Small mammals of a forest reserve and adjacent stands of the Kelečská pahorkatina Upland (Czech Republic) and their effect on forest dynamics

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ABSTRACT: The community of small terrestrial mammals (STM) was studied on seven experimental plots characterizing forest stands in various stages of succession development and with different level of management from plantings through production/commercial stands to a forest reserve. Increased attention was paid to dominant species and their effects on the dynamics of the forest reserve. In total, eight species of STM were detected with the highest dominance and abundance of *Apodemus flavicollis* and *Myodes glareolus.* The total relative abundance of STM was significantly highest in plantings ($P < 0.05$). *A. flavicollis* was significantly most abundant in production beech stands ($P < 0.05$), differences in the abundance among the other STM species being insignificant. The highest diversity was also determined in plantings ($P < 0.05$) as typical ecotone sites. Different natural conditions of open and high forest sites were also reflected in different weight of specimens of dominant species of STM from these biotopes. In *A. flavicollis*, the difference was highly significant ($P < 0.01$) and in *M. glareolus* significant ($P < 0.05$). Both species significantly affected the forest reserve dynamics through the consumption of forest seeds, particularly of beechnuts (100% consumption of the 2007 crop). However, according to the proportion of natural regeneration from previous years, the reserve proved resistance to the impact of rodents caused by the consumption of seeds in a long-term horizon.

Keywords: *Apodemus flavicollis*; forest natural regeneration; *Myodes glareolus*; nature reserve; small terrestrial mammals; tree seed crop

Thanks to their life strategy, small terrestrial mammals are characterized by high reproduction capacity and thus also by considerable fluctuation of the population dynamics, being important consumers and secondary producers in ecosystems. The ability to reach considerable population densities under optimum conditions significantly affects the site character occupied by the mammals, which can be well documented also on forest ecosystems (Pucek et al. 1993; Wolff 1996; Jedrzejewska et al. 2004). There, the rate of their impact is dependent on the level of ecological stability closely related with anthropogenic effects (Heroldová et al. 2007, 2008; Suchomel 2008). As compared to cultivated stands, natural and close-to-nature forests show a number of self-regulation mechanisms allowing to suppress impacts of the possible effect of rodents in the period of their population peak (Pucek et al. 1993; Heroldová et al. 2007, 2008). On the other hand, production stands represent a more optimum biotope for small mammals from the aspect of their population density (Zejda et al. 2002; Suchomel, Heroldová 2004, 2008), being therefore reservoirs of stable and abundant populations also for the surrounding area of natural character including nature reserves. Small-area forest reserves surrounded by commercial production stands and easily colonisable due to their insufficient area can be potentially more stressed by the impact of small mammals than extensive natural sites.

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In the present paper, problems of small terrestrial mammals are analysed in relation to various types of forest sites with an increased emphasis on dominant species of rodents the role of which is crucial in the dynamics of forest ecosystems (e.g. Jensen 1982, 1985; Pucek et al. 1993; Jedrzejewska et al. 2004). Data on other species of small terrestrial mammals including insectivores were used to evaluate the diversity of communities in particular monitored biotopes and to assess their importance for the species diversity of these animals.

Study Area

For the study of populations experimental plots in the Valšovice Training Forest Range (Přerov District) were used, which is a special-purpose area of the Secondary Forestry School in Hranice na Moravě. The studied plots are situated in Natural Forest Area No. 37 – the Kelečská pahorkatina Upland (in total 1,003.47 ha) on the boundary line of the Oderské and Hostýnské vrchy Hills. They create a promontory of the Oderské vrchy Hills terminated by the Maleník plateau. The highest peak in the management-plan area (MPA) is Maleník with its height of 479 m. Mean altitude a.s.l. ranges between 300 and 400 m. The lowest point of the MPA is situated on the Bečva riverbank in the northern part at an altitude of about 240 m. As for climate, the locality belongs to a moderately warm region with warm subregion B3, hilly country, slightly humid, with mild winters. Mean annual temperatures are 7 to 8°C. Mean annual precipitation amounts to 600–700 mm, in recent years only to 450–500 mm. Prevailing winds blow from NW–W–SW (according to the Forest Management Plan 2001–2010). In total, seven experimental plots were chosen with a different level of management, which included different forest sites from early succession stages to natural forests free of management measures. Three of the plots represented commercial stands nearly of the character of beech monocultures (P1–P3), two plots represented stands in the nature reserve (P4, P5) and two plots were plantings of various age (P6, P7):

