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EFFECT OF FELLING ON THE DISTRIBUTION OF RODENTS AND THEIR PREDATORS IN A TRANSITIONAL MIXED FOREST

ABSTRACT: The influence of felling on the distribution of rodents and their predators in a transitional coniferous-deciduous forest in northern Belarus was investigated in relation to stand age, forest type, and soil richness. The study was conducted in two areas differing by top-grounds (clay and sand soils) and, in turn, having different habitat carrying capacities. Three forest parts were investigated: 1) 10%, 2) 20–30%, and 3) 40–60% covered by recent clearcuts. Three age classes of the clearcuts, namely 1) less than 2 years old, 2) 2–5 years old and 3) 6–12 years old, were considered. In total, we obtained data on small rodent numbers in 84 clearcuts, and the data on predators – in 67 clearcuts and the woodland parts differed by logging rate. Eventually, we became convinced that felling generally led to an increase in the abundance and species richness of rodents and their predators and that was attributable in the clearcuts aged up to 12 years. First, logging led to higher densities of *Apodemus* mice, the red fox *Vulpes vulpes* L., weasel *Mustela nivalis* L., tawny owl *Strix aluco* L., common buzzard *Buteo buteo* L. and adder *Vipera berus* L. Also, with the increased felling rate *Microtus* voles and the long-eared owl *Asio otus* L. penetrated in transitional woodlands. Too intensive forest harvesting (more than 40% of recent clearcuts) led to the decline in the populations of several predatory species such as the pine marten *Martes martes* L., Tengmalm's owl *Aegolius funereus* L., Ural owl *Strix uralensis* Pall., and pygmy owl *Glaucidium passerinum* L. The decline in rodent predators found in the conditions of too intensive logging rate was different in the woodlands on sand and clay top-grounds. In the conditions of clay soil too intensive felling led to the pronounced decline of a marked part of the rodent predatory guild inhabiting woodlands, and the species densities decreased to the level that was lower than the initial one. Conversely, in initially poor habitats in the woodland on sandy deposits, logging of any rate led to the increase in numbers of rodents and their predators compared to undisturbed forest. But moderate logging was found to be the most favourable for the community there.

KEY WORDS: rodents, carnivores, raptors, logging, clearcut

1. INTRODUCTION

Clear cutting is an important form of man-made disturbance in woodlands. As a result, the majority of recent clearcuts look like grasslands that are gradually transformed into young forests due to natural reforestation and/or forest plantation. Indeed, felling impacts not only forest plant communities, but it also disturbs animal populations inhabiting woodland (Hansson 1978, 1994, Wołk E. and Wołk K. 1982, Jensen 1984, Kirkland *et al.* 1985, Aksenova and Buljuk 1986, Hakkarainen *et al.* 1996, Bryja *et al.* 2002). Particularly, this affects rodents as small herbivores and, in turn, their predator guild (Hansson 1978, 1994, Wołk E. and Wołk K. 1982, Jensen 1984, Kirkland *et al.* 1985, Aksenova and Buljuk 1986, Hakkarainen *et al.* 1996, Bryja *et al.* 2002).

However, it is worthwhile to get to know whether timber harvest has only a negative effect on the community of rodents and their predators or whether there is some positive effect on the species diversity and density. Such positive influences on rodents (Hansson 1978, Wołk E. and Wołk K. 1982, Bryja *et al.* 2002) and their predators (Hakkarainen *et al.* 1996, Petty 1999, Bryja *et al.* 2002) in a forest-clearcut interface with increasing of species diversity and biomass in recent clearcuts are known in the literature. Nevertheless, to date, no study has simultaneously addressed the responses of an entire community of rodents and their predators to clear cutting. Moreover, published studies on the issue were mostly conducted in boreal coniferous woodlands in Sweden (Hansson 1978, 1994, Kirkland *et al.* 1985, Hakkarainen *et al.* 1996) and Finland (Jensen 1984, Sami *et al.* 1998) and in more nemoral pine-deciduous (mostly broad-leaved) woodlands (Wołk E. and Wołk K. 1982, Aksenova and Buljuk 1986, Bryja *et al.* 2002), but none of them related to the transitional boreo-nemoral coniferous-deciduous (mostly small-leaved) woodlands of the European forest zone. In our study, we measured the response of the entire rodent and predator community to timber harvest. Taking into account previously obtained results on the community of rodents and their predators in transitional woodlands in northern Belarus (Sidorovich *et al.* 2003a, b, 2005, 2006), we predicted that felling influence on the community structure varies relating to clearcut age, habitat type (centre compared to edge of clearcut) and type of top-ground (sand or clay). Respectively, the research design established was applied to test the above hypotheses.

2. STUDY AREA

Our study took place in northern Belarus, in mixed coniferous-small-leaved forests, where the more southerly deciduous (mostly broad-leaved) forests merge with boreal coniferous forests. Common deciduous trees include the black alder *Alnus glutinosa* L. and grey alder *A. incana* L. Moench, birches *Betula pendula* Roth, *B. pubescens* and aspen *Populus tremula* L., whereas there are few masting broad-leaved trees such as the oak *Quercus robur* L., lime *Tilia cordata* Mill., maple *Acer platanoides* L. and ash *Fraxinus excelsior* L.

