

Population ecology of *Apodemus flavicollis* in two lowland forest habitats (Rodentia: Muridae)

Populačná ekológia *Apodemus flavicollis* v dvoch typoch nížinného lesa (Rodentia: Muridae)

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received on 12 June 2006

Abstract. Several population characteristics were studied and compared between populations of *Apodemus flavicollis* inhabiting two different lowland forest habitats. Small mammals were live-trapped during 2000–2002 on two 1.44 ha plots in alder forest and oak-elm forest (Nature Reserve Jurský Šúr, Slovakia). The density of *A. flavicollis* was 0.0–25.3 individuals per ha in alder forest and 3.1–28.0 individuals per ha in oak-elm forest. Throughout the study, *A. flavicollis* was the most numerous species in oak-elm forest (72–100%), while in alder forest its proportion was much lower (0–50%). Higher reproductive activity in alder forest was probably caused by higher food and shelter availability in this area during breeding season. Animals of both sexes were heavier in oak-elm forest which suggests a better fitness of individuals in this habitat. While the degree of male residency was significantly higher in oak-elm forest, we did not find any difference in resident rate of females. Different occurrence and residency of individuals on the study plots are probably caused by higher heterogeneity and larger total area of alder forest together with temporary winter insufficiency of resources on the local study plot.

INTRODUCTION

The structure and dynamics of a population represent the outcome of the interactions between life histories of its individuals and the spatial and temporal variations in its environment (ZENG & BROWN 1987). Local populations of widely distributed species living in different environmental conditions may exhibit different demographic parameters in relation to ecological characteristics of habitats (MONTGOMERY & GURNELL 1985). The yellow-necked mouse, *Apodemus flavicollis* (Melchior, 1834), as one of the most ubiquitous and abundant small mammals in the western Palaearctic, utilises a variety of habitat types throughout its geographical range. It is primarily a woodland rodent preferring mature successional stages of deciduous forests with an open ground layer. However, it can also inhabit field-forest ecotones, grassy areas and brushwood sets (GURNELL 1985, JENSEN 1984). Its occurrence in coniferous forests, subalpine and alpine zone is mainly seasonal (KRATOCHVÍL & ROSICKÝ 1952, ZIMA et al. 1984), depending on local seed supply and immigration from nearby stable populations with higher densities (MARTÍNKOVÁ et al. 2001). Populations of *A. flavicollis* are able to persist in different habitat types because of their broad flexibility in demography and habitat selection as well as high adaptability to different environmental conditions (DOUGLASS et al. 1992, MONTGOMERY & GURNELL 1985).

In the present study we compared several demographic parameters (abundance, residency, age composition breeding activity and body mass) between two populations of *A. flavicollis* inhabiting different lowland forest habitats in National Nature Reserve Jurský Šúr.

MATERIAL AND METHODS

Study area

The study was carried out in the Jurský Šúr National Nature Reserve, 12 km north-east of Bratislava (128–132 m a. s. l., DFS 7769c). Study sites were situated in two different forest habitat types, an alder forest (study plot A) and an oak-elm forest (plot B).

The alder forest forms an isolated complex of swampy boggy forest in the centre of wet meadows. It spreads over an area of 334.7 ha and forms the greatest part of the Jurský Šúr National Nature Reserve. The alder forest belongs phytoecologically to the *Carici elongatae-Alnetum medioeuropaeum* association. The tree layer of study plot A is formed by the following species: *Alnus glutinosa*, *Quercus robur* and *Ulmus laevis*. The shrub layer develops mainly in the sites with loose canopy and is formed by the species *Alnus glutinosa*, *Salix cinerea*, *Prunus spinosa* and *Rosa* spp. The herb layer is formed by the species *Iris pseudacorus*, *Urtica kiovenensis*, *Alisma plantago-aquatica* and *Carex* spp. This plot is characterised by the presence of surface floods (XI–II/III) when the water level reaches 20–50 cm (KUPCOVÁ 1980).