P1 (49.525658 N, 17.6862752 E): stand part 4A14, mean altitude 410 m, age 144 years, HS (management group of stands) 4446, forest type 4B1. The high-quality fruit-bearing beech (*Fagus sylvatica*) stand of genetic classification B, European larch (*Larix decidua*) – 6%, small-leaved linden (*Tilia cordata*) ‑ 2%, sessile oak (*Quercus petraea*) ‑ 1%. Sporadically, natural regeneration of beech, sessile oak, hornbeam (*Carpinus betulus*), smooth-leaved elm (*Ulmus carpinifolia*), European ash (*Fraxinus excelsior*), sycamore maple (*Acer pseudoplatanus*), small-leaved linden and larch. *Convallaria majalis*, *Lathyrus vernus* and *Carex pilosa* occur in undergrowth.

P2 (49.526033 N, 17.6875392 E): stand part 4A6a, mean altitude 390 m, age 60 years, HS 4446, forest type 4B1. Mainly a pole-stage stand to a large-diameter stand of European beech (*Fagus sylvatica*) with an admixture of small-leaved linden (*Tilia cordata*). The herb layer consists of *Convallaria majalis*, *Lathyrus vernus* and *Carex pilosa*.

P3 (49.523157 N, 17.6763829 E): stand part 5C12, mean altitude 400 m, age 127 years, HS 16, forest type 3J2. Protection forest – "lime-tree little rock". A mixed large-diameter stand (European beech 60%, small-leaved linden 32%, European larch 2%, sessile oak 2%, European ash 2%, hornbeam 1% and sycamore maple 1%) on a steep stony to boundary slope, N–NW slope orientation with protruding rocks. *Convallaria majalis* and *Carex pilosa* occur in undergrowth.

P4 (49.5156567 N, 17.6964967 E): stand part 13C13, mean altitude 368 m, age 131 years, HS 4446, forest type 3B2. Eastern part of the nature reserve called "Dvorčák". A quality oak stand with *Fagus sylvatica* and *Quercus petraea* grows on a gentle SE–S slope, sporadically with gaps. European ash and small-leaved linden self-seeding or even advance growth occur in undergrowth. *Carpinus betulus* and *Acer pseudoplatanus* with interspersed *Tilia cordata* predominate in the tree layer. Dominant species of the herb layer are as follows: *Lathyrus vernus*, *Convallaria majalis*, *Tithymalus amygdaloides*, *Polygonatum multiflorum*, *Petasites albus*, *Carex pilosa*, *Poa nemoralis* etc.

P5 (49.5141806 N, 17.6887167 E): stand part 13C13, mean altitude 360 m, age 131 years, HS 4446, forest type 3B2. The "Dvorčák" Nature Reserve was established on 31 July 1962 by the decree of the Ministry of Education and Culture on an area of 11.71 ha as an evidence of the natural structure of forests of the Moravian Gate. *Fagus sylvatica* with interspersed *Tilia cordata*, *Quercus petraea*, *Carpinus betulus* and *Acer pseudoplatanus* predominate in the tree layer. Dominant species of the herb layer are: *Lathyrus vernus*, *Convallaria majalis*, *Tithymalus amygdaloides*, *Polygonatum multiflorum*, *Petasites albus*, *Carex pilosa*, *Poa nemoralis* etc.

P6 (49.30889 N, 17.41449 E): stand part 5G1b, mean altitude 460 m, age 10 years, HS 446, forest type 4B1. Artificial regeneration of beech *Fagus sylvatica* (95%) with an admixture of ash *Fraxinus* *excelsior* (3%), silver fir *Abies alba* (1%), larch *Larix decidua* (1%), *Alnus glutinosa*, and *Acer pseudoplatanus*, mainly with grasses (*Calamagrostis arundinacea*) and *Rubus fruticosus* in its undergrowth.

P7 (49.31304 N, 17.41118 E): stand part 10C1, mean altitude 380 m, age 9 years, HS 446, forest type 3B2. The planting of *Fagus sylvatica* (74%) with an admixture of *Quercus petraea* (10%), *Fraxinus excelsior* (5%), *Tilia cordata* (5%), *Carpinus betulus* (3%), *Picea abies* (1%), *Acer pseudoplatanus* (1%) and *Ulmus carpinifolia* (1%). The stand is situated on a gentle SE slope dissected by watercourses. Grasses (*Calamagrostis arundinacea*) and *Rubus fruticosus* are dominant in the herb layer.