In the transitional mixed forest in northern Belarus there is a diverse predatory guild of rodent consumers that mainly consists of the weasel *Mustela nivalis* L., pine marten *Martes martes* L., red fox *Vulpes vulpes* L., Ural owl *Strix uralensis* Pall., tawny owl *S. aluco* L., Tengmalm's owl *Aegolius funereus* L., pygmy owl *Glaucidium passerinum* L., common buzzard *Buteo buteo* L., and adder *Vipera berus* L. Concerning rodent species, the bank vole *Myodes glareolus* Schr. and several mouse species of genus *Apodemus* are common in the woodland, and the species compose the main part of the forest rodent community (Sidorovich *et al.* 2003 a, b). *Microtus* voles, mostly living in open grasslands, rarely occur in forest habitats of transitional woodlands.

In European woodlands, presence of masting broad-leaved forests, which periodically produce a big amount of nourishing seeds that are important for rodents, leads to a pronounced cyclicity in rodent populations inhabiting such woodlands (Jędrzejewska and Jędrzejewski 1998). In transitional woodlands that are prevailed by coniferous and small-leaved trees, food supply for rodents is markedly more stable on multiannual scale. Therefore, in the transitional woodlands the bank vole and other forest rodent species have only seasonal fluctuations with no recurrent cycles of outbreaks and crashes (Jędrzejewski and Jędrzejewska 1996, Sidorovich *et al.* 2003a, 2005).

This study was conducted in semi-natural landscapes of northern Belarus. There is a rather dense river network, numerous glacial lakes, large forests and bog ecosystems on rough glacial terrain, whereas a man-made part (villages and fields) constitutes only 8–14% of the landscape. The data have been collected in two areas substantially differing in top grounds originated from the last glaciation that resulted in considerably different carrying capacities of the community habitats (Solovej *et al.* 2001, 2003).

The first study area is situated on the upper reaches of the Lovat River (Gorodok district, Vitebsk region, NE Belarus; 55°N, 31°E) and covers an area of approximately 300 km^2. Surface ground deposits are rich in clay, which ensures good water supply and abundant trace elements, and, consequently, rich soil (hereafter "clay" area). Plant communities in the "clay" area have a high species diversity and productivity, and habitats with high carrying capacity for herbivores dominate. Forest types, characterised by abundant and diverse vegetation (mature forests dominated by spruce, medium-aged deciduous forests and black alder swamps) make up to 53% of the woodland structure. Therefore, species richness and population biomass of rodents in the "clay" area are high (Sidorovich *et al.* 2003b).

The second study area (Polotsk district, Vitebsk region, central north of Belarus; 55°N, 29°E), covers an area of approximately 250 km^2. Surface ground deposits consist of sand mainly (hereafter "sandy" area), with clay only in valleys of glacial lakes and rivers. Soils of the area are barren because of poor water supply. Therefore, the woodland is dominated by pine stands with very poor ground vegetation, constituting about 60% of forest on dry land and 19% in raised bogs. Consequently, a species-poor rodent community with very low biomass is characteristic of the "sandy" area (Sidorovich *et al.* 2003b).

During the study period, as well as before, the woodlands in both study areas were intensively exploited by human to get timber. There, timber harvest was widespread and occurred in nearly all forest types. Clear cutting was the most common practice of the local forestry, and entirely logged areas ranged from 1–100 ha (usually 10–20 ha). Shape of a clearcut was mostly rectangle or any other. Also in some places local forestry did selective tree harvesting. Usually newly planned clearcut plots were scattered by forestry through the woodlands. In effect recent clearcuts in the woodlands are interspersed with either earlier clearcuts reforested naturally or forest plantations or undisturbed forest types.

In northern Belarus, severity of winters varies from year to year. Some of winters are rather mild with a fairly short snowy period (1.5–2 months), but the majority of them are quite severe, with a snow cover ranging from 30 to 90 cm, and an air temperature of about -20°C and lower for several weeks. Such hard frost periods usually alternate with thaws lasting for several weeks.

3. MATERIAL AND METHODS

The research design was established to reveal the variation in the distribution of rodents and their predators along the gradient of felling rate and taking into account the age of clearcuts and soil richness. We used felling rate expressed by proportion of recent clearcuts (that have been done for the last 7 years) as an index of the extent and intensity of logging in the woodlands. We used the age of clearcuts as a gauge of habitat recovery time due to reforestation. Soil richness determines species diversity and productivity of plant communities in forest habitats and clearcuts in course of their reforestation. In both study areas we worked in three parts of the woodlands that had been chosen along the gradient of felling rate as follows: 1) 10%, 2) 20–30%, and 3) 40–60% covered by recent clearcuts. Three age classes of clearcuts, namely 1) less than 2 years old, 2) 2–5 years old and 3) 6–12 years old, were considered. Felling plots aged older than 12 years looking as succession young forests were out of the study. In both "clay" and "sandy" study areas, we investigated the model types of undisturbed forest (forest dominated by spruce in the "clay" area and dry land pine stand in the "sandy" area) and their clearcuts of the different age classes. Three types of transects were placed in a particular felling area: 1) within clearcut in the centre (hereafter clearcut centre); 2) in ecotone between forest and clearcut (hereafter clearcut edge or ecotone); 3) within undisturbed forest of the same type as it had been felled (hereafter unharvested forest). The transect in the clearcut ecotone was placed in a 10 m wide stripe that overlapped 5 m in the clearcut and 5m in unharvested forest. Transects in the unharvested forest were situated at the distance approximately 300 m from the clearcut edge. Length of the clearcut transects (i.e. centre and edge ones) was chosen to be maximally possible for 10–20 ha clearcuts that are common in Belarus, and it varied from 0.4 to 1.5 km, while transect length in adjacent unharvested forest was about 1 km. These three transects were used to estimate the abundance index of rodents and register activity of rodent predators in felling plots of different age in both "sandy" and "clay" areas. Additionally, to reveal an influence of logging on the density and distribution of rodent predators, we did their census (see the used methods below) along the transects placed in the three mentioned woodland parts differing by felling rate. The transects were 15 km long and crossed the whole variety of habitats in such a forest part and were directed northwards to be random.