The oak-elm forest is a remnant of old thermophilous mixed forests of the Pannonian basin, partly it keeps its forest-steppe character. It spreads over an area of 42.38 ha. The tree layer of study plot B is represented by the species *Quercus robur*, *Q. cerris*, *Ulmus laevis*, *Acer campestre*, and *Carpinus betulus*. Shrub layer is formed by the species *Prunus spinosa*, *Rosa canina* and *Crataegus* spp. The herb layer is formed mainly by grasses (Poales). Besides them, the species *Viola* sp., *Geum urbanum*, *Alliaria petiolata*, *Allium ursinum*, *Lamium maculatum*, and *Galium aparine* occur most frequently (KUPCOVÁ 1980, MIKLOS 1999). The study sites were separated by approximately 1 km wide corn field.

Methods

Small mammals were live-trapped every six weeks between February 2000 and November 2002 on two 1.44 ha plots. Live-traps were set 15 m apart in a 9×9 matrix on each grid. A single Chmela-type live trap baited with oats was placed at each station. Traps were set during six consecutive nights and checked twice a day, mornings and evenings. All captured small mammals were individually marked by toe-clipping and released at trapping points immediately after data collection. Upon capture the following parameters were noted for each individual animal: capture point co-ordinates, species, individual number, sex, weight and status of external sexual characters to assess reproductive individuals (males: scrotal testes; females: enlarged nipples, perforated vagina or pregnancy). Monthly population abundance was estimated by direct enumeration of mice captured on the study plot, and population densities were obtained by dividing abundance by the trapping area, increased by one trap distance per side. Abundance variation was compared between habitats using the chi-square goodness of fit test. All the individuals caught were divided into three groups according to their residential status. The first group (long time residents) comprised animals present throughout at least two series of trapping, the second group (short time residents) included individuals captured several times during the sampling session. The third group (transients) encompassed those individuals that were caught only once and no more. Resident rate was expressed as the proportion of long time residents excluding mice captured in the last trapping period of a year. The age of each individual was estimated on the basis of body weight according to GLIWICZ (1988) and all individuals were divided into adult ($m > 25$ g) and young (subadult and juvenile; $m < 25$ g) age classes. The following characteristics were analysed for each trapping session, individual years and also jointly for the three years of study: sex ratio, age structure (proportion of young), breeding intensity (proportion of reproductively active females) and resident rate. These characteristics were compared between habitats using chi-square analysis of contingency tables. The body weights of sexually active and adult individuals of both sexes

were compared between habitats using the Mann-Whitney test. We tested the spatial distribution of either sex as well as that of both sexes together to find possible departures from random (Poisson) distribution using the χ^2 -test. When we found non-random spatial distribution, we used LLOYD (1967) index to decide whether the distribution was clumped or even.

RESULTS

The total material consisted of 1,927 captures of 617 individuals of *Apodemus flavicollis* (Melchior, 1834), comprising 914 captures of 301 individuals in alder forest and 1,013 captures of 316 individuals in oak-elm forest. Besides that, the following species were recorded: in the alder forest *Clethrionomys glareolus* (Schreber, 1780), *Sorex araneus* Linnaeus, 1758, *Neomys fodiens* (Pennant, 1771), *Micromys minutus* (Pallas, 1771) and *Mustela nivalis* Linnaeus, 1766, and in the oak-elm forest *Clethrionomys glareolus*, *Sorex araneus*, *Crocidura leucodon* (Hermann, 1780), *Micromys minutus* and *Mustela nivalis*.

The density of *A. flavicollis* was 0–25.33 individuals per ha on plot A and 3.11–28 individuals per ha on plot B. During the reproduction season (III/IV–IX/X) we did not find any differences in abundance variation between the study sites. Statistically significant difference ($\chi^2=105.8139$, $p<0.01$, $df=19$) in variation of abundance found, when comparing the whole study period, was caused by much lower minimum numbers and even absence of individuals on plot A during winter months (II–IV 2000, II 2001, III 2002).