Sites in the nature reserve, where the majority of studies regarding the impact of small rodents on forest stands were carried out, represented basic plots. Other plots served as comparative plots and for obtaining a comprehensive view of the variety of the small mammal synusia in the monitored region.

MATERIAL AND METHODS

The community of small mammals was studied for a period of three years (2006–2008). In 2006, two trappings were carried out in the spring (June) and autumn season (October) and in 2007 and 2008, three trappings were carried out in the spring (April), summer (July) and autumn (October) season. On each of the plots (P1–P5), 80–100 snap traps were laid in a line at 3-m spacing (Table 1). A kerosene lamp wick parched on oil and flour or smeared with peanut butter was used as bait. On plots P6 and P7, 20–50 traps were laid. The low number of traps in exclusion fences was used because the original intention was to trap small mammals only in order to determine the species which could be potential causal agents of damage to tree plantings without another plan to study the population dynamics or other properties of the community. The smaller number of traps was also given by the limited size of these two experimental plots.

The traps were exposed for the period of 4 days (i.e. 3 nights) and checked in the morning every day (Pelikán 1976). The species, body length and weight of caught individuals were determined in the laboratory. In species that can be confounded (the genera *Apodemus* and *Sorex*) other length measures were also determined. Particular animals were dissected in order to determine sex and sexual activities. Only those animals were considered to be adult that showed characteristic features of maturity, i.e. developed seminal vesicles and large testicles in males, and embryos in the uterus or scars on the uterus after birth – *maculae cyaneae* in females (Zejda et al. 2002).

Basic ecological characteristics of the community were evaluated, namely the dominance and relative abundance of selected species (according to Losos et al. 1985), diversity (Shannon, Weaver 1963) and equitability (Sheldon 1969). In total, 654 small mammals were caught (Table 1).

Statistical evaluation was carried out by means of the Statistica.cz version 8 programme. The *t*-test was used for independent samples (comparisons of the weight of animals, diversity of two sites and relative abundance of two types of sites and two domi-

Table 1. Values of dominance (D), relative abundance (rA), diversity (H') and equitability (E) at communities of small terrestrial mammals detected at studied plots (Σ(n) – total number of individuals, NTP – number of traps and nights, P1 to P7 – experimental plots, description see Chapter of the studied area)

Species	P1		P2		P3		P4		P5		P6		P7	
	D (%)	rA	D (%)	rA	D (%)	rA	D (%)	rA	D (%)	rA	D (%)	rA	D (%)	rA
Apodemus flavicollis	76.3	3.63	64.1	2.08	78.2	3.87	56.9	2.58	62.1	1.62	17.8	1.72	10.5	1.08
Apodemus sylvaticus	7.9	0.38	10.3	0.33	6.4	0.32	6.4	0.29	12.1	0.32	6.7	0.65	2.1	0.22
Apodemus agrarius	0	0	0	0	0	0	6.4	0.29	3.5	0.09	32.2	3.12	28.4	2.9
Myodes glareolus	15.8	0.75	24.4	0.8	15.5	0,77	28.4	1.29	22.4	0.59	37.8	3.66	39.0	3.98
Microtus agrestis	0	0	0	0	0	0	0.9	0.04	0	0	1.1	0.11	11.6	1.18
Sorex araneus	0	0	1.3	0.04	0	0	0.9	0.04	0	0	2.2	0.22	5.3	0.54
Sorex minutus	0	0	0	0	0	0	0	0	0	0	1.1	0.11	3.2	0.32
Talpa europaea	0	0	0	0	0	0	0	0	0	0	1.1	0.11	0	0
Σ*n*	114	78	110	109	58	90	95							
NTP	2,400		2,400		2,220		2,400		2,220		930		930	
H'	0,678		0.912		0.7		1.117		1.003		1.456		1.557	
E	0.617		0.658		0.637		0.623		0.724		0.7		0.8	

nant species of rodents), ANOVA was used to compare the diversity of all trial plots, and Tukey's HSD test and Duncan's post-hoc test were employed to compare the diversity of three types of sites.

Effects of small mammals on forest regeneration were assessed according to the consumption of tree seeds and the amount of emerged seedlings. The actual food offer of seeds was determined in the nature reserve (P4, P5) in the autumn season (2007), namely from ten randomly selected small plots 50 × 50 cm in size converted to ha. The total number of rodents per ha to estimate the seed consumption was calculated according to Zapletal et al. (2000). The total estimate of seed consumption (beechnuts) per ha by the rodent species (*Apodemus flavicollis*, *Myodes glareolus*) was calculated according to Heroldová et al. (2008). The level of natural regeneration in the reserve was evaluated for the purpose of its effectiveness, namely by a single application (in 2008) through checking the number of the youngest tree individuals (up to 3 years of age) on ten randomly selected 10 m^2 plots and then also converted to hectares (Table 2).