Our analysis entailed many pairwise comparisons of species richness and abundance between: 1) different parts of clearcut (centre and edge) and unharvested forest within the same study area; 2) the same parts of clearcuts of different age classes within the same study area; 3) woodland parts differing by felling rate. We did not make similar comparisons between the "clay" and "sandy" areas, because the community is markedly differently structured there (Sidorovich *et al.* 2003b), while the purpose of this study was only to analyse the impact of felling on the same community, but initially differently structured in the areas characterized by different habitat carrying capacity (Solovej *et al.* 2003). Statistical analysis of the data obtained was done using the Spearman correlation (r_s) between species parameters (abundance index, activity registration) and logging parameters (age of clearcuts, felling rate); t-test of the difference between two means, and G-test for homogeneity of proportional data (Sokal and Rohlf 1995). We used Simpson's index (*S*) to estimate the diversity of rodent species (Krebs 1998):

$$S = 1 - \sum (p_i)^2 \qquad (1)$$

where *S* – Simpson's index of diversity, p_i – proportion species *i* in the species structure of rodent community.

We used the simplified Morisita's index (*M*) to examine structural similarity (Krebs 1998). Overlap between the species structure of rodent communities in habitat *j* and *k* is calculated as follows:

$$M = \frac{2\sum_i^n p_{ij}\, p_{ik}}{\sum_i^n p^2_{ij} + \sum_i^n p^2_{ik}} \qquad (2)$$

where p_{ij} – proportion species *i* in the species structure of the community in habitat *j*; p_{ik} – proportion species *i* in the species structure of the community in habitat *k*; *i* = 1, 2, 3,..., *n*; *n* – number of rodent species.

Rodent number was investigated by snap trapping during the post-reproductive period (late October – early November). As it is commonly used (Jędrzejewski and Jędrzejewska 1996), efficiency of rodent snap trapping was applied as well-known rodent abundance index (hereafter *RAI*) that was expressed as follows:

$$RAI = \frac{RC}{d \times st} \times 100 \qquad (3)$$

where *RC* – number of rodents captured by given number of snap traps (*st*) and during snap trapping duration, *d* – snap trapping duration in days.

The number of rodents captured during 100 snap trap-nights was used as a proxy of rodent density; the species proportions in trapping bags were applied to approximate their proportions in the living rodent community (hereafter species structure of the rodent community). Such data on rodent numbers may be obtained during snowless season only. So as the data on the distribution of rodent predators were gathered by snowtracking in winter, the most relevant data on rodent numbers could be gained in late autumn. Also, autumn (i.e. post-reproductive) data on rodent numbers indicate habitat differences in carrying capacity for rodents better due to higher numbers of each species. To do rodent census in a given place, from 20 to 50 snap traps were set in a line at approximately 5 m intervals for three days and checked daily. Fried bread was used as bait. In total, we obtained data on small rodent numbers from 84 clearcuts, where about 30,000 snap trapping were completed.

We evaluated adder distribution using visual censuses on 3 m wide transects in 53 clearcuts in May. Transects were allocated evenly to clearcut centres, edges, and unharvested forest, and were only performed under suitable weather conditions (Pikulik *et al.* 1988).

Activities of red foxes, weasels, polecats and pine martens in 67 felling plots were determined through snowtracking. For that in winter we counted the species trails on the same transects situated in the clearcut centre, clearcut edge and unharvested forest. Activity index of the species (hereafter *PAI*) was calculated as follows:

$$PAI = \frac{PT}{d \times l} \times 100 \qquad (4)$$

where PT – the number of the species trails crossed the transects, l –the transect length (in km) and d – the number of days passed since the last snowfall. As a result, we obtained the average number of trails per 1 km daily. This activity index was used as a proxy of the species selection of various habitats in felling plots.

Similar counting of trails of red foxes, polecats and pine martens was done along the 15 km transects established in the woodland fragments with different felling rates. Based on these data, the species densities were estimated by the Priklonsky's formula (Priklonsky 1965, see Jędrzejewska and Jędrzejewski 1998 for details). The formula was adapted to the habitat conditions of northern Belarus involving data on daily movement distance of red foxes and pine martens. By combining snowtracking and radiotracking studies, we estimated the daily movement distance of the species in the variety of snow conditions (Brzeziński *et al.* 1992, Zalewski *et al.* 1995).