Throughout the study, the proportion of *A. flavicollis* in small mammal community was different between the two study sites. In the oak-elm forest, *A. flavicollis* was the most numerous

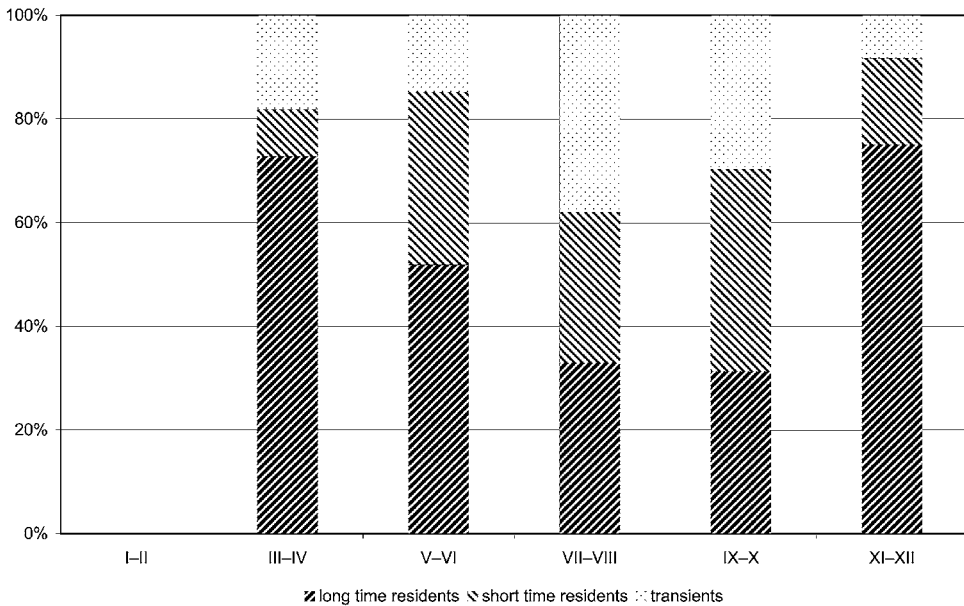


Fig. 1. Resident rate of males in alder forest (pooled data for 2-months intervals).
Obr. 1. Rezydencia samcov v jelšovom lese (zhrnuté dáta pre dvojmesačné obdobia).

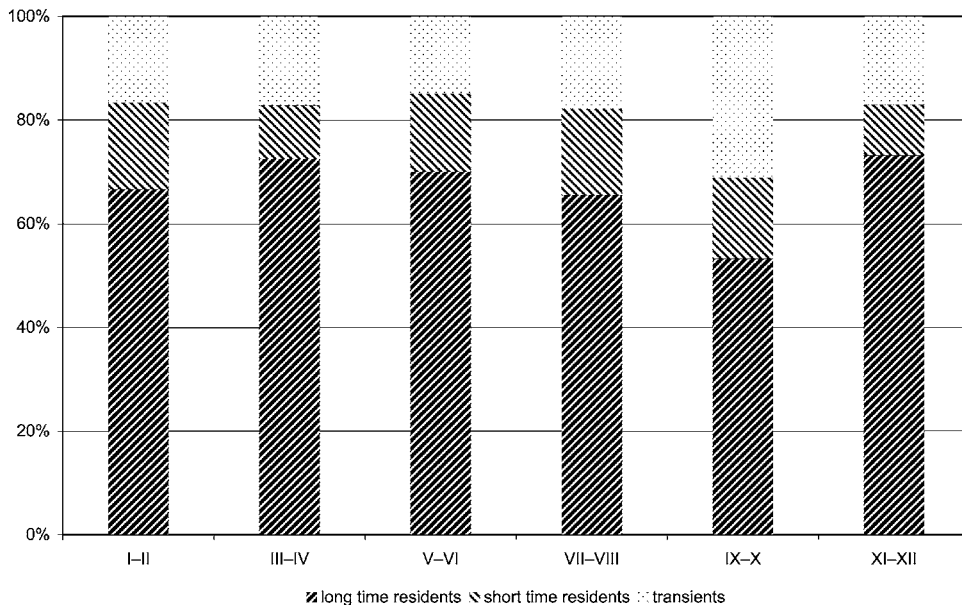


Fig. 2. Resident rate of males in oak-elm forest (pooled data for 2-months intervals).
 Obr. 2. Rezidencia samcov v dubovo-brestovom lese (zhrnuté dáta pre dvojmesačné obdobia).

species, its proportion in small mammal community reaching 72 to 100%. In the alder forest, the proportion of *A. flavicollis* ranged from 0 to 50%. Small mammal abundance was always higher in the alder forest (on the average 3.5-times higher, during peak abundance 2.8–4.3 times).