RESULTS

In total, eight species of small mammals were found out in the studied area, namely 5 species of rodents and 3 species of insectivores (*Eulipotyphla*, syn. *Insectivora*). *Apodemus flavicollis* with the total dominance D = 53.1% together with *Myodes glareolus* with D = 25.8% was the most abundant species in the area. The rodents represented the group of eudominant species (D > 10%). Moreover, the following species occurred on these plots: dominant (D = 5–10%) *A. agrarius* with D = 9.9%, *A. sylvaticus* with D = 7.0%, recedent (D = 1–2%) *Microtus agrestis* with D = 1.99 % and *Sorex araneus* with D = 1.38% and subrecedent (D < 1%) *S. minutus* with D = 0.61% and *Talpa europaea* with D = 0.15%. The proportions of all determined species on particular plots and their abundance are given in Table 1.

The total abundance (rA) of small mammals significantly fluctuated depending on the site character (Fig. 1) while populations of open sites reached markedly higher abundance (t= –2.698; P = 0.017, t-test). *Apodemus flavicollis* and *Myodes glareolus* were the most important species of small mammals thanks to the values of dominance and relative abundance. A sufficient amount of data made it possible to monitor also the fluctuation of their population dynamics with a possibility to predict effects on the regeneration of forest stands (Figs. 2–5). However, there were considerable disproportions in dominance and abundance revealed by the evaluation of particular types of sites which were related with the biotope preferences of both species (Table 1; Figs. 2–5).

Apodemus flavicollis was the most abundant at localities P1–P5 with high-quality stands of seed-bearing trees (particularly beechnuts). It markedly predominated in commercial stands representing nearly pure beech stands (P1–P3; D >75%; rA > 3.6). Its abundance was significantly higher than the abundance of *Myodes glareolus* (t = 2.358; P = 0.033, t-test). Natural sites of forest reserves (P4, P5) were also a suitable biotope. However, the dominance and abundance of the species was naturally lower there (D = 57–62%; rA = 1.6–2.6) with respect to the higher species and structural diversity of trees and microbiotopes limiting the ecological niche of *Apodemus flavicollis* and allowing the occurrence of a number of other species of small mammals (Table 1). Open sites of plantings were substantially less suitable for *Apodemus flavicollis* (P6, P7; D = 10–18%; rA = 1–1.7). However, the differences in abundance from mature stands were not significant (P > 0.05, t-test).

On the other hand, *Myodes glareolus* was the most abundant species at open sites of plantings (D = 38–39%) reaching the highest abundance out of all local small mammals (rA = ca 4.0). The differences in abundance from mature stands were not however significant (P > 0.05; t-test). Thus, both species showed quite different fluctuations of population dynamics at sites of full-grown stands (P1–P5) and in the early succession stages of plantings (P6, P7) (Figs. 2–5) although significant differences were found only between populations of both species in mature forest stands.

As for the other species of marked dominance which can be important consumers in local forest ecosystems thanks to their abundance, we can

Table 2. The number of seedlings of various tree species (pcs·ha^{-1}) and their proportion (%) in natural regeneration in the Dvorčák nature reserve

	Fagus sylvatica	*Quercus petraea*	*Fraxinus excelsior*	*Tilia cordata*	*Carpinus betulus*	*Acer pseudoplatanus*
pcs·ha^{-1}	10,600	7,600	3,400	1,600	7,400	100
(%)	34.53	24.76	11.07	5.21	24.1	0.33

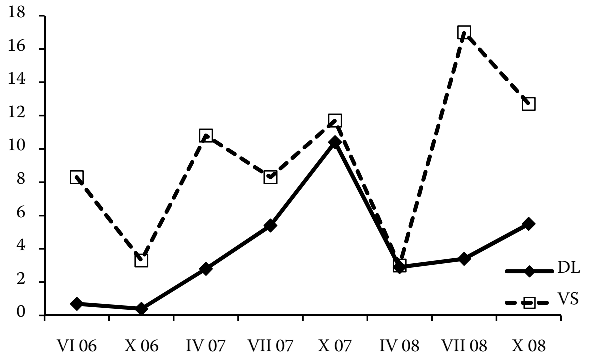

Fig.1. Fluctuations of the abundance of small mammals in various succession stages of forest ecosystems (DL – mature stands, VS – plantings) in the monitored area