We conduced owl censuses along the same 15 km transects in late March and April following the published methods (Holmberg 1979, Fuller and Mosher 1981, Johnson *et al.* 1981), which are based on a species-specific territorial call of owls. We assumed that 600 m would be an appropriate census transect width that was based on our previous experiences of numerous attempts to listen to such calls at a distance. Along census transects, we repeated calls of different owl species (the Ural owl, tawny owl, Tengmalm's owl, pygmy owl and long-eared owl) every 600 m. To call owls, we played a tape with owl calls on a tape-recorder. Owl censuses were conducted from dusk until about 1am and from about 3 am until dawn mainly by one person on foot. The transects were investigated twice, with a second control census done in the opposite direction. One stop took about 15–20 minutes until territorial calls of all owl species were played. We surveyed only under suitable weather conditions (with no rain or strong wind). The following assumption was used. If a territorial call of an individual owl of a particular species was recorded at least twice in one place during the initial and second control census, one active territory was noted, for which we formally stated the presence of a couple of the owl species. The neighbouring territories of each owl species were separated one from another on the basis of simultaneous observations of two or more calling individuals. Thus, our estimates of owl density were slightly inflated (in an active territory there may be only one individual) but comparable because the same method was used in each census transect.

To estimate numbers of common buzzards, we searched for all their nests in each forest fragment, and then checked the nests in the breeding period. Additional pointed long-lasting (3–5 hours) visual observations of flying couples with or without fledglings was helpful to detect several extra pairs of the species.

Doing census of weasels, we counted the species track concentrations by shuttle inspecting of a particular plot (2–4 km^2) in early winter in the conditions of little snow cover. We did census of weasels only if there was no snowfall for one or two day. Weasel track concentration was presumably accepted as presence of an individual weasel.

4. RESULTS

4.1 Rodents and predators in "clay" area in connection with forest exploitation

Overall in both the unharvested forests dominated by spruces and clearcuts, we captured eleven rodent species during snap trapping census, including the yellow-necked mouse *Apodemus flavicollis* Melch., wood mouse *A. sylvaticus* L., pygmy field mouse *A. microps* Krat. *et* Ros., striped field mouse *A. agrarius* Pall., common rat *Rattus norvegicus* Berk., harvest mouse *Micromys minutus* Pall., bank vole, common vole *Microtus arvalis* Pall., field vole *M. agrestis* L., forest dormouse *Dryomys nitedula* Pall., and birch mouse *Sicista betulina* Pall. (Table 1A). The bank vole was the most common species in clearcuts (63% of rodents captured), edge (78%) and unharvested spruce forest (84%). In clearcuts, we additionally captured the field vole and common rat; however these were not captured in the unharvested spruce forest, while the forest dormouse was merely revealed in fairly old forest habitats (Table 1A). Also, common voles were caught much more frequently in clearcuts than in the unharvested spruce forests, where this rodent species was registered only a few times. The mean number of species recorded in one census transect in a clearcut centre was 1.4 fold higher than that in an unharvested forest habitat (2.9 *versus* 2.1; t = 3.74, $P = 0.001$). Heterogeneity in the species structure of the rodent communities assessed by Simpson's index (S, see formula 1) appeared to be higher in the clearcut centre compared to the initial forest biotope dominated by spruces ($S = 0.52$ versus $S = 0.28$). Looking at the rodent species richness in clearcuts of different age classes, the following differences were found. The mean number of species recorded in one census transect in the centres of clearcuts aged up to 2 years and 2–5 years was 1.3–1.4 fold higher compared to that in the centres of clearcuts older than 5 years (3.1–3.3 versus 2.4, t = 1.8–2.2, $P = 0.03–0.05$). We did not find similar significant differences in the clearcut edges of different age classes (t = 0.73–1.49, $P = 0.10–0.26$), where the mean number of rodent species recorded in one census transect varied from 2.3 to 2.6. Species proportions in rodents inhabiting the centres and edges of clearcuts of different age classes and unharvested forests were very similar: the centres of clearcuts of different age classes – the unharvested spruce forests (Morisita's index M = 0.92–0.98, see formula 2; G-test = 4.4–16.6; P = 0.12–0.95); the clearcut centre – the clearcut ecotone ($M = 0.93–0.99$; G-test = 2.6–13.3, $P = 0.28–0.99$); the clearcut ecotone – the unharvested spruce forest ($M = 0.99$; G-test = 1.3–3.6, $P = 0.97–1.00$); between the centres of clearcuts of different age classes ($M = 0.97–0.99$; G-test = 3.6–7.7, $P = 0.73–0.98$); between the clearcut ecotones of different age classes ($M = 0.98–0.99$; G-test = 1.5–4.2, $P = 0.96–1.00$).

Similarly to the rodent species richness, the abundance index of rodents (*RAI*; see formula 3) in both the centres and ecotones of clearcuts of all age classes was higher than that in the unharvested spruce forests (Table 1A): clearcut centres – 1.2–1.6 fold (t = 0.80–2.66, $P = 0.01–0.22$), clearcut ecotones – 1.1–1.7 fold (t = 0.29–3.13, $P = 0.003–0.42$). The rodent numbers in felling plots was found to be different according to clearcut age. Mean score of rodents captured per 100 snap-trap-nights (*RAI*) in the centres of clearcuts aged 2–5 years was found to be 1.2–1.4 fold higher than that in both the centres of clearcuts older than 5 years and aged up to 2 years (statistically not significant, t = 0.77–1.48, $P = 0.09–0.25$). Among clearcut ecotones the highest abundance index of rodents was found in logging plots up to 2 years old compared to that of older age classes (t = 1.79–1.91, $P = 0.05–0.07$).

