

Microhabitat selection by three small mammal species in oak-elm forest

Peter MIKLÓS¹ and Dávid ŽIAK²

Faculty of Natural Sciences of Comenius University, Department of Zoology, Mlynská dolina B1, 842 15 Bratislava, Slovakia; e-mail: ¹ miklos@fns.uniba.sk, ² ziak@fns.uniba.sk

Received 14 February 2001; Accepted 7 February 2002

A b s t r a c t. Between 1996 and 1998, microhabitat selection by three small mammal species was studied in oak-elm forest using the catch-mark-release (CMR) method. Microhabitat selection by these species was assessed by Discriminant Function Analysis (DFA) and Canonical Correspondence Analysis (CCA). *Apodemus flavicollis* was shown to prefer dense young forest and shrubs, but the presence of dead woody material was also important. In *Microtus arvalis* the data confirmed a negative relationship with stands with higher tree and shrub cover and a preference for open meadows. *Clethrionomys glareolus* was found to prefer non-fragmented tree microhabitats, preferring sites with developed undergrowth and ample hiding places amongst fallen logs and branches. Although *C. glareolus* did not change its microhabitat requirements during the year (spring to autumn), within forest stands it was connected with undergrowth regardless of species composition; this highlights the importance of undergrowth for *C. glareolus*. Seasonal changes in microhabitat selection could not be confirmed unambiguously.

Key words: microhabitat selection, microhabitat preference, seasonality of microhabitat requirements, *Apodemus flavicollis*, *Microtus arvalis*, *Clethrionomys glareolus*, oak-elm forest

Introduction

Analysis of animals' utilisation of their environment is supposed to be one of the fundamental necessities in understanding species' ecologies. Microhabitats represent the space characterised by various factors with value changes within the home range of a single individual (A d l e r 1989 in L i n & S h i r a i s h i 1992). In fact, an individual's home range is defined as the area traversed by the individual during its normal activities of food gathering, mating and caring for young (B u r t 1943). The area used by an individual within a population affects population density, intrapopulation competition, reproductive success, resource partitioning, social organisation, interspecific relationships and other aspects of community and population ecology (B o n d r u p - N i e l s e n 1985). However, environment selection itself is influenced by biotope characteristics, interspecific and intraspecific relationships, and by the particular features of a given individual, which may change throughout the year.

The aim of our work was to study the microhabitat requirements of various small mammal species in oak-elm forest, to describe their most suitable microhabitats, and to find those factors most markedly influencing their presence within certain habitats, thus allowing prediction of community composition.

Study Area

Research was undertaken within the National Nature Reserve Šúr, 12 km north-east of Bratislava. Study sites were situated in the part of the reserve covered with oak-elm forest, with a less dense cover of trees locally having forest-steppe characteristics. According to the composition of the vegetation strata, three study plots were chosen to reflect typical habitats within this forest:

M – predominantly meadow stands with isolated stands of shrubs and trees.

F – relatively homogenous and poorer stands of trees and shrubs, undergrowth being rarely represented, but with frequent fallen logs.

S – meadow stands covering one third of the area, with transition into young tree stands with dense cover through to a very dense shrub stratum, gradually changing to older tree stands with poorer cover.

Material and Methods

The M and F study plots were 1.08 ha each, but S was 0.95 ha. In determining the size of the study areas, quadrat side length was taken as the distance between traps placed in corners of a particular quadrat (Peľíkán 1975). Within individual quadrats a regular network of capture points was established at distances of 13 m. These were arranged in parallel 13 m from each other (M, F 9 × 9, S 9 × 8 trapping points). One wooden Chmela-type live trap was placed at every capture point.

We captured small mammals at quadrats M and F between July 1996 and October 1998, but at quadrat S captures were performed between April 1997 and October 1998. There were six-week intervals between the individual trapping periods and traps were placed for six nights during each period.

The CMR method was used to obtain data on populations of *Apodemus flavicollis* (Melchior, 1834), *Microtus arvalis* (Pallas, 1779) and *Clethrionomys glareolus* (Schreber, 1780). The traps were baited with oat flakes and usually checked twice a day (mornings and evenings). During frosty weather a third night-time trap inspection was undertaken, whilst during hot summer days a third afternoon inspection was added. The trapped mammals were marked individually by toe-clipping. Upon capture the following parameters were noted for each individual animal: capture point co-ordinates, species, individual number, sex, weight, body length, status of external sexual characters. For the purposes of statistical analyses of microhabitat selection the following individual groups were formed:

Residents - individuals captured three or more times. In addition, individuals trapped once or twice during a certain trapping period were considered resident if they had been trapped at the same plot during the previous or subsequent trapping period. These individuals were included in analyses of microhabitat selection.

Transients – individuals captured once or occasionally twice within one plot, but not recorded in the previous or subsequent capture set. Transients were not included in analyses of microhabitat selection because, based on their position within the population, these individuals can occur permanently in microhabitats that are suboptimal for that particular species.

The detailed description of microhabitats was taken from James & Shugart (1970) and Noon (1981) and modified for our purposes. Measurements of horizontal vegetation cover were made once per season. Measurement and assessment of further factors was performed once during the whole research period. Microhabitat characteristics

were measured at each capture point within a circle (radius = 6.5 m) around the trap. The factors measured were: total cover of trees and shrubs, herbs, grass, O-horizon, bryophytes and bare soil, cover of individual trees and shrubs and herb species, number of trunks at various thickness intervals, cover of dead wood at various thickness intervals, sum of living tree trunks, standing and fallen dead trunks, number of tree and herb species, height of herb stratum, and horizontal cover of vegetation. The descriptions of the important environmental variables (along with their abbreviations) are shown in Table 1.