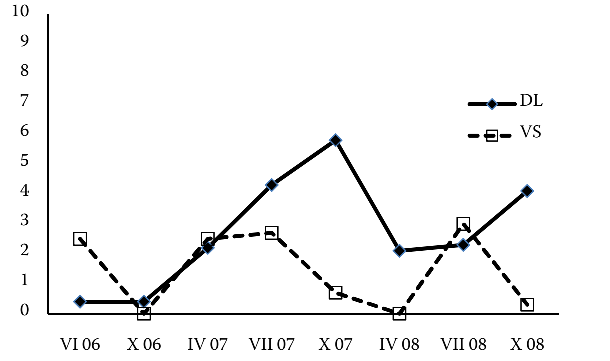

Fig. 2. Fluctuations of the abundance of *Apodemus flavicollis* in various succession stages of forest ecosystems (DL – mature stands, VS – plantings) in the monitored area

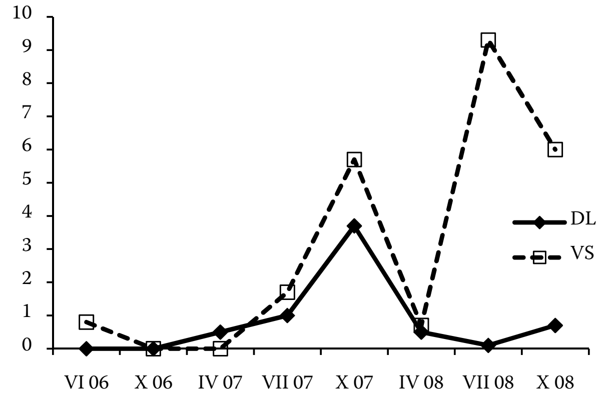

Fig. 3. Fluctuations of the abundance of *Myodes glareolus* in various succession stages of forest ecosystems (DL – mature stands, VS – plantings) in the monitored area

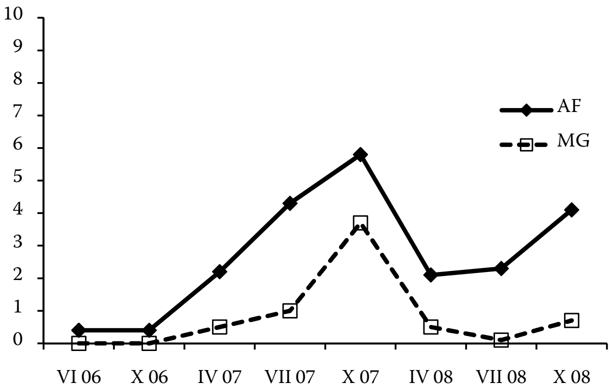

Fig. 4. Differences in the relative abundance fluctuation of *Apodemus flavicollis* (AF) and *Myodes glareolus* (MG) in mature forest stands

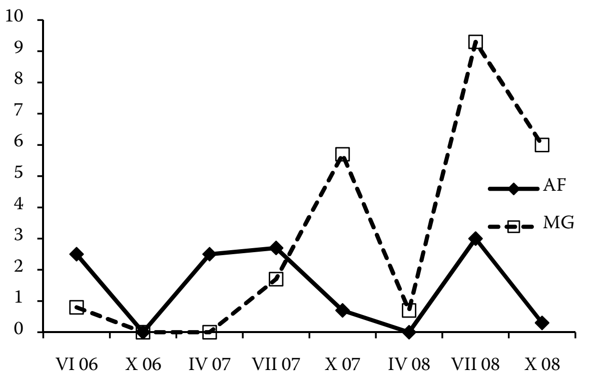

Fig. 5. Fluctuations of population dynamics of *Apodemus flavicollis* (AF) and *Myodes glareolus* (MG) in plantings in the monitored area

mention *Apodemus agrarius* with D = 3.5–6.4% in mature stands (P4, P5) and with D = 28.4–32.2% in plantings (P6, P7) and *Microtus agrestis* on a clearing P7 (D = 11.6%) (Table 1).