Carnivore activity (*PAI*, see formula 4) was higher in the clearcut ecotones compared to the clearcut centres and unharvested spruce forests (Fig. 1): the red fox – 1.5–2.3 fold more frequently (t = 1.33–2.62, $P = 0.01–0.09$), weasel – 1.5–2.3 fold (t = 2.20–2.32, $P = 0.02–0.03$), pine marten – 1.2–2.0 fold (t = 0.31–0.84, $P = 0.22–0.38$). Indices of carnivore activity recorded in logging plots of different ages were not significant (t = 0.23–1.05, $P = 0.17–0.42$). Considering the variation in indices of rodent abundance (*RAI*) and carnivore activity (*PAI*) through the various habitats appeared in the woodland affected by logging (i.e. centre and edge of clearcuts of different age classes, unhar-

Table 1. Rodent abundance index (*RAI*, formula 3) estimated in different habitat types in relation to felling in woodlands on clay and sand top-grounds, October 1999–2003. Mean number of individuals captured per 100 snap trap-nights, its standard deviation (SD) and number of census plots investigated (n) are given.

A. "Clay" area

Rodent species	Unharvested spruce forest (n=61)	Central part of clearcuts aged as:			Clearcut ecotone aged as:		
		up to 2 years (n=8)	2–5 years (n=8)	> 5 years (n=8)	up to 2 years (n=5)	2–5 years (n=6)	>5 years (n=5)
Field striped mouse	0.06±0.53	1.2±2.31	0.3± 0.96	–	–	–	–
Yellow-necked mouse	2.9± 3.25	8.4± 6.23	11.2± 6.46	6.0± 5.89	5.6 ± 5.04	6.3 ± 2.92	4.3 ± 3.7
Pigmy field mouse	0.02± 0.17	0.8±2.19	–	0.2± 0.46	0.3± 0.63	–	–
Wood mouse	0.3±0.63	0.8±1.64	0.3± 0.61	0.3± 0.96	0.7 ±1.03	–	0.2 ± 0.54
Bank vole	18.1±10.18	16.4±15.36	21.1± 12.3	18.3±11.28	29.5 ± 7.27	22.7 ± 9.17	18.8 ±9.12
Harvest mouse	0.2±0.97	0.2±0.40	1.2± 2.41	0.5 ± 1.27	–	0.2 ± 0.49	–
Field vole	–	0.3± 0.59	0.5± 1.01	0.2 ± 0.42	0.6 ± 1.28	–	–
Common vole	0.02± 0.09	0.4± 0.39	0.2± 0.50	–	–	0.6 ± 1.47	–
Common rat	–	–	0.2 ± 0.46	–	–	–	–
Forest dormouse	0.05± 0.37	–	–	–	–	–	–
Birch mouse	0.02± 0.09	–	–	–	–	–	–
Pooled abundance	21.7± 11.3	28.5± 9.73	35.0± 13.55	25.5±12.73	36.7 ±10.22	29.8 ±14.77	23.3±11.94
Number of species	9	8	8	6	5	4	3

B. "Sandy" area

Rodent species	Unharvested pine forest (n=23)	Central part of clearcut aged as:			Clearcut ecotone aged as:		
		up to 2 years (n=6)	2–5 years (n=7)	> 5 years (n=10)	up to 2 years (n=3)	2–5 years (n=3)	> 5 years (n=3)
Field striped mouse	–	–	0.1 ± 0.49	–	–	–	–
Yellow-necked mouse	0.17 ±0.83	0.5 ± 1.09	2.2 ± 2.08	1.3±1.12	0.9 ±1.56	0.9±0.78	0.9 ± 0.75
Pigmy field mouse	–	–	0.1 ± 0.49	0.4± 0.93	–	0.4 ± 0.75	–
Wood mouse	0.12 ±0.56	–	1.0 ± 1.55	1.2 ± 2.08	–	–	–
Bank vole	1.35 ±1.58	–	1.2 ± 1.98	2.4± 2.71	–	3.6 ± 2.08	0.9 ± 1.56
Harvest mouse	–	–	1.0 ± 1.31	0.6 ± 1.35	–	0.4 ± 0.75	–
Field vole	–	–	0.4 ± 1.02	–	–	0.4 ± 0.68	–
Common vole	–	–	0.8± 1.07	0.1 ± 0.41	–	0.9 ± 1.56	–
Pooled abundance	1.64 ± 1.9	0.5 ± 1.09	6.8 ±4.92	5.9 ± 6.2	0.9 ± 1.56	6.6 ± 3.59	1.8 ± 2.04
Number of species	3	1	8	6	1	6	2

vested forest), we found out positive correlations between the indices: weasel – $r_s = 0.67$, $P = 0.05$; the red fox – statistically not significant, $r_s = 0.37$, $P = 0.41$; pine marten – $r_s = 0.88$, $P = 0.005$.

Three different trends in changes of densities of rodent predators in the woodland parts differently affected by logging were found (Table 2). The first one was the density increasing with a higher rate of felling. This trend was attributable to the red fox (the increase was 1.4 fold), weasel – (1.8 fold), tawny owl (2.5 fold), long-eared owl (12.0 fold), common buzzard (3.1 fold), adder (5.9 fold). Another trend was an opposite one, when species density decreased with higher felling rate. Such response was demonstrated by the Ural owl (2.1 fold). The third trend was an increase of species density in the moderately logged woodland fragment compared to the less disturbed forest, but when the felling rate became higher, its population declined to the density level that was lower than initial one. The pine marten, polecat, Tengmalm's owl and pygmy owl showed such features (Table 2). If we consider the above predatory species altogether, an increase in numbers of rodent predators about 2.5 fold was found, while comparing the forest fragments having less than 10% of recent clearcuts and 40–60% of recent clearcuts.