We found higher resident rate on plot B when comparing pooled data for the whole study period for all individuals ($\chi^2=8.37$, $p<0.05$) and for males ($\chi^2=13.27$, $p<0.05$) (Figs. 1, 2). Higher resident rate of males on plot B was statistically significant also for pooled data for 2000 ($\chi^2=6.42$, $p<0.05$), 2001 ($\chi^2=4.01$, $p<0.05$), and in 2002 it was close to the limit of statistical significance ($\chi^2=3.73$, $p=0.054$). A similar trend can be observed also in the individual trapping series, but the difference was statistically significant only in IX 2000 ($\chi^2=8.31$, $p<0.05$), VIII 2001 ($\chi^2=4.82$, $p<0.05$) and VIII 2002 ($\chi^2=9.72$, $p<0.05$). We did not find any difference in resident rate of females.

We did not find any difference in timing of reproduction (sexually active individuals and juveniles were recorded during the same trapping series on both plots). Reproduction period started in III/IV and ended in IX/X.

In the alder forest we found a higher proportion of sexually active females, this difference being statistically significant for the pooled data for the whole study period ($\chi^2=5.7$, $p<0.05$), and for the pooled data for the year 2001 ($\chi^2=8.14$, $p<0.05$) (Fig. 3a, b).

In alder forest we found also a higher proportion of young (subadult and juvenile) individuals, this difference being statistically significant for the pooled data for the whole study period ($\chi^2=4.17$, $p<0.05$) (Fig. 4a, b). A higher proportion of young individuals in the alder forest was observed also in individual trapping series, the difference being statistically significant in VIII 2001 ($\chi^2=4.37$, $p<0.05$) and X 2002 ($\chi^2=5.2$, $p<0.05$).

Table 1. Mean body weights and standard deviations for sexually active and adult individuals of *Apodemus flavicollis*

Tab. 1. Priemerné hmotnosti pohlavne aktívnych a adultných jedincov *Apodemus flavicollis*

	alder forest (m±SD) [g]		oak-elm forest (m±SD) [g]	
	active	adult	active	adult
females	29.98±3.68	28.78±4.68	31.45±4.21	31.79±4.59
males	31.96±5.00	30.60±6.23	32.25±4.99	33.32±5.95

Average weights of sexually active and adult individuals were higher in the oak-elm forest, this differences being statistically significant only for females (sexually active females: $w=5,340$, $p<0.01$, adult females: $w=9,433$, $p<0.01$) (Table 1).

Spatial distribution of long-time residents on plot A was random in most trapping series, with the exception for females in November 2000 ($\chi^2=6.50$, $p<0.05$, $L=1.22$) and August 2001 ($\chi^2=6.10$, $p<0.05$, $L=2.24$) and for both sexes together in October 2001 ($\chi^2=9.63$, $p<0.01$, $L=1.68$), when the spatial distribution was aggregated. Spatial distribution of males was random in all trapping series. On plot B we found aggregated spatial distribution for males in February ($\chi^2=20.01$, $p<0.001$, $L=3.83$), April ($\chi^2=18.12$, $p<0.001$, $L=4.13$), June 2001 ($\chi^2=12.66$, $p<0.01$, $L=2.88$) and in August 2002 ($\chi^2=6.57$, $p<0.05$, $L=2.88$). For both sexes together we found aggregated distribution in September ($\chi^2=53.59$, $p<0.001$, $L=1.97$) and November 2000 ($\chi^2=10.44$,