We used Discriminant Function Analysis (DFA) and Canonical Correspondence Analysis (CCA) to evaluate the relationship between the various small mammal species and their habitats. The effects of a particular set of environmental variables on species were analysed using CCA. Species were represented by the number of captures of resident animals. During analysis variables were chosen by the forward selection technique.

In DFA we investigated the differences between preferred and non-preferred capture points. Points were regarded as being preferred if more than the average number of captures per species per capture point were trapped. This average was calculated from points with at least one trapped individual of a particular species. This calculation was important for us, suggesting that these trapping points were most suitable (or preferred) by the particular species (Van Horne 1982). In each analysis combinations of environmental factors were formed whose number did not exceed 10% of the amount of samples, i.e. the number of trapping points (Paul 1990). With the aid of DFA exactness tests (eigenvalue, canonical correlation coefficients, Wilks Lambda test, Chi-square test, degrees of freedom, significance level, posterior probabilities) we obtained final factor combinations by the gradual selection of environmental variables.

By the use of two methods for the statistical evaluation of microhabitat selection, and by comparison of these results, we tried to find potential mistakes occurring through the different affinities of different individuals to traps. Namely, some of the individuals were captured regularly at the same capture point, so it cannot be excluded that some of these could be attracted to the trap – this leading to the overvaluation of certain points. This phenomenon could be reduced by multiple captures of a certain individual at the same point during one trapping period being considered as one record. On the other hand, this would also undervalue the higher suitability of the trapping point for certain species. In addition, we were unable to estimate how much individuals were attracted by live traps (Doughlass 1989).

By the use of these methods we evaluated “general selection of microhabitat” when data from all study plots relating to the 1997 (without the February set) – 1998 research period were entered into the analysis. We also studied (DFA only) whether microhabitat selection changed according to stand structure (selection at each study plot). Selection, preference for particular microhabitats, can differ in different seasons. Selection can be affected by seasonal changes in vegetation (Doughlass et al. 1992), population dynamics, or species social structure. At lower population density values, rodents occupy the most suitable (optimal) areas (Mazurkiewicz & Rajska-Jurgiel 1987). In an analyses to estimate seasonal changes in microhabitat utilisation, species data from 1997 and 1998 were used as follows: spring season – trapping period from March to June, summer time – from July to September, autumn season – October trapping period (the distribution being dependent mainly on changes in vegetation cover). The winter season could not be evaluated due to insufficient data. In these analyses we used the indices of relative horizontal cover obtained in the respective season.

Table 1. List of environmental variables.

Description	Abbreviation
horizontal cover of vegetation in high 0-5 cm	0-5
horizontal cover of vegetation in high 5-10 cm	5-10
horizontal cover of vegetation in high 10-30 cm	10-30
horizontal cover of vegetation in high 30-50 cm	30-50
horizontal cover of vegetation in high 50-100 cm	50-100
horizontal cover of vegetation in high beyond 100 cm	100+
cover of genus <i>Acer</i>	ACER
number of individuals of genus <i>Acer</i> in thickness interval 69-84 cm	AC-F
number of individuals of genus <i>Acer</i> in thickness interval < 8 cm	AC-S
cover of genus <i>Achillea</i>	ACH
cover of genus <i>Alium</i>	ALIUM
cover of species <i>Alliaria petiolata</i>	AP
bare soil	BS
cover of genus <i>Carex</i>	CAREX
cover of genus <i>Centaurea</i>	CENT
cover of dead woody material	DWM
cover of genus <i>Euonymus</i>	EUO
cover of fallen dead trunks	FDT
number of fallen trunks in thickness interval 8-15 cm	FDT-A
number of fallen trunks in thickness interval 15-23 cm	FDT-B
number of fallen trunks in thickness interval 23-38 cm	FDT-C
number of fallen trunks in thickness interval 38-53 cm	FDT-D
number of fallen trunks in thickness interval < 8 cm	FDT-S
cover of genus <i>Fragaria</i>	FRAG
cover of genus <i>Fraxinus</i>	FRAX
number of individuals of genus <i>Fraxinus</i> in thickness interval 15-23 cm	FR-B
number of individuals of genus <i>Fraxinus</i> in thickness interval < 8 cm	FR-S
cover of species <i>Galium aparine</i> in spring	GASPR
cover of genus <i>Geum</i>	GEUM
cover of species <i>Glechoma hederacea</i>	GLE
cover of grass	GRASS
cover of species <i>Galium verum</i>	GV
cover of herbs	HERB
cover of species <i>Ligustrum vulgare</i>	LV
number of individuals of species <i>Ligustrum vulgare</i> in thickness interval < 8 cm	LV-S
cover of genus <i>Malus</i>	MALUS
number of fallen trunks	NRFT
number of herbaceous species	NRHERB
number of standing dead trunks	NRSDT
number of tree and shrub individual's	NRTS
number of tree and shrub genera	NRTSG
cover of O-horizon	OH
cover of species <i>Potentilla heptaphylla</i>	PH
number of individuals of genus <i>Pirus</i> in thickness interval 15-23 cm	PI-B
number of individuals of genus <i>Pirus</i> in thickness interval 38-53 cm	PI-D
number of individuals of genus <i>Pirus</i> in thickness interval 53-69 cm	PI-E
cover of genus <i>Polygonatum</i> in spring	POLSPR
cover of species <i>Potentilla reptans</i>	POR
number of individuals of genus <i>Prunus</i> in thickness interval < 8 cm	PR-S
cover of genus <i>Prunus</i>	PRUN
cover of species <i>Quercus robur</i>	QR
number of individuals of <i>Quercus robur</i> in thickness interval 8-15 cm	QR-A
number of individuals of <i>Quercus robur</i> in thickness interval 38-53 cm	QR-D

