risk assessment: a case study on the potential risk of cadmium for the little owl in a Dutch river floodplain. *Environmental Science & Technology* 39: 2177–2187.
- Korn H. 1986. Changes in home range size during growth and maturation of the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*). *Oecologia* 69: 623–628.

- Křištofik J. 1999. Small mammals in floodplain forests. *Folia Zoologica* 48: 173–184.
- Lange R., Twisk P., Van Winden A. and Van Diepenbeek A. 1994. [Mammals of Western Europe]. KNNV-uitgeverij, Utrecht, The Netherlands: 1–400. [In Dutch]
- Leuven R. S. E. W., Wijnhoven S., Kooistra L., De Nooij R. J. W. and Huijbregts M. A. J. 2005. Toxicological constraints for rehabilitation of riverine habitats: a case study for metal contamination of floodplain soils along the Rhine. *Archiv für Hydrobiologie Suppl.* 155: 657–676.
- Ma W.-C. and Talmage S. 2001. Insectivora. [In: Ecotoxicology of wild mammals. R. F. Shore and B. A. Rattne, eds]. John Wiley & Sons Ltd: 123–158.
- Montgomery W. I. 1989. Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. *Journal of Animal Ecology* 58: 465–475.
- Myllymäki A. 1977a. Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos* 29: 468–493.
- Myllymäki A. 1977b. Interactions between the field vole *Microtus agrestis* and its microtine competitors in Central-Scandinavian populations. *Oikos* 29: 570–580.
- Nelson J. 1995. Intrasexual competition and spacing behaviour in male field voles, *Microtus agrestis*, under constant female density and spatial distribution. *Oikos* 73: 9–14.
- Pachinger K. and Haferkorn J. 1998. Comparisons of the small mammal communities in floodplain forests at the Danube and Elbe rivers. *Ekológia (Bratislava)* 17: 11–19.
- Pelikán J., Zejda J. and Holišová V. 1974. Standing crop estimates of small mammals in Moravian forests. *Zoologické Listy* 23: 197–216.
- Pernetta J. C. 1976. Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grassland. *Journal of Animal Ecology* 45: 899–912.
- Pusenius J. and Schmidt K. A. 2002. The effects of habitat manipulation on population distribution and foraging behavior in meadow voles. *Oikos* 98: 251–262.
- Randolph S. E. 1977. Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding. *Journal of Animal Ecology* 46: 653–676.
- Rudge M. R. 1968. The food of the common shrew *Sorex araneus* L. (Insectivora: Soricidae) in Britain. *Journal of Animal Ecology* 37: 565–581.
- Smyth M. 1966. Winter breeding in woodland mice, *Apodemus sylvaticus*, and voles, *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford. *Journal of Animal Ecology* 35: 471–485.
- Southern H. N. 1965. Handbook of British Mammals. Mammal Society of the British Isles. Blackwell Scientific Publications, Oxford, UK: 1–465.
- Stelter C., Reich M., Grimm V. and Wissel C. 1997. Modelling persistence in dynamic landscapes: Lessons from a metapopulation of the grasshopper *Bryodemys tuberculata*. *Journal of Animal Ecology* 66: 508–518.
- Szacki J. 1987. Ecological corridor as a factor determining the structure and organization of a bank vole population. *Acta Theriologica* 32: 31–44.
- Tapper S. 1979. The effect of fluctuating vole numbers *Microtus agrestis* on a population of weasels *Mustela nivalis* on farmland. *Journal of Animal Ecology* 48: 603–617.
- Ter Braak C. J. F. and Smilauer P. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Centre for Biometry, Wageningen, The Netherlands.
- Van Apeldoorn R. C., Oostenbrink W. T., Van Winden A. and Van der Zee F. F. 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. *Oikos* 65: 265–274.
- Van der Velde G., Leuven R. S. E. W. and Nagelkerken I. 2004. Types of river ecosystems. [In: Fresh surface water. Encyclopedia of life support systems (EOLSS). J. C. I. Dooge, ed]. Developed under the auspices of the UNESCO, EOLSS Publishers Co. Ltd., Oxford, UK: 1–29, ([www.eolss.net](http://www.eolss.net)).
- Ward J. V., Tockner K., Uehlinger U. and Malard F. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated Rivers: Research & Management* 17: 311–323.