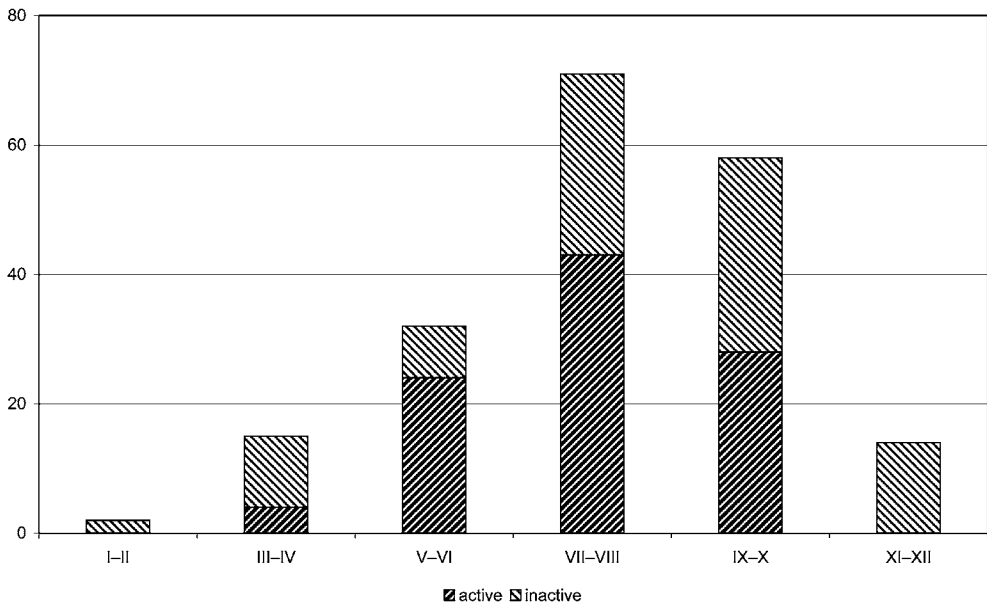


Fig. 3a. Proportion of sexually active females in alder forest (pooled data for 2-months intervals).

Obr. 3a. Zastúpenie pohlavne aktívnych samíc v jelšovom lese (zhrnuté dáta pre dvojmesačné obdobia).

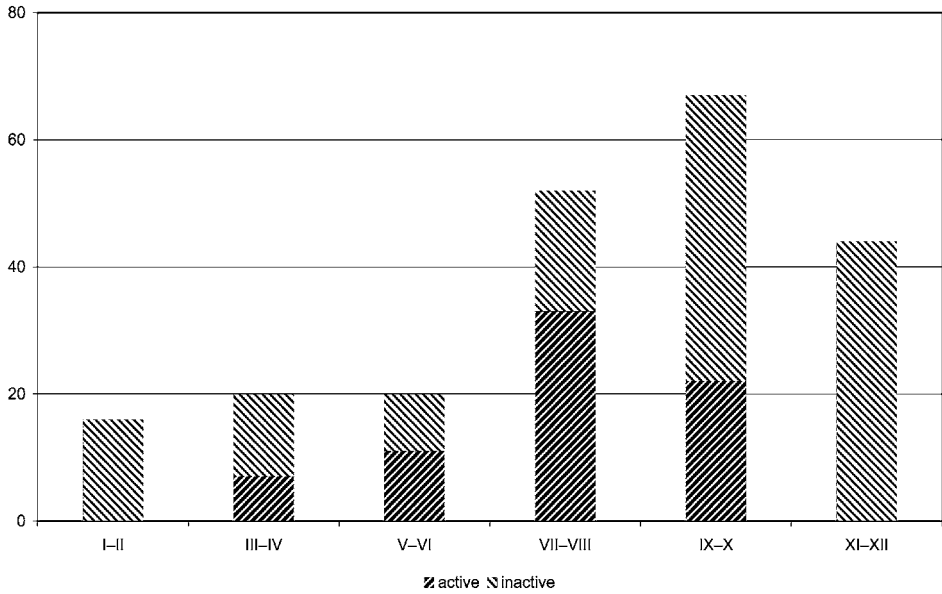


Fig. 3b. Proportion of sexually active females in oak-elm forest (pooled data for 2-months intervals).
 Obr. 3b. Zastúpenie pohlavne aktívnych samic v dubovo-brestovom lese (zhrnuté dáta pre dvojmesačné obdobia).