Table 1. Continued

Description	Abbreviation
number of individuals of <i>Quercus robur</i> in thickness interval 53-69 cm	QR-E
number of individuals of <i>Quercus robur</i> in thickness interval 69-84 cm	QR-F
number of individuals of <i>Quercus robur</i> in thickness interval < 8 cm	QR-S
cover of species <i>Rhamnus cathartica</i>	RC
number of individuals of genus <i>Rosa</i> in thickness interval < 8 cm	RO-S
cover of genus <i>Rumex</i>	RUMEX
cover of standing dead trunks	SDT
number of standing dead trunks in thickness < 8 cm	SDT-S
cover of genus <i>Stellaria</i>	STELL
cover of genus <i>Tithymalus</i>	TIT
total cover of trees and shrubs	TS
cover of trees and shrubs over 70 cm	TS>70
cover of trees and shrubs under 70 cm	TS<70
number of trees and shrubs in thickness 8-15 cm	TS-A
number of trees and shrubs in thickness 15-23 cm	TS-B
number of trees and shrubs in thickness < 8 cm	TS-S
cover of genus <i>Ulmus</i>	ULMUS
cover of genus <i>Viola</i>	VIOLA

Results

A total of 5,802 captures of 1,555 individuals of three species were recorded. Microhabitat utilisation analyses were performed on data from residents only: 431 individuals of *A. flavicollis* (2,877 captures), 293 individuals of *M. arvalis* (1,388 captures) and 62 individuals of *C. glareolus* (458 captures).

Apodemus flavicollis (Table 2)

The microhabitat preferred by *A. flavicollis* was a place positively associated with an abundance of fallen logs (NRFT) and twigs (FDT-S) in the forest stand (TS) or with dense shrub stands. The shrub stand is described by the variables PRUN and PR-S because the genus *Prunus* was the most frequent component of the dense shrub sections. The forest stand and dense shrub stand are together in young forest successional stages, where there is sporadic occurrence of fallen woody material.

Microtus arvalis (Table 2)

On the basis of a negative relationship of *M. arvalis* with the most important variables (TS, TS>70, OH) it can be concluded that this species prefers places with meadow vegetation and without trees or shrubs. This is in agreement with the positive relationship of *M. arvalis* with the density of the vegetation stand at a height of 50–100 cm (grass stand) and with *Galium verum* (GV) cover, which is typical of meadow communities.

Clethrionomys glareolus (Table 2)

This species lives in places with a larger amount of dead woody material (DWM) and high tree cover (TS>70, TS). Within these places *C. glareolus* prefers microhabitats with frequent fallen logs and dead wood (DWM, SDT, FDT) – typical of older forests. Also, the higher discrimination coefficient for *Fraxinus* cover (FRAX), represented in older forest parts more than in younger stands, may be a result of this preference.

Table 2. Discriminant function analyses of microhabitat preference in *Apodemus flavicollis*, *Microtus arvalis* and *Clethrionomys glareolus* in oak–elm forest, respectively. Explanations: AF – *Apodemus flavicollis*; MA – *Microtus arvalis*; CG – *Clethrionomys glareolus*; Affinity – preference of higher (+) or lower (–) amount of concrete variable; SDFC – standardized discriminant function coefficient; n – absence in the final variable combination of concrete analysis; for description of variable abbreviation see Table 1.

Variable	Affinity	AF		MA		CG	
			SDFC	Affinity	SDFC	Affinity	SDFC
0-5	–		-0,1483		n		n
30-50			n		n	–	0,2900
50-100			n	+	-0,1807		n
ACER	+		-0,1197	–	0,1207	+	0,2155
ALIUM			n	+	-0,2781		n
DWM			n	–	0,2812	+	-0,6070
FDT	+		-0,5582		n	+	0,4482
FDT-B			n		n	+	0,2938
FDT-C			n		n	+	0,3899
FDT-S	+		-0,6525		n		n
FRAG			n	–	0,3343	+	0,2207
FRAX			n		n	+	0,4826
GV			n	+	-0,1435		n
LV-S			n	–	0,1582		n
NRFT	+		1,2807		n		n
NRSDT	+		0,4772		n		n
NRTS			n	–	-0,2965		n
OH	+		0,5419	–	0,6253		n
PR-S	+		-0,6813		n		n
PRUN	+		1,0036		n		n
QR-F			n		n	+	0,2434
QR-S			n		n	+	0,2957
RO-S	+		0,1178		n		n
RUMEX	–		-0,2526	+	-0,1150		n
SDT	+		0,1818		n	+	0,4866
STELL			n		n	+	0,2098
TS	+		-0,5804	–	-1,1029	+	1,0373
TS<70			n		n	+	0,4218
TS>70	+		0,2396	–	1,1129	+	-1,2833
TS-A			n	–	0,2665		n
TS-S	+		0,2986		n		n
ULMUS			n	–	0,0744		n