4.2. Rodents and predators in "sandy" area in connection with forest exploitation

In total, in pine stands and their clearcuts, eight rodent species were captured during the census by means of snap-traps (Table 1B). The species were as follows: the yellow-necked mouse, wood mouse, pygmy field mouse, striped field mouse, harvest mouse, bank vole, common vole, and field vole. The bank vole was one of the predominant rodent species: in clearcut centres (20% of rodents captured), clearcut ecotones (48%) and unharvested pine forests (82%) (Table 1B). Another species frequently composed the rodent community in the "sandy" area was the yellow-necked mouse: in clearcut centres (51%), clearcut edges (29%) and unharvested pine forests (10% of rodents captured). Generally, bank voles were more often caught in the pine stands (82 *versus* 20%; G-test = 41.29, $P < 0.01$), while *Apodemus* mice in the clearcuts (67 versus 18%; G-test = 30.22, $P < 0.01$). In the clearcuts, we also captured

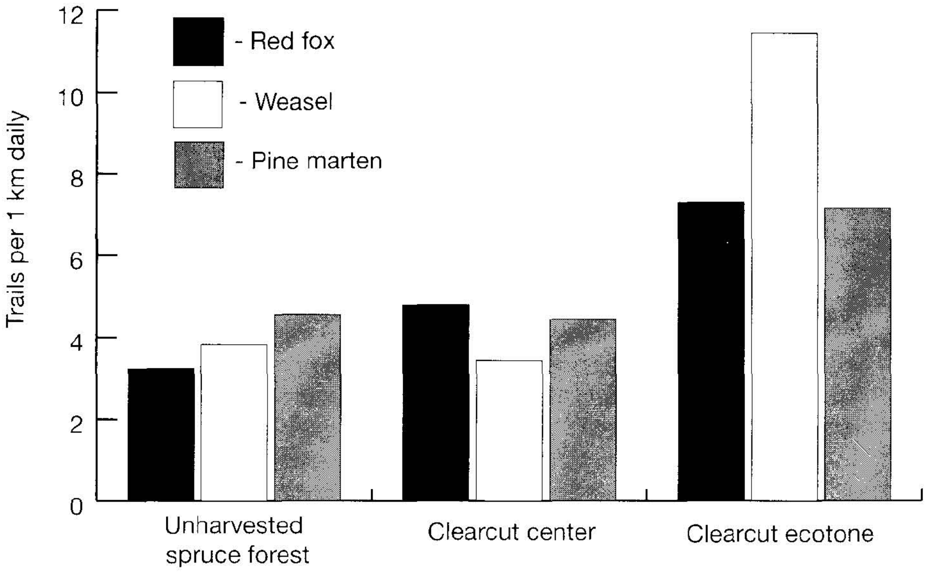

Fig. 1. Difference in the usage of old spruce woods and their clearcuts by red foxes, weasels and pine martens in the woodland of the "clay" area. Early winter of 1999–2003. The habitat usage was estimated as the predator activity (*PAI*, formula 4), i.e. the counts of the species trails crossed the transects per 1 km daily.

the pygmy field mouse, striped field mouse, harvest mouse, common vole and field vole (Table 1B). Heterogeneity in the species structure of rodent communities assessed by Simpson's index (*S*, see formula 1) was mostly higher in the clearcut centres (0.75 in the second age class and 0.80 in the third age class) compared to the initial pine forests (0.31), with the exception of the recent clearcuts aged up to 2 years (0), where merely yellow-necked mice were snap-trapped. Considering the rodent species richness in the logging areas up to 2 years old, the mean number of rodent species revealed per one census transect was 4.5 fold lower in the clearcut centres (0.2 *versus* 0.9; $t = 2.4$, $P = 0.01$) and 1.1 fold lower in the clearcut ecotone (0.8 versus 0.9; statistically not significant $t = 1.1$, $P = 0.17$) than that in the unharvested pine forests. Conversely, the mean number of rodent species that was revealed per one census transect was markedly higher (2.1–2.5 fold) in the logging areas older than 2 years than in the unharvested forests: clearcut centres (2.1–2.3 *versus* 0.9; t = 2.96–3.85, $P = 0.001$–0.006); clearcut ecotones (1.9–2.0 *versus* 0.9; t = 0.51–3.90, $P = 0.001$–0.31). Species proportions in rodents inhabiting the centres and edges of clearcuts of different age classes and unharvested forests were fairly dissimilar (with some exceptions): the centres of clearcuts of different age classes – the unharvested pine stands (Morisita's index $M = 0.12$–0.78, see formula 2; G-test = 1.6–196.7, $P < 0.001$); the clearcut centres – the clearcut ecotones ($M = 0.63$–0.81; G-test = 50.7–51.4, $P < 0.001$, with the exception of the clearcuts up to 2 years old); the clearcut ecotones of different age classes – the unharvested pine stands ($M = 0.12$–0.89; G-test = 42.4–196.7, $P < 0.001$); between the centres of clearcuts of different age classes ($M = 0.34$–0.81; G-test = 30.5–142.1, $P < 0.001$); between the clearcut ecotones of different age classes ($M = 0.20$–0.81; G-test = 52.1–172.2, $P < 0.001$).