The diversity of monitored sites showed a significant effect on the character of diversity of small mammals (Table 1). The highest index of diversity was shown by plantings as early succession stages of forest stands (P6, H' = 1.46; P7, H' = 1.56). Forest reserves (P4, P5) showed somewhat lower diversity (H' = 1.0–1.12) due to the limited amount of open sites and thus the absence of specialized species. Commercial beech stands (P1–P3) with the limited diversity of habitats and low differentiation of food sources (H' = 0.68–0.9) showed the lowest diversity. However, in spite of the given differences, no statistically significant differences (ANOVA) were detected among the particular experimental plots. At a simpler division only into open sites (plantings) and closed mature stands diversity was significantly different ($t = -2.586$; $P = 0.012$, *t*-test) similarly like among the three types of biotopes according to the method of management representing the given plots, i.e. seed-bearing cultivated beech stands (P1–P3), forest reserve (P4, P5) and plantings ($F = 3.342$; $P = 0.043$, ANOVA). At a subsequent multiple comparison (ANOVA, Tukey's HSD test), a significant difference in diversity was determined between seed-bearing beech monocultures and plantings ($P = 0.043$). No difference between these two types of sites and the forest reserve was found out. However, using Duncan's post-hoc test, a statistically significant difference was calculated even between the planting and the forest reserve (P = 0.042) as well as between the planting and the seed-bearing cultivated beech stand (P = 0.026). Communities of small mammals of mature forest stands were also less equalized (E) than in plantings (Table 1).

Forest plantings as succession-initial stages of the forest development show quite different life conditions from those of high forests, which became evident also on the fitness of local populations of small mammals. Thus, some differences were determined between the weights of populations of dominant species (*Apodemus flavicollis*, *Myodes glareolus*) from both types of sites. The values were significant both in adult *Myodes glareolus* (t = –2.143, P = 0.037, t-test) when the mean weight of individuals in forests was 20.38 ± 2.79 g and in plantings 22.22 ± 3.47 g and in all individuals including subadult ones (t = –2.246; P = 0.026, t-test) when the mean weight was 17.76 ± 3.41 g in forests and 19.01 ± 3.74 g in plantings.

In *A. flavicollis*, the weight difference in all individuals without exception of sex activities was even highly significant (t = 3.808; P = 0.00017, t-test). Individuals showed the mean weight of 30.26 ± 9.01 g in the forest and only 23.4 ± 5.95 g in plantings. Similarly, there was a high significance also in the case of separation of adult, i.e. sexually active, individuals, when their weight was 35.65 ± 6.84 g in the forest and 27.2 ± 4.31 g (t = 3.850; P = 0.00017, t-test) in plantings.

The population of granivorous species of small mammals was also affected by food offer in the form of tree seeds. Their actual amount aimed at beech was studied in the nature reserve in autumn 2007. The total number of fallen seeds reached (after conversion) 824,000 per ha. The highest production was found in beech, viz 596,000 seeds per ha (D = 72.3%). Hornbeam also provided a significant source of food, namely 184,000 seeds per ha (D = 22.3%). The other two detected tree species produced seeds rather sporadically in the given year. Small-leaved linden provided about 40,000 seeds per ha (D = 4.85%) and sessile oak only 4,000 seeds per ha (D = 0.5%).

Depending on the food offer mentioned above the total numbers of individuals of *A. flavicollis* and *Myodes glareolus* were determined in the forest reserve in autumn 2007, namely about 111 yellow-necked mice·ha^{-1} and about 92 bank voles·ha^{-1}.

With respect to the low crop of seeds of other woody species attention was paid only to the impact of rodents on the food offer of beechnuts. The consumption of beechnuts by *A. flavicollis* was estimated to be 2,109 beechnuts·day^{-1}·ha^{-1}, i.e. within the next 10 months when seeds were utilizable by rodents the potential consumption amounted to about 632,700 beechnuts·ha^{-1}. As for *Myodes glareolus*, its consumption was 1,104 beechnuts·day^{-1}·ha^{-1}, which amounted to about 331,200 beechnuts/ha/ten months. It follows that a loss of seeds caused by rodents was virtually 100% making the stand regeneration impossible in the next year. Checking the natural regeneration also proved it.

To assess the function of self-regulation mechanisms in the reserve in spite of the high consumption of seeds by small rodents the inspection of natural regeneration was carried out. In total, the inspection recorded 30,700 seedlings of various species per ha in 2008. The predominance of beech (34.5%; see Table 2) was marked. However, these were mostly older individuals (aged minimally 2–3 years) while new regeneration from beechnuts (crop of 2007) was virtually absent.