Results of CCA (Fig. 1)

Describing canonical axes can be realised with the help of the lengths and structures of each variable in an ordination diagram, as well as by correlation coefficients with individual axes (see Table 3). A high correlation with the first axis (horizontal axis) is considered to relate to high tree and shrub cover (TS) with a negative coefficient. Besides that, other variables with notable correlations oriented in a similar direction. For example *Quercus robur* (QR) cover, or the number of tree species (NRTSG) and also the only variable oriented positively – horizontal cover 50–100 cm (50–100) – possess considerable gradients on this axis as well. This axis gradually leads (from left to right) from forest stands to open meadow stands. The variable for the number of fallen logs in C thickness interval (FDT-C), *Quercus robur* (QR) cover, and the cover by herbs of genus *Viola* (VIOLA) correlate positively with the second canonical axis. At the same time, *Ligustrum vulgare* (LV) cover showed a negative correlation. This is connected with a gradient (from top to bottom) from older forest stands

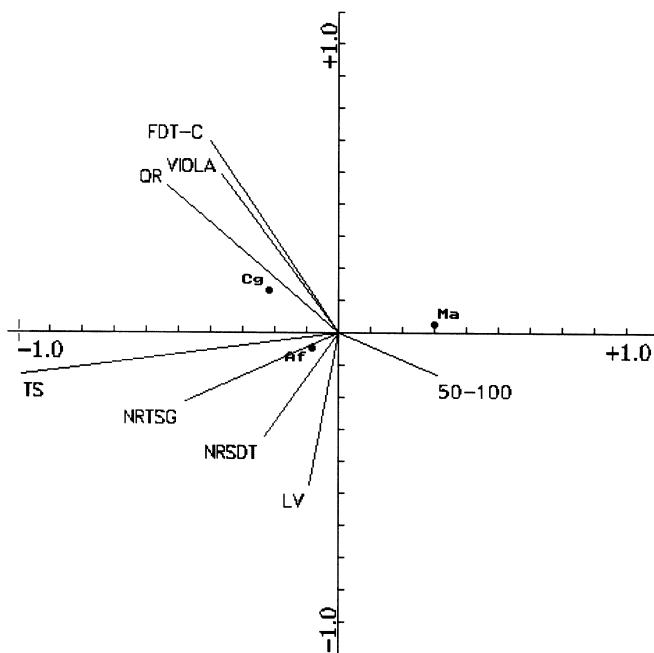


Fig. 1. Ordination diagram of Canonical correspondence analysis. Explanation: Cg – *Clethrionomys glareolus*; Af – *Apodemus flavicollis*; Ma – *Microtus arvalis*; for description of variable abbreviation see Table 1.

with frequent fallen logs and relatively poor undergrowth (which meets the requirements of genus *Viola*) towards dense shrub stands at forest fringes.

Apodemus flavicollis is located relatively near the centre of the ordination diagram, indicating a lower specificity for a certain type of habitat, yet with some preference for tree stands with denser cover; this is shown by the short vector distances for number of tree species (NRTSG) and the sum of standing dead trunks (NRSDT).

Microtus arvalis apparently prefers open vegetation with a higher degree of grass cover and low values of tree cover.

Clethrionomys glareolus markedly prefers forest stands. Here it occurs amongst older forest vegetation with many fallen logs and a certain amount of undergrowth.

Table 3. Correlations between variables and ordination axes in Canonical correspondence analysis; for description of variable abbreviation see Table 1.

variable	ax 1	ax 2	ax 3	ax 4
TS	-0,913	-0,061	-0,016	-0,003
QR	-0,496	0,235	-0,051	0,003
LV	-0,083	-0,224	-0,073	0,055
FDT-C	-0,374	0,301	-0,008	-0,021
NRSDT	-0,233	-0,181	0,191	-0,051
VIOLA	-0,350	0,241	0,035	-0,055
NRTSG	-0,439	-0,100	0,127	0,108
50-100	0,289	-0,067	0,066	0,033

Microhabitat selection in particular study plots

Apodemus flavicollis (Table 4)

Plot M: the preferred microhabitat was perfectly described by the presence of dead woody material (FDT, FDT-D) occurring exclusively within islets of trees (AC-S, EUO).

Plot F: as for the older forest stand habitat, *A. flavicollis* preferred sites with higher amounts of dead woody material (FDT, DWM, SDT) – especially those with more standing dead woody material (NRSDT, SDT-S). The high number of standing dead logs occurred at sites with a shrub stratum (TS-S) and hence in relatively dense tree and shrub vegetation. Variables TS>70 and TS refer to forest stand.

Plot S: *A. flavicollis* markedly preferred sites with high tree and shrub cover (TS, TS>70) and, within such places, microhabitats with higher numbers of trees (trunks, wooden stems), denser tree cover (NRTS, TS-S) and a higher amount of dead woody material (NRSDT). *Apodemus flavicollis* tends to have a negative relationship with grass cover (GRASS). These microhabitats are present in young successional-stage forests with continual overgrowth of meadow stands by shrubs and young trees, but with a poor herb layer.

Table 4. Discriminant function analyses of microhabitat preference in *Apodemus flavicollis* at plot M, F and S, respectively. Explanations: Affinity - preference of higher (+) or lower (-) amount of concrete variable; SDFC - standardized discriminant function coefficient; n – absence in the final variable combination of concrete analysis; for description of variable abbreviation see Table 1.