Patterns of rodent abundance index (*RAI*, see formula 3) across habitat types in the logging areas generally matched those of species richness (Table 1B). In the clearcuts up to 2 years old the rodent abundance index was 3.2 fold lower in the centres ($t = 1.91$, $P = 0.04$) and 1.8 fold lower in the ecotones, but statistically not significant ($t = 0.75$, $P = 0.25$)

Table 2. Mean density of rodent predators (individuals per 10 km^2) in woodland fragments differently affected by felling in "clay" and "sandy" areas, 1999–2003.

Predatory species	Census season	<10% covered by recent clearcuts		20–30% covered by recent clearcuts		40–60% covered by recent clearcuts	
		"Clay" area	"Sandy" area	"Clay" area	"Sandy" area	"Clay" area	"Sandy" area
Red fox	December	12.9	1.6	16.8	3.0	18.7	4.1
Weasel	December	42.7	2.9	54.6	8.4	75.9	10.4
Pine marten	December	7.1	0.7	10.2	2.5	4.5	1.5
Polecat	December	6.8	0.5	9.9	1.2	5.2	0.9
Ural owl	April	6.2	1.0	5.1	1.8	2.9	1.3
Tawny owl	April	3.8	0.6	6.8	1.9	9.4	4.0
Long-eared owl	April	0.5	0	3.3	0	6.0	1.3
Tengmalm's owl	April	3.4	0.9	6.7	3.1	2.0	1.1
Pigmy owl	April	5.8	3.9	8.8	4.9	4.2	2.8
Common buzzard	May	3.8	1.2	9.1	2.5	11.6	2.4
Adder	May	40.2	3.9	88.9	12.8	239	19.3
All species pooled		133.2	17.2	202.2	42.1	379.4	49.1

than in the unharvested pine forests. The rodent abundance index *RAI* in the clearcuts aged 2–5 years compared to the unharvested pine forests appeared to be higher: clearcut centres – 4.3 fold (t = 2.70, $P = 0.01$); clearcut ecotones – 4.1 fold (t = 2.35, $P = 0.03$). The further trend in the rodent abundance index (*RAI*) was gradual decreasing with reforestation (Table 1B).

Low-disturbed fragment of the pine-dominated woodland, having less than 10% of recent clearcuts (done for the last 7 years), was rarely populated by the predatory species eating rodents (Table 2). Intensive logging led to a marked increase in the numbers of rodent predators in the woodland (Table 2). The majority of the predatory species responded absolutely positively on intensive forest exploitation. When there were 40% and higher of recent clearcuts, the red fox density was found to be 2.6 fold higher than that in fairly undisturbed pine forests; similarly, the weasel density increased in 3.6 fold, the tawny owl density – in 6.7 fold, the long-eared owl density – manifold (the owl species was not detected in the slowly exploited pine forests), the adder – 5.0 fold. Modest rate of logging of the pine-dominated woodland, when there were 20–30% of recent clearcuts, favoured pine martens, polecats, Tengmalm's owls, Ural owls, pygmy owls and common buzzards. These species responded with the decreased densities to the increased felling rate, but only the density of pygmy owls dropped to the level that was lower than the initial one. In the woodland in the "sandy" area, the pooled increase in rodent predator densities was about 2.9 fold, while comparing the forest fragments having less than 10% of recent clearcuts and 40–60% of recent clearcuts.

Concerning the obtained results on the index of carnivore activity (*PAI*, see formula 4) in relation to logging (Fig. 2), the following data were gained. Trails of red foxes and weasels were more frequently found in the clearcuts compared to low-disturbed pine stands: clearcut ecotone, the red fox – 2.3 fold (t = 1.79, $P = 0.06$); clearcut centre, the red fox – 2.8 fold (t = 1.93, $P = 0.05$); clearcut ecotone, the weasel – manifold (the species was not detected in undisturbed pine forests in the "sandy" area); clearcut centre, the weasel – manifold. Considering the variation in indices of rodent abundance (*RAI*) and carnivore activity (*PAI*) through the various