DISCUSSION

Forest stands in the monitored area represent suitable biotopes for eudominant species of small mammals such as *Apodemus flavicollis* and *Myodes glareolus*, significantly affecting the dynamics of forest ecosystem by the consumption of tree seeds (Jensen 1985; Pucek et al. 1993; Wolff 1996; Jedrzejewska et al. 2004; Heroldová et al. 2008; Suchomel, Heroldová 2008). Particularly sites with the predominance of fructiferous beech (*Fagus sylvatica*) trees, the seeds of which represent a substantial part of food of both species (Holišová 1971; Obrtel, Holišová 1974; Holišová, Obrtel 1980; Pelikán et al. 1974; Abt, Bock 1998), are an important reservoir of populations for the whole monitored area particularly in years of seed crop (there in 2007). The dominance of *Myodes glareolus* was, however, substantially lower in these biotopes than that of *Apodemus flavicollis* by reason of its high abundance, aggressiveness and competitiveness (Montgomery, Gurnell 1985; Zejda 2002). It became evident particularly on plots in commercial stands (P1, P3; D < 16%, rA < 0.8; Table 1).

On the contrary, *Myodes glareolus* was the most abundant in plantings representing an optimum biotope for this species due to the dense herb layer providing necessary protection cover and enough food in the form of green plant matter (e.g. *Rubus* spp.), which is, in addition to seeds, the most important component of food (Holišová 1971; Obrtel, Holišová 1974; Abt, Bock 1998; Heroldová et al. 2007). On the other hand, plantings were unsuitable for *Apodemus flavicollis* (lack of food offer in the form of tree seeds), which rather uses them as migration routes (Niethammer, Krapp 1978; Zejda et al. 2002).

The occurrence of *A. agrarius* can be considered interesting in these stands. It is commonly reported as a species of open sites, particularly in agricultural landscape, with close relations to moist biotopes (Niethammer, Krapp 1978; Zejda et al. 2002). The high abundance and dominance in forest plantings (rA about 3) can evidence rather humid microclimate of the site. Its food preferences include a high proportion of invertebrates and small seeds (weeds, grasses), therefore its effect on forest regeneration is negligible having quite a positive role by the consumption of animals (Zejda et al. 2002). The marked dominance of bank vole in plantings (D = 11.6%) was also important. This species is potentially an important pest of local beech stands due to bark browsing (Gill 1992; Heroldová et al. 2007).

Soricidae showed rather low dominance as well as relative abundance in the area (Table 1), which can be related with the total fall of the group in Moravia in the last decades (Suchomel, Heroldová 2004). Generally, small mammals showed slightly higher abundance at open sites (Fig. 1) which represent an important reservoir of rodents there (particularly of Arvicolidae). These rodents can affect forest regeneration by bark browsing (Gill 1992; Heroldová et al. 2007; Suchomel 2008).

In addition to the high abundance of small mammals higher species diversity was also observed at open sites of plantings. It corresponds to the level of richly structured biotopes (Pelikán 1986, 1989; Stanko et al. 1996; Bryja et. al. 2001; Suchomel, Heroldová 2004, 2007) being related with the site character, which represents (thanks to its limited size and vicinity of forest stands) a characteristic ecotone zone with a marked ecotone effect, i.e. the occurrence of both forest and nonforest species of small mammals (Pelikán 1986; Stanko et al. 1996; Suchomel, Heroldová 2004, 2007).

It means that the structure of the community of small terrestrial mammals and population dynamics as well as the fitness of particular species are dependent on the site character. Similarly, populations of small mammals affect the site, in forest ecosystems particularly by the intensity of their impact on forest regeneration. In this sense, the most important are dominant species of rodents affecting forest regeneration mainly by the consumption of tree seeds and seedlings (Pucek et al. 1993; Jedrzejewska et al. 2004; Heroldová et al. 2008; Suchomel, Heroldová 2008) or bark browsing in the winter season under the shortage of food offer (Gill 1992; Heroldová et al. 2007). The resistance of forest biotope to damage caused to (natural and artificial) regeneration depends on its ecological stability and structure (Heroldová et al. 2007; Suchomel 2008).

Effects of small mammals on the forest dynamics resulting from the consumption of tree seeds as well as their dependence on food offer were quite frequently studied under conditions of this country (e.g. Pelikán et al. 1974; Heroldová et al. 2008; Suchomel, Heroldová 2006, 2008) and particularly elsewhere in Europe (e.g. Jensen 1982, 1985; Flowerdew et al. 1985; Pucek et al. 1993; Wolff 1996; Jedrzejewska et al. 2004 etc.). In the area under study, the seed crop caused an increase in the small mammal population (particularly of *A. flavicollis*) during two successive years (2007, 2008, Figs. 1, 2, 4) with the population peak in 2007. Because small mammals respond to the increased food offer by an increase of their populations with some (sometimes even one-year) delay (Jensen 1982; Flowerdew et al. 1985), their population peak in 2007 was affected by the crop of oak (*Quercus* spp.) trees in 2006 and then the higher abundance in 2008 (as against 2006) by the beech crop in 2007. Although the inspection of oak seed crop was not carried out in the studied region in 2006, it is possible to suppose it both according to the high populations of rodents and according to the crop of acorns at other localities in Moravia (Suchomel, Heroldová 2008). In 2007, the crop of beechnuts occurred at the locality synchronously with the crop of beechnuts in piedmont and mountain areas (Heroldová et al. 2008).