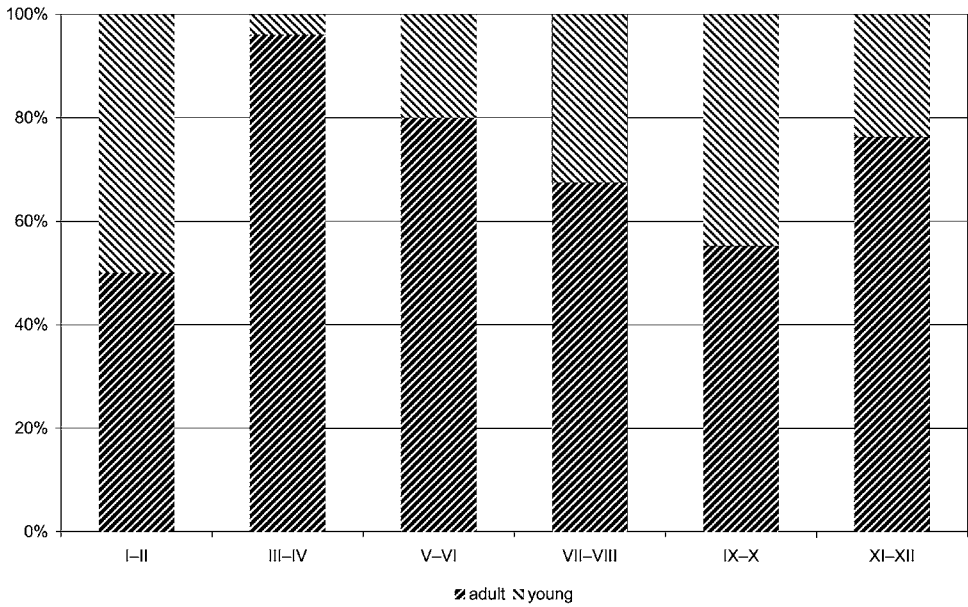


Fig. 4a. Proportion of young individuals in alder forest (pooled data for 2-months intervals).
 Obr. 4a. Zastúpenie mladých jedincov v jelšovom lese (zhrnuté dáta pre dvojmesačné obdobia).

$p < 0.05$, $L = 1.84$), February ($\chi^2 = 6.05$, $p < 0.05$, $L = 2.43$), April ($\chi^2 = 8.05$, $p < 0.05$, $L = 2.45$) and July 2001 ($\chi^2 = 15.22$, $p < 0.01$, $L = 1.79$) and February ($\chi^2 = 11.69$, $p < 0.001$, $L = 3.31$) and August 2002 ($\chi^2 = 9.32$, $p < 0.01$, $L = 2.80$). Spatial distribution of females was random in all trapping series.

DISCUSSION

Populations under study revealed typical seasonal trend of abundance fluctuation known for this species (FLOWERDEW 1985, GURNELL 1985, MONTGOMERY 1979, PUCEK et al. 1993) with peak numbers in late summer/early autumn and decrease during late autumn and winter months. Maximal densities achieved on both plots are consistent with published data for *A. flavicollis* in Central Europe (MAZURKIEWICZ & RAJSKA-JURGIEL 1998, WOJCIK & WOLK 1985).

The most part of the study plot A was flooded and frozen during winter (XI–II/III), so as regards abundance and availability of food, which is the most important factor governing local distribution and abundance of *A. flavicollis* (ANGELSTAM et al. 1987, MONTGOMERY 1979), as well as regarding the availability of shelters, it represents an unfavourable environment for this species (MONTGOMERY 1978). The animals retreat from this study plot during winter. However, after a temporary absence during winter we repeatedly captured the same individuals on plot A as in the previous year, and in quite high numbers (TRUBENOVÁ et al. 2004). The animals inhabiting study plot A are able to survive winter, despite the fact that they are forced to seek out more favourable refuges for overwintering, and probably the refuges inhabited during winter are within easy reach for this species. In contrast to study plot in alder forest, the continuous