Variable	Affinity	M	SDFC	F	SDFC	Affinity	S	SDFC
				Affinity				
100+	+	0,2263			n		n	
AC-S	+	1,1265			n		n	
DWM		n		+	-0,1734		n	
EUO	+	-1,0693			n		n	
FDT	+	2,7548		+	0,6011		n	
FDT-D	+	-1,6210			n		n	
GRASS		n			n	–	-1,2019	
HERB		n			n	–	0,5056	
NRSDT		n		+	-1,3172	+	-1,0585	
NRTS		n			n	+	-1,2300	
SDT		n		+	0,5885		n	
SDT-S	+	0,6202		+	1,5621		n	
TS	+	-0,5261		+	0,9923	+	3,5189	
TS>70	+	0,8371		+	-1,0500	+	-3,2331	
TS-S		n		+	0,5869	+	0,5657	

Microtus arvalis

The results of microhabitat selection by *M. arvalis* at plots M and S were very similar to those for all study plots together (general selection of microhabitat, Table 2), i.e. there was a negative relationship with stands with higher tree and shrub cover, including isolated areas in plot M. In plot F *M. arvalis* was captured only rarely during the October trapping period, and these captures were never of resident animals.

Clethrionomys glareolus (Table 5)

Plot M: *C. glareolus* was hardly ever captured at this site, and then only near continuous forest stands.

Plot F: as in forest stands of middle or older age, *C. glareolus* preferred sites with lower tree cover (NRTS, AC-S), more developed undergrowth (AP) and the presence of fallen dead woody material (FDT-C).

Plot S: *C. glareolus* preferred sites with forest stands (TS, TS>70) of the older age categories (QR, TS-S, FDT-C) and with larger amount of fallen dead woody material (FDT-C, FDT, DWM).

Seasonal changes in microhabitat preference

Unlike *C. glareolus* (Table 6) we did not find any seasonal changes in requirements in *A. flavicollis* or *M. arvalis* during the study period. In each part of the year *C. glareolus* preferred forest habitats with a large amount of dead woody material (spring: GRASS, FR-B, FRAX, FR-S, FDT, FDT-C, NRFT, FDT-A, summer: QR, QR-D, QR-E, FRAX, FDT, NRFT, FDT-C, autumn: TS, FR-B, TS>70, FDT-B, NRFT), however, the difference amongst study seasons was always in preference to different plant species (spring: GASPR, POLSPR, summer: AP, autumn: GEUM). Since these plant species were the most important components of the undergrowth during a particular season, the relationship is supposed to be related to the species' requirements for microhabitat structure, rather than *C. glareolus*' affinity for a particular plant species in a certain season. According to these results we can state that in *C. glareolus* there is some seasonality apparent, but that it is connected more with microhabitat structural changes than with changing microhabitat preferences in different seasons.

Discussion

Microhabitat selection by individual species

Apodemus flavicollis

Apodemus flavicollis is generally described as a species of mature forests, but the presence of shrub cover and a thin herb layer is also important (Niethammer 1978, Gurnell

Table 5. Discriminant function analyses of microhabitat preference in *Clethrionomys glareolus* at plot F and S, respectively. Explanations: Affinity - preference of higher (+) or lower (-) amount of concrete variable; SDFC - standardized discriminant function coefficient; n - absence in the final variable combination of concrete analysis; for description of variable abbreviation see Table 1.

Variable	Affinity	F	SDFC	Affinity	S	SDFC
AC-F	-		-0,5625			n
AC-S	-		-0,6623			n
AP	+		0,7101			n
DWM			n		-	
FDT			n		+	0,7500
FDT-C	+		0,6130		+	0,4099
FR-B	+		0,5933			n
NRTS	-		0,8032			n
OH	+		-0,4484			n
QR			n		+	0,5773
TS			n		+	-2,4953
TS<70	-		-0,3485			n
TS>70			n		+	1,9759
TS-S			n		-	1,0496

Table 6. Discriminant function analyses of microhabitat preference in *Clethrionomys glareolus* in spring, summer and autumn. Explanations: Affinity - preference of higher (+) or lower (-) amount of concrete variable; SDFC – standardized discriminant function coefficient; n – absence in the final variable combination of concrete analysis; for description of variable abbreviation see Table 1.

Variable	Affinity	SPRING		SUMMER		AUTUMN	
		SDFC	Affinity	SDFC	Affinity	SDFC	Affinity
10-30		n	–	0,4373		n	
AP		n	+	0,4836		n	
CENT		n		n	+	-0,2236	
FDT	+	0,7485	+	-1,0557	+	0,0548	
FDT-A	+	0,1278		n		n	
FDT-B	+	-0,2808		n	+	-0,5293	
FDT-C	+	-0,5554	+	0,4181		n	
FDT-D		n		n	+	0,1351	
FRAX	+	-0,4019	+	0,5628		n	
FR-B	+	-0,6490	+	0,0978	+	-0,5041	
FR-S	+	0,4134		n		n	
GASPR	+	-0,4474		n		n	
GEUM		n		n	+	-0,4006	
GRASS	–	-0,7692		n		n	
GV		n		n	–	0,3130	
NRFT	+	-0,3879	+	0,5935	+	0,4209	
NRSDT		n		n	+	0,2027	
OH	+	-0,1773		n		n	
PI-D		n	+	0,2069		n	
PI-E		n	–	-0,3129		n	
POLSPR	+	-0,3859		n		n	
QR		n	+	0,3457		n	
QR-D		n	+	-0,7067		n	
QR-E		n	+	0,6060		n	
SDT		n		n	+	-0,2131	
TIT		n		n	+	-0,1959	
TS	+	-0,2907	+	-0,1259	+	0,6645	
TS<70		n		n	+	-0,3968	
TS>70	+	0,2747	+	0,2290	+	-0,4250	
TS-B		n	+	0,2310	+	-0,3019	