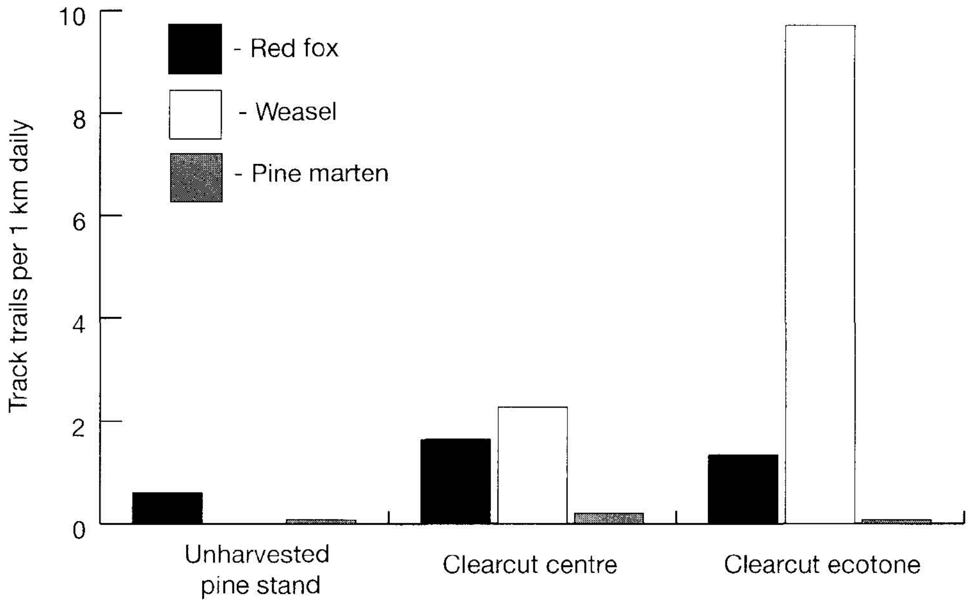

Fig. 2. Difference in the usage of old pine stands and their clearcuts by red foxes, weasels and pine martens in the woodland of the "sandy" area. Early winter of 1999–2003. The habitat usage was estimated (*PAI*, formula 4), i.e. the counts of the species trails crossed the transects per 1 km daily.

habitats appeared in the woodland affected by logging (i.e. centre and edge of clearcuts of different age classes, unharvested forest), we found positive correlations between the indices, but merely that for the pine marten is statistically significant ($r_s = 0.85$, $P = 0.02$).

5. DISCUSSION

Our results suggest that clear cutting generally leads to an increase in the numbers and species richness of rodents and their predators in stands up to 12 years. Similar results were gained in boreal coniferous woodlands in Scandinavia (Hansson 1978, 1994, Hakkarainen *et al.* 1996, Sami *et al.* 1998) as well as in coniferous – broad-leaved forest in eastern Poland (Wołk E. and Wołk K. 1982) and northern England (Petty 1999). Therein, a particular positive role of clearcut ecotones was evidently shown (Jensen 1984, Hansson 1994, Lidicker 1999).

In clearcuts aged older than 12 years, which look like a young succession forest, negative changes in the community may happen that would consist of a decline in the species richness and their population density. Our preliminary observations offer this inference, but this is a particular question to continue the study. Coming back to the revealed results relating to the positive influence of logging on rodents and their predators, it should be noted the following. First of all, logging led to higher densities of *Apodemus* mice, the red fox, weasel, tawny owl, common buzzard and adder. Also, with the increased felling rate *Microtus* voles and the long-eared owl penetrated in transitional woodlands, whereas these species were rather rare before the intensive felling. Nevertheless, too intensive clear cutting (more than 40% of fairly recent clearcuts) led to population decline of several predatory species. Those are the pine marten, Tengmalm's owl, Ural owl and pygmy owl. So, as all these species were frequently found nested in various tree holes, one of the possible causes may be limitation of suitable nesting sites in the condition of small proportion of oldgrowth having a lot of such hollows. Such results were numerically obtained on owls (Lundberg 1979, Mikkola 1983, Mebs and Scherzinger 2000, Scherzinger 2003, and references therein). On the other hand, a decreased biomass of rodents may not be the cause, because we found the higher rodent biomass in the majority of clearcuts that suggests the increasing prey supply for rodent predators with intensifying of forest exploitation.

However, the decline in rodent predators found in the conditions of too intensive logging rate was different in the woodlands on sand and clay top-grounds. In the conditions of clay soil and, in turn, ecologically rich initial forest habitats, too intensive felling led to the pronounced decline of a marked part of the rodent predatory guild inhabiting woodlands, and the species densities decreased to the level that was lower than the initial one. That may be explained by several negative factors. First, habitats of intensively exploited woodland with low proportion of mature forest patches and presence of a few old trees became much poorer sheltered, first of all for owls, compared to extended oldgrowth slightly fragmented by clearcuts. Also, in clearcuts, especially in large ones, there is an unfavourable structure of snow cover that is often crusted and usually harder than that under the forest canopy, and in such snow conditions it is much harder for predators to catch rodents (Jędrzejewska and Jędrzejewski 1998). Conversely, in initially poor habitats in the woodland on sandy deposits, logging of any rate conditioned plausibly higher habitat carrying capacity for the community of rodents and their predators, and the species densities were higher in intensively exploited forest than in undisturbed forest. But, nevertheless, moderate logging appeared to be the most favourable for the community there too.

We found markedly different age-related trends in the community structure in clearcuts in the woodlands on sand and clay top-grounds. In clearcuts on rich clay soil rather high species diversity and biomass of herbal vegetation usually appeared in a year after felling. That favoured rodents mostly being herbivorous immediately and, in turn, their predators. In contrast, in clearcuts on sandy soil, the habitats of a very poor quality including many open sand layers were found during the first years after the logging. Such unfavourable habitats were hardly populated by rodents and, hence, were hardly used by rodent predators. However, with time (during 3–5 years after the logging) herbal vegetation covered such clearcuts, while a grassy covering was almost absent in former pine stands that mostly had mosses and lichens in the forest floor. We hypothesize that while logging heavy forestry machines get sand mixed with remains of the terrestrial vegetation and tree branches. Such organic matter mixed with sand layers keeps water and gradually produces chemical substances containing nutrient elements available for herbal vegetation. In effect, grass appears in such clearcuts, and, consequently, rodents populate them, which, in turn, attract predators.

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