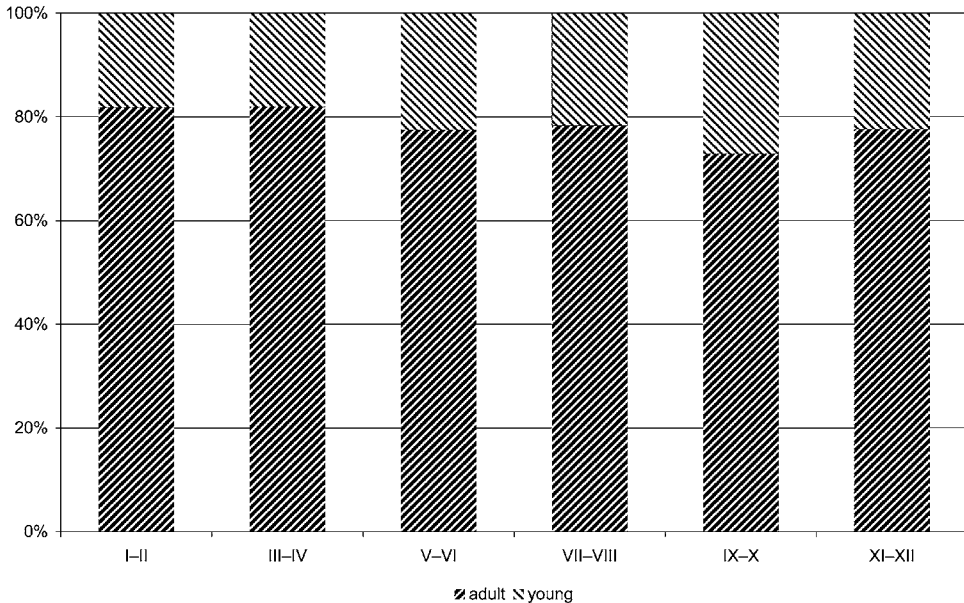


Fig. 4b. Proportion of young individuals in oak-elm forest (pooled data for 2-months intervals).

Obr. 4b. Zastúpenie mladých jedincov v dubovo-brestovom lese (zhrnuté dáta pre dvojmesačné obdobia).

occurrence of individuals of *A. flavicollis* on the study plot in oak-elm forest suggests that this habitat is suitable for *A. flavicollis* all year over, also during winter months (TRUBENOVÁ et al. 2004). This seems consistent with the findings of CASTIEN & GOSALBEZ (1994) and MONTGOMERY (1979), according to whom *A. flavicollis* is quite rare in many forest types during winter and the populations are restricted to one habitat type characterised by the presence of a number of seed-bearing tree species and by a dense entanglement of branches above ground level. This way could be characterised the study plot in the oak-elm forest as well as the oak-elm forest as a whole.

Distinct difference in the proportion of *A. flavicollis* in the small mammal community between these two habitats is caused by the much higher numbers of small mammals in the alder forest (especially *Clethrionomys glareolus*), which suggests higher productivity and/or higher heterogeneity of this habitat (M'CLOSKEY 1976, VAN HORNE 1983). Almost monospecific occupancy of plot B by *A. flavicollis* is in contrast with the situation in alder forest, where the numbers of *A. flavicollis* were similar or lower than the numbers of *C. glareolus*. However, we do not suppose that the presence of *C. glareolus* limits the numbers achieved by *A. flavicollis* population. Where these two species occur together, *A. flavicollis* is generally considered dominant (ANDRZEJEWSKI & OLSZEWSKI 1963, BERGSTEDT 1965, GRÜM & BUJALSKA 2000), affecting population dynamics, spatial distribution and/or demographic variables of *C. glareolus* population, but not conversely.

The different residency of males and females is caused by different reproductive strategies between sexes. Females are characterised by lower mobility, higher residency and selection of places providing secure cover for rearing the young, while males are distributed with respect to breeding opportunity (OSTHELD 1985). As we have found difference only in the resident rate of males, while the resident rate of females did not differ between the plots, we can suppose that higher residency of males in oak-elm forest was not caused only by higher quality of this habitat. In oak-elm forest we have found also longer residency time of individuals of both sexes, significantly for males (TRUBENOVÁ et al. 2004). Differences in male residency could be associated with more opportunity to disperse in alder forest, and also with higher heterogeneity of this habitat (TRUBENOVÁ et al. 2004). The alder forest seems to be a highly seasonal environment in which different habitat patches may be preferred at different seasons. Spatial activity and residency of *Apodemus* spp. are affected not only by the woodland habitat itself but also by the surrounding landscape, distances to neighbouring woodlands and connectivity between them (KOZAKIEWICZ 1993, YLÖNEN et al. 1991). In smaller woodlands, where the surrounding area of ancient woodland tends to be lower, there is less opportunity to disperse (MARSH & HARRIS 2000). BROWN (1966) concluded that a substantial proportion of male *Apodemus* have different areas of activity at different times. She reported that the individuals concerned were the dominant males having very large home-ranges and visiting various parts of these ranges on a regular rotation basis. So the lifetime home ranges of *A. flavicollis* males in oak-elm forest are probably smaller, the animals have fewer seasonal centres of activity, and they stay longer in the same place. Aggregated distribution of males in oak-elm forest can be connected with their higher residency and restricted spatial activity in this habitat.