1985, M á s k y 1985). According to M á s k y (1985), in floodplain forest *A. flavicollis* markedly preferred older tree stands to younger ones; a finding with which our results disagree. Comparison of the results from DFA and CCA showed that both indicated identical or markedly similar microhabitat selection (a microhabitat of dense, young forest or shrubs), while the amount of dead woody material was also important. Our findings rather support the H a m a r et al. (1996) findings that *A. flavicollis* prefers dense forests. This preference for dense tree cover in young forest stands may be due to the low numbers of shrubs in mature forest. According to C a s t i e n & G o s a l b e z (1994) *A. flavicollis* occupies adjacent bramble or stream hedges that have higher food availabilities due to their structure and floral composition during seasons with low seed crops. *Apodemus flavicollis* consumes food consisting largely of high calorie components, especially seeds (O b r t e l & H o l i š o v á 1974) – which can cause a preference for stands with more abundant live woody material (T u r č e k 1960); this may also be the case here. Moreover, dense tree and shrub strata are important for protection against predators (C h ě t n i c k i & M a z u r k i e w i c z 1994). D u d i c h (1970) also points out the function of food and shelter availabilities in habitat

selection by *A. flavicollis*. As for the herb layer, we did not see any markedly negative relationship with factors relating to this stratum in general habitat selection. However, on the other hand, in plot S there was a considerable negative relationship between the high herb layer cover and an increased occurrence of *A. flavicollis* (Table 4). This phenomenon is probably caused by *A. flavicollis*' preference for habitats with dense tree stands at this site and a poor herb layer caused by increased shadowing. Also, we did not see any notably negative relationship with undergrowth in the herb layer in plot F (Table 4). These results indicate *A. flavicollis*' probable tolerance of the presence of and various degrees of undergrowth density in the herb layer. At plot M the presence or absence of undergrowth was considerably exceeded by other factors that markedly influenced the occurrence of *A. flavicollis*, so this factor is not decisive from the point of view of species occurrence. Furthermore, the fact that *A. flavicollis* occupies this plot and microhabitats that are suitable, despite being scattered across a habitat with dense grass stands, indicates a considerable tolerance to undergrowth and especially to herb layer density. However, to prove or disprove this would only be possible by more detailed analyses of the individual home ranges of each species. According to a detailed analysis of habitat selection *A. flavicollis* utilises sites with larger tree stands but without a preference for denser tree and shrub stands at this site. This phenomenon is probably caused by the fact that the tree islets are too small to show a deeper preference for areas with denser tree and shrub stands. Thus, if we accept the assumption that dense tree stands are an optimal habitat for *A. flavicollis*, it is possible that the conditions provided by this area are not optimum for the species – resulting in its occurrence in habitats with suitable tree stands, but whilst tree density is not important.

Microtus arvalis

Both analyses (DFA, CCA) suggested *M. arvalis* largely lives in (or prefers) habitat with open meadow stands lacking tree cover. According to Pe likán (1959) *M. arvalis* shows a strong tendency to occupy free grassy places among shrubs on meadows, however, in some cases it prefers solitary trees and shrubs. We can confirm the preference of grassy places among groups of trees and shrubs, but not for solitary trees and shrubs occurring as small patches surrounded by meadow vegetation. Moreover, according to Pe likán (1959), the structural features of grass stands are not a limiting factor for *M. arvalis*, even though it is encountered more frequently in places with dense and high stands: we came to similar conclusions. The results of both analyses (CCA, DFA) showed a certain preference for sites with higher grass stands (variable: 50–100). Besides that, a suitable or less suitable habitat type is not occupied regularly, but we can find dispersed colonies of *M. arvalis* in it (Pe likán 1959). This could lead to our being unable to determine significant variables explaining the distribution of individual *M. arvalis* in suitable conditions by DFA. As for social structure, individual microhabitat selection can be influenced markedly by colony localisation as young individuals tend to occupy its margins (Pe likán 1959). Another possible explanation is that almost the whole area of study plot M (*i.e.* with the highest occurrence of *M. arvalis* of all study sites) was burnt in March 1998. This burning included the old grass stands, or the dry grass leaves, respectively, which form the fundamental component of the undergrowth at this site. This stratum was restored by June 1998 and formed structural conditions that appeared to be similar to those seen before the fire. However, we are unable to estimate what changes occurred in vegetation composition at this site as floristic variables were only measured in summer 1998. Data from this locality markedly influenced the results of the analysis of habitat selection by this species – largely

because of the permanent presence of *M. arvalis* in a large portion of the capture quadrat. However, undergrowth species composition could have changed markedly due to the effects of the fire. As for the trophic needs of *M. arvalis*, some plants are differentially attractive to the species (Holíšová 1959) and may thus influence its occurrence (Pelikán 1959). In 1998 these rodents probably found different conditions at this site than in previous years. The estimation of floristic variables was performed only once (in summer 1998) so our analyses could not show which plants *M. arvalis* preferred.