The crop of beechnuts was completely consumed by rodents, which was caused partly by its rather small amount (e.g. in the Beskids in the same year, the crop was 1,600,000 beechnuts·ha^{-1} – Heroldová et al. 2008) and partly by the high abundance of rodents (e.g. in the Beskids Mts. in the same time, only twelve *A. flavicollis* per ha were found and one *Myodes glareolus* per ha – Heroldová et al. 2008), which was a result of the population density increase as a response to high food offer from the oak crop in 2006. The total consumption of seed reserves was also affected by the unsuitable timing of beechnut crop to the year of the highest abundance of small mammals on plots P1–P5 for the monitored three-year period (2007; Figs. 2 and 4).

At the surplus of seeds, rodents feed nearly exclusively on them, which may result in 100% losses (Jedrzejewska et al. 2004) already mentioned above. For example, at sites with fructiferous beech trees in the Beskids, the consumption of seeds and beechnuts by *Myodes glareolus* accounted for even 80% of the stomach content (Bryja et al. 2001).

However, at really high amounts of seeds, small mammals are not able to consume the crop totally (Jensen 1985; Wolff 1996; Jedrzejewska et al. 2004). It became evident e.g. in the Beskids Mts., where the two species consumed about 42.75% of the beechnut crop in the given year (Heroldová et al. 2008).

In addition to the actual consumption of beechnuts which is mostly considered to be negative, small mammals also play a positive role in the distribution of seeds at a site. For example, *A. flavicollis* prepares seed reserves for the winter season (as many as 4 kg) which are not, however, fully used and thus the species contributes to the distribution of beechnuts (Niethammer, Krapp 1978; Zejda et al. 2002).

In spite of the considerable stress on the seed crop through the small rodent predation natural regeneration was found out in the reserve, particularly from the previous year dispersion when lower numbers of rodents occurred (Figs. 2–5) and potentially also a higher crop. The occurrence of seedlings from previous years evidences the long-term sufficient regeneration capacity of this forest stand and a certain level of resistance to the impact of small rodents in spite of unfavourable years of the total disposal of seed crop.

In addition to the effect of small mammals on stands through the consumption of seeds their impact by bark browsing was also described in the monitored nature reserve (Suchomel 2008). Analyses confirmed the substantially higher resistance of natural regeneration to browsing in the reserve than in plantings (Gill 1992; Zejda et al. 2002; Heroldová et al. 2007).

Thus, it is possible to state that the impacts of bark browsing exert substantially smaller effects on forest regeneration in forest reserves than the consumption of tree seeds (Gill 1992; Heroldová et al. 2008; Suchomel 2008). Unsuitable site conditions for rodents particularly of the genus *Microtus*, such as sparse herb layer, easier accessibility to predators, intense competition of *A. flavicollis*, protection of seedlings by their accumulation into groups of high densities when only individuals along the margins are available etc. are the reasons for the low rate of damage and higher resistance of young trees.

CONCLUSION

Thanks to their different character, the studied forest sites affected the population dynamics, diversity and fitness of selected species of small terrestrial mammals to a different extent evidencing the importance of biotope differentiation for the species diversity of these animals. The nature reserve, which was in the foreground of our interest, proved resistance to the impact of rodents caused by the consumption of seeds in the long-term horizon. With respect to specific conditions which resulted in the presence of a large population of rodents at the locality in the period of beechnut crop, intensive consumption of this food offer occurred as well as its subsequent disposal and thus new natural regeneration in the next year was prevented. It was a marked intervention into the forest stand dynamics. Natural regeneration in the reserve showed substantially higher resistance to bark browsing than plantings, thus representing a smaller intervention into the stand dynamics than the seed consumption. Plantings and cultivated beech stands are reservoirs of populations of dominant species of small mammals which can intensively colonize surrounding natural forests and affect the dynamics of these ecosystems depending on their population dynamics.

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