Balanced sex ratio found in both populations (TRUBENOVÁ et al. 2004) is a characteristic feature of stable populations living in optimal habitats. Although we have found no difference in timing and duration of reproduction period, the higher proportion of sexually active females and young individuals in alder forest indicate a higher intensity of reproduction in this habitat. As the numbers of females active sexually may be a good indicator of the quality of a given

habitat (MAZURKIEWICZ 1991, 1994), the alder forest seems more suitable for *A. flavicollis* during breeding season. Aggregated spatial distribution of females in alder forest can be connected with locally and temporally more favourable conditions, which cause concentration of females in this habitat during the time it provides suitable conditions for weaning the litter.

Higher numbers of sexually active females in alder forest could have also another reason. In oak-elm forest the individuals remain all year over, as they find suitable conditions for surviving the winter there. So the structure of the local population is stable, with well-defined dominance hierarchy. Social interactions may prevent young animals from entering the reproducing part of population (MAZURKIEWICZ & RAJSKA-JURGIEL 1998). In contrast, the study plot in alder forest is not populated by *A. flavicollis* individuals during winter and the population in spring consists mainly of immigrants. In such environment, where there is no stable structure of the population and where at that time there is no social interaction factor, every spring and early-summer immigrant may mature and breed (MAZURKIEWICZ & RAJSKA-JURGIEL 1998, VAN HORNE 1983).

The higher body weight of individuals in the oak-elm forest found, when comparing all individuals (TRUBENOVÁ et al. 2004), can be partly caused by the higher proportion of adults in this habitat. However, higher body weights were found in this habitat also when comparing sexually active individuals (although significantly only for females), and also when comparing adult individuals (significantly for females), which suggest that individuals living in the oak-elm forest are heavier. It is used to present body weight as one of the measures of fitness, which provides information about habitat quality for the studied species, as animals in higher-quality habitats tend to be heavier (VAN HORNE 1983). Higher body weight of animals of both sexes in oak-elm forest suggests better fitness of individuals in this habitat, which is probably caused by more suitable year-long conditions here in comparison to the alder forest, where the fitness of individuals may be lowered by the cost of winter migration.

SÚHRN

V práci sú vyhodnotené a porovnané demografické parametre populácií *Apodemus flavicollis*, obývajúcich dva typy nížinného lesa. Terénny výskum prebiehal v rokoch 2000–2002 v jelšovom lese a dubovo-brestovom lese (NPR Šúr, SR) na odchytočných kvadrátoch veľkosti 1,44 ha s použitím CMR metódy. Počas obdobia výskumu bolo v jelšovom lese zaznamenaných 914 odchytovcov 301 jedincov a v dubovo-brestovom lese 1013 odchytovcov 316 jedincov *A. flavicollis*. Densita druhu dosahovala hodnoty 0,0–25,3 jedincov na hektár v jelšovom lese a 3,1–28,0 jedincov na hektár v dubovo-brestovom lese. Zatiaľ čo v dubovo-brestovom lese bol *A. flavicollis* najpočetnejším druhom počas celého obdobia (72–100 %), v jelšovom lese bolo jeho zastúpenie výrazne nižšie (0–50 %). Obdobie rozmnožovania, stanovené na základe odchytyvania pohlavne aktívnych a juvenilných jedincov trvalo v jednotlivých rokoch v oboch prostrediach rovnako. Vyšší podiel pohlavne aktívnych samíc, ako aj juvenilných jedincov v jelšovom lese poukazuje na vyššiu reprodukčnú aktivitu v tomto prostredí. V dubovo-brestovom lese bol zistený vyšší podiel dlhodobu rezidentných samcov, rezidencia samíc sa medzi sledovanými prostrediami nelíšila. U oboch pohlaví bola zistená vyššia hmotnosť jedincov v dubovo-brestovom lese, čo naznačuje lepšiu kondíciu jedincov v tomto prostredí. Rozdiely v rezidencii jedincov medzi sledovanými lokalitami boli pravdepodobne spôsobené väčšou rozlohou a heterogenitou jelšového lesa, súčasne s jeho nevhodnými podmienkami počas zimného obdobia.

ACKNOWLEDGEMENTS

This work was carried out with the financial support of the grants by VEGA No. 1/7197/20 and 1/0017/03. We also thank Lenka TREBÁČKÁ for her help with the field-work.

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