Clethrionomys glareolus

The optimal habitat for *C. glareolus* is usually reported as wet forest biotopes with rich undergrowth and large amounts of fallen branches and logs (Pucek 1983, Mazurkiewicz & Rajska - Jurgiel 1987, Smaha 1996). According to our results *C. glareolus* prefers older forest stands with fallen tree trunks. This dead woody material provides hiding places (Mazurkiewicz & Rajska - Jurgiel 1987) for this species, which has rather poor burrowing abilities (Pucek 1983). However, other authors have not confirmed a preference for older forest stands; Mazurkiewicz (1991) found no relationship with tree stands with a certain age structure, and hence with older forests. We suppose that the preference for older forest stands at our study sites is a secondary phenomenon, probably related to choice of habitats with more developed undergrowth (compared with the younger, denser parts of the forest). The importance of undergrowth presence, density and spatial distribution for *C. glareolus* has been stressed in several studies (Mazurkiewicz 1986, 1991, Mazurkiewicz & Rajska - Jurgiel 1987, Chętnicki & Mazurkiewicz 1994). The food of *C. glareolus* consists mainly of the vegetative parts of plants, seeds and, to a lesser extent, fungi and animal foods (Watts 1968, Obrtel & Holíšová 1974, Gębczyńska 1983). Therefore, in *C. glareolus* undergrowth is important as a source of food and also for protection against predators (Mazurkiewicz 1986, Chętnicki & Mazurkiewicz 1994). Chętnicki & Mazurkiewicz (1994) stressed that the shrub substratum had the same importance, underlining its protective function. In our study, *C. glareolus* especially preferred sites either entirely lacking or without a well-developed shrub stratum. This may have been due to sites with more continual shrub stands having no undergrowth or lacking well-developed undergrowth. An alternative (or complementary reason) was that there was an increased occurrence of *A. flavicollis* in these areas, therefore *C. glareolus* does not prefer sites with dense shrub stands. The dominant position of *A. flavicollis* in interspecific relationships with *C. glareolus* was reported by Andrezewski & Olszewski (1963). These workers found that the bigger, more aggressive *A. flavicollis* physically attacks *C. glareolus* and expels it from food sources. Similarly, Wójcik & Wołk (1985) found that at higher population densities *C. glareolus* adapts its daily activities to avoid *A. flavicollis*. Another factor in areas with a developed shrub stratum seems to be the small amount of fallen woody material that could provide suitable hiding places for the species. As for study plot M, *C. glareolus* was captured very rarely and only near a continual forest stand. This shows that scattered forest stands occurring at this site do not provide suitable conditions for the species. According to Nagyová (1998) the forest fringe forms a barrier to *C. glareolus*, which dislikes the absence of a shrub and tree stratum. This allows us to suppose that this species avoids living, or even passing through, habitats without tree stands, although in some cases it can occur in them (Pucek 1983). We can assume that this species is unable to tolerate increased fragmentation of small areas with theoretically suitable conditions in habitats unsuitable for

its occurrence. *Clethrionomys glareolus* is known for its high trophic plasticity and no deep specialisation on any particular plant species has been shown (Gebčík & Václav 1983); this supports our conclusions on seasonal changes in microhabitat preference for the species. Moreover, Chetnicki & Mazzoni (1994) underlined the protective function of undergrowth, which supports the relationship of *C. glareolus* to undergrowth probably having a structural rather than a trophic basis.

Acknowledgements

This work was carried out with financial support of grants VEGA 1/4140/97 and 1/7197/20. We also thank RNDr. J. Šeffer for allowing us to use the CANOCO statistical programme, Mgr. D. Němethová and Mgr. N. Martínková for their help in statistical analyses. Furthermore, we thank Mgr. P. Meredá, Mgr. M. Perný and Mgr. J. Rípká for the determination of some plants, and Mgr. I. Nagyová for her help with field work.