- Wolff J. O. 1998. Behavioural model systems. [In: Landscape ecology of small mammals. G. W. Barrett and J. D. Peles, eds]. Springer: 11–40.
- Wolton R. J. and Flowerdew J. R. 1985. Spatial distribution and movements of woodmice, yellow-necked mice and bankvoles. *Symposium of the Zoological Society of London* 55: 249–275.
- Zandberg B. 1999. [‘Afferdensche en Deestsche Waarden’ floodplain; Plan of arrangement]. Report 99.001. Directorate-General of Public Works and Water Management, Arnhem, The Netherlands. [In Dutch]
- Zejda J. 1976. The small mammal community of a lowland forest. *Acta Scientiarum Naturalium Brno* 10: 1–39.
- Zejda J. 1991. A community of small terrestrial mammals. [In: Floodplain forest ecosystem 1. M. Penka, M. Vyskot, E. Klimo and F. Vašiček, eds]. Elsevier: 357–371.
- Zejda J. and Pelikán J. 1969. Movements and home ranges of some rodents in lowland forests. *Zoologické Listy* 18: 143–162.
- Zorn M. I., Van Gestel C. A. M. and Eijsackers H. 2005. Species-specific earthworm population responses in relation to flooding dynamics in a Dutch floodplain soil. *Pedobiologia* 49: 189–198.

*Received 30 August 2004, accepted 19 May 2005.*

*Associate Editors were Leszek Rychlik and Karol Zub.*

Appendix. Home ranges and densities of small mammals. All data are from West- and North-European studies in environments comparable to floodplain habitats. Symbols indicate where specific data about males (M), females (F) or juveniles (juv) have also been incorporated. Besides general data, specific data on biotopes comparable to those found in the 'Afferdenschche en Deesische Waarden' floodplain have been incorporated when available between brackets, which means data on grassland for *M. arvalis*, *M. agrestis* and *S. araneus*; deciduous and mixed forests for *C. glareolus*, *S. araneus* and *A. sylvaticus*; pine forests for *C. glareolus*; scrubs for *S. araneus*; gardens for *C. russula* and plantations for *A. sylvaticus*. Specific data for summer and winter were also available for *C. glareolus*, *S. araneus* and *A. sylvaticus*.

Species	Recorded mean size of home ranges in m <sup>2</sup> (total recorded range)	Recorded densities (n/ha) (recorded densities specific for floodplains)	References
<i>Microtus arvalis</i> (F, M, juv)	161–1350 (118–1500)	up to >1000 (64.1)	Myllymäki 1977b, Boyce and Boyce 1988b, Lange <i>et al.</i> 1994
<i>Microtus agrestis</i> (F, M)	250–500 (200–700)	8–350	Myllymäki 1977a, b, Tapper 1979, Erlinge <i>et al.</i> 1983, Gurnell and Flowerdew 1990, Agrell <i>et al.</i> 1992, Nelson 1995
<i>Clethrionomys glareolus</i> (F, M)	260–4100 (200–11000)	some–250 (1.7–139)	Kikkawa 1964, Bergstedt 1966, Crawley 1969, Zejda and Pelikan 1969, Bujalska 1970, Pelikán <i>et al.</i> 1974, Zejda 1976, 1991, Alibhai and Gipps 1985, Geuse <i>et al.</i> 1985, Wolton and Flowerdew 1985, Andrzejewski and Babińska- -Werka 1986, Korn 1986, Szacki 1987, Gliwicz 1989, Gurnell and Flowerdew 1990, Lange <i>et al.</i> 1994, Pachinger and Haferkorn 1998, Kristófik 1999
<i>Sorex araneus</i> (F, M)	360–1400 (90–2800)	a few–50 (0–114.4)	Pelikán <i>et al.</i> 1974, Dickman 1975, Churchfield 1980, Gurnell and Flowerdew 1990, Lange <i>et al.</i> 1994, Pachinger and Haferkorn 1998, Kristófik 1999, Ma and Talmage 2001
<i>Crocidura russula</i>	50–200	up to 100	Lange <i>et al.</i> 1994, Favre <i>et al.</i> 1997
<i>Micromys minutus</i>	200–900	up to 250	Lange <i>et al.</i> 1994
<i>Apodemus sylvaticus</i> (F, M)	230–12200 (230–21772)	<1–190 (1.7–19)	Kikkawa 1964, Randolph 1977, Erlinge <i>et al.</i> 1983, Geuse <i>et al.</i> 1985, Montgomery 1989, Gurnell and Flowerdew 1990, Zejda 1991, Lange <i>et al.</i> 1994, Pachinger and Haferkorn 1998, Kristófik 1999