LITERATURE

- ANDRZEJEWSKI, R. & OLSZEWSKI, J., 1963: Social behaviour and interspecific relations in *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolus* (Schreber, 1780). *Acta Theriol.*, 7: 155–168.
- BONDRUP-NIELSEN, S., 1985: An evaluation of the effects of space use and habitat patterns on dispersal in small mammals. *Ann. Zool. Fenn.*, 22: 373–383.
- BURT, W. H., 1943: Territoriality and home range concepts as applied to mammals. *J. Mammal.*, 24(3): 346–352.
- CASTIEN, E. & GOSALBEZ, J., 1994: Habitat selection of *Apodemus flavicollis* in a *Fagus sylvatica* forest in the Western Pyrenees. *Folia Zool.*, 43(3): 219–224.
- CHĘTNICKI, W. & MAZURKIEWICZ, M., 1994: Dispersion of the bank vole in fine- and coarse-grained mosaics of deciduous and mixed coniferous forests. *Acta Theriol.*, 39(2): 127–142.
- DOUGLASS, R. J., 1989: The use of radio-telemetry to evaluate microhabitat selection by deer mice. *J. Mammal.*, 70: 648–652.
- DOUGLASS, R. J., DOUGLASS, K. S. & ROSSI, L., 1992: Ecological distribution of bank voles and wood mice in disturbed habitats: preliminary results. *Acta Theriol.*, 37(4): 359–370.
- DUDICH, A., 1970: Mikromammalia Demänovskéj doliny (Micromammalia of the Demänovská valley). *Ochrana fauny*, 4(1): 10–18 (in Slovak, with summaries in English, Russian and German).
- GEBCZYŃSKA, Z., 1983: Feeding habits. In: Petrusewicz, K. (ed.), Ecology of the bank vole. *Acta Theriol.*, 28, Suppl. 1: 40–49.
- GURNELL, J., 1985: Woodland rodent communities. *Symposia of the Zoological Society of London*, 55: 377–411.
- HAMAR, M., SIMONESCU, V. & THEISS, F., 1966: Biometrische und zoogeographische Untersuchungen der Gattung *Apodemus* (Kaup, 1829) in der Sozialistischen Republik Rumänien. *Acta Theriol.*, 11(1): 1–40.
- HOLIŠOVÁ, V., 1959: Potrava hraboše polního (Food of common vole). In: Kratochvíl, J. et al. (eds), Hraboš polní *Microtus arvalis* (Common vole *Microtus arvalis*). ČSAV, Prague: 100–129 (in Czech, with a summary in German).
- JAMES, F. C. & SHUGART, H. H., 1970: A quantitative method of habitat description. *Audubon Field Notes*, 24(6): 727–736.
- LIN, L.-K. & SHIRAISHI, S., 1992: Home range and microhabitat utilization in the formosan wood mouse, *Apodemus semotus*. *Journal of the Faculty of Agriculture Kyushu University*, 37(1): 13–27.
- MÁJSKY, J., 1985: Drobné zemné cicavce lužných lesov a vetrolamov hornej časti Žitného ostrova (Small mammals in floodplain forests and windbreaks of upper part of Žitný ostrov). *Biologické práce*, 31(2): 1–116 (in Slovak, with summaries in Russian and English).
- MAZURKIEWICZ, M., 1986: The influence of undergrowth distribution on utilization of space by bank vole populations. *Acta Theriol.*, 31(4): 55–69.
- MAZURKIEWICZ, M., 1991: Population dynamics and demography of the bank vole in different tree stands. *Acta Theriol.*, 36(3–4): 207–227.
- MAZURKIEWICZ, M. & RAJSKA – JURGIEL, E., 1987: Numbers, species composition and residency of a rodent community in forest and field – forest ecotones. *Acta Theriol.*, 32 (25): 413–432.

- NAGYOVÁ, K., 1998: Sezónne zmeny štruktúry populácie a disperzie hrdziaka lesného (*Clethrionomys glareolus* Schreber, 1780) [Seasonal changes in structure and dispersation of a bank vole population (*Clethrionomys glareolus* Schreber, 1780)]. *Prirodovedecká fakulta UK, Bratislava, Diploma thesis*, 40 pp. (in Slovak).
- NIETHAMMER, J., 1978: *Apodemus flavicollis* (Melchior, 1834) – Gelbhalsmaus. In: Niethammer, J. & Krapp, F. (eds), *Handbuch der Säugetiere Europas*. Akademische Verlagsgesellschaft, Wiesbaden: 325–336.
- NOON, B. R., 1981: Techniques for sampling avian habitats. In: The use of multivariate statistics in studies of wildlife habitat. *USDA Forest Service*: 42–53.
- OBRTEL, R. & HOLIŠOVÁ, V., 1974: Character of foods eaten by *Apodemus flavicollis Clethrionomys glareolus* in a lowland forest. *Lynx (Prague)*, 16: 37–45 (in Czech, with a summary in English).
- PAUL, G., 1990: Geschlechtsbestimmung von Skeletten mit Diskriminanzfunktionen für bleibende Zähne. *Fakultät für Theoretische Medizin der Universität Ulm, Ulm, PhD thesis*: 77 pp.
- PELIKÁN, J., 1959: Bionomie hraboše polního (Bionomy of common vole). In: Kratochvíl, J. et al. (eds), Hraboš polní *Microtus arvalis* (Common vole *Microtus arvalis*). ČSAV, Prague: 80–129 (in Czech, with a summary in German).
- PELIKÁN, J., 1975: K ujednocení odchytového kvadrátu a linie pro zjištování populační hustoty drobných savců v lesích (On the standardization of the trapping quadrat and line for estimating the population density of small mammals in forests). *Lynx (Prague)*, 17: 58–71 (in Czech, with a summary in English).
- PUCEK, M., 1983: Habitat preference. In: Petrusewicz, K. (ed.), Ecology of the bank vole. *Acta Theriol.*, 28, Suppl. 1: 31–40.
- ŠMAHA, J., 1996: Soupis poznámek o theriofauně biosférické rezervace Křivoklátsko (Notes on the mammal fauna of the Krivoklatsko Biosphere Reserve. *Lynx (Prague)*, 27: 37–56 (in Czech, with an abstract in English).
- TURČEK, F. J., 1960: Sídelné vzťahy niektorých drobných lesných hlodavcov zistené na podklade mapovania (Habitat requirements of some woodland rodent species find out by mapping). *Biológia (Bratislava)*, 15: 729–737 (in Slovak, with a summary in English).
- VAN HORNE, B., 1982: Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. *Ecology*, 63: 992–1003.
- WATTS, C. H. S., 1968: The food eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *J. Anim. Ecol.*, 37: 25–41.
- WÓJCIK, J.M. & WOLEK K., 1985: The daily activity rhythm of two competitive rodents: *Clethrionomys glareolus* and *Apodemus flavicollis*. *Acta Theriol.*, 30(14): 241–258.