

## Demography of woodland rodents in fragmented habitat

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Populations of two species of woodland rodents were studied: *Apodemus flavicollis* (*A. f.*) and *Clethrionomys glareolus* (*C. g.*), inhabiting a set of small wood patches, isolated from large, continuous forest. The species composition, density and population dynamics differed from those in the forest. The rodents used the entire area as a patchy habitat, moving between the woodlots. In the breeding season high mobility caused higher mortality among males, especially in *C. g.* Sex ratio in *C. g.* was female biased. In *A. f.* females prevailed in spring whereas there was a prevalence of males in autumn. Seasonal changes in age structure followed different patterns in females and males. Males prevailed in first spring litters in both species. Males also prevailed among numerous immigrants of *A. f.* but females prevailed among immigrants of *C. g.* The demographic processes in these species resulted from habitat fragmentation and different life strategies.

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### Introduction

It is commonly accepted that persistence of a metapopulation is affected by habitat fragmentation (Merriam 1984, Gilpin 1987, Opdam 1988, Wiens 1989, Saunders *et al.* 1991). The probability of extinctions of local populations increases as their size decreases, and the isolation of habitat patches lessens the probability of potential recolonization. According to theoretical models (Fahring and Merriam 1985, Henein and Merriam 1990) connectivity between local populations decreases extinction probability of local populations and increases stability of the whole system (metapopulation). In man-dominated landscape, it is mainly the woodland species that are offered small, discrete habitat patches, compared with former extensive tracts of forests.

The populations of the woodland rodents inhabiting farm woodlots are a typical example of local populations isolated by inhospitable landscape matrix. The aim of this paper was to compare the effects of habitat fragmentation on demography of two woodland species: the yellow-necked mouse *Apodemus flavicollis* (Melchior,

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1834) and the bank vole *Clethrionomys glareolus* (Schreber, 1780) inhabiting small forest remnants.

### Methods and materials

The study was carried out in Białowieża Landscape Park, in northeastern Poland. The Park, situated in the centre of Białowieża Glade, is isolated from the vast tracts of Białowieża Forest by 1–3 km wide belt of crop fields, meadows and dwellings.

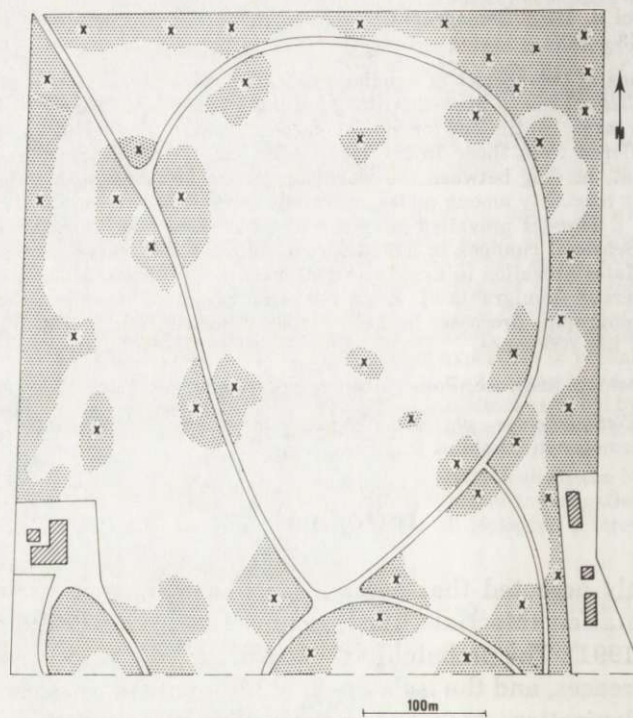


Fig. 1. A sketch map of the northern part of Białowieża Landscape Park. Trapping plots in the woodlots were marked with crosses.

The Park, of area of 50 ha, was established a hundred years ago by enriching the remnants of natural forest with introduced species of trees and shrubs. The severe climate and expansion of native plant species caused numerous exotic plants species to extinct. *Picea excelsa*, *Carpinus betulus*, *Quercus robur*, *Tilia cordata*, *Acer platanoides* and *Betula verrucosa* occur as the dominant tree species, alike in the surrounding forests. In the under storey common self-seeding trees and shrubs dominate. The herb layer is rich in species typical of forests. Among the woodlots, the spacious fertile meadows took over former forest sites. At present, the park represents a mosaic of woodlots and meadows mowed once a year remaining of the modern, patchy landscape.

Because of tourist visiting the park, the northern part of the park was chosen for study. The wood patches occupied 25% of that area and total area of the woodlots was 6.5 hectares (Fig. 1). The sizes and shapes of woodlots were variable. The width of woodlots surrounding the park as well as the



length of small, isolated ones did not exceed 50 meters. The maximum distance between the neighbouring woodlots was no more than 100 meters. Forty two trapping plots were located at random in the woodlots (Fig. 1), each of 100m<sup>2</sup> area and 4 live-traps in each plot.

The CMR technique was applied. Between June 1987 and June 1989, eleven trapping sessions were carried out (during breeding seasons only), with seven-week intervals between five-day sessions. The traps were inspected twice a day (in the morning and in the evening). The rodents were marked by toe clipping and their identity number, sex, reproductive status, weight, age (determined on the basis of body size and pelage colour) and the place of capture were recorded.

In total, 570 individuals of *Apodemus flavicollis* (*A. f.*) and 320 *Clethrionomys glareolus* (*C. g.*) were captured. Additionally, 108 individuals of *Apodemus agrarius* (Pallas, 1771) (*A. a.*) and a few individuals of *Microtus arvalis* (Pallas, 1771), *Mus musculus* (Linnaeus 1758), *Sorex araneus* (Linnaeus, 1758), *Neomys fodiens* (Pennant, 1771), and *Mustella nivalis* (Linnaeus, 1766) were also captured. Two forest species: *A. f.* and *C. g.* were analyzed thoroughly in this paper.

## Results

### Rodent community structure

During the study, the park woodlots were permanently populated by both *A. f.* and *C. g.* *Apodemus agrarius* occurred in lesser numbers and was not present at all time. Such pattern could be caused by seasonal migration, typical of this species (Rajska-Jurgiel and Mazurkiewicz 1988). *A. f.* was most numerous species throughout the study (Fig. 2). The domination of *A. f.* was most evident in 1987. The population numbers of *C. g.* was lower in 1987, then there were more individuals of *A. f.* compared with 1988 (Fig. 2). In 1988 the decrease in number of *A. f.* and increase in *C. g.* caused different species structure. Throughout the study, the rodent community structure in the woodlots was different from that in the surrounding forests, where *C. g.* occurred in the highest number and the percentage of *A. f.* ranged from 20% in spring to 40% in autumn (E. Rajska-Jurgiel and J. Kot, in prep.).

Rodent densities were estimated as Minimum Number Present per 1 ha of total area of woodlots for all trapping sessions. The density of *A. f.* was 6 – 25 per ha of woodlots and density of *C. g.* was 2 – 14 per ha (Fig. 2). The density of *A. f.* was equal or higher and density of *C. g.* was 2 – 3 times less than that in the forests (E. Rajska-Jurgiel and J. Kot, in prep). Hence the community structure, in woodlots different from that in the surrounding forests, resulted mainly from low density of *C. g.* in the woodlots.

### Space use

In 1987 and 1988, *A. f.* and *C. g.* were recorded in each woodlot and each plot in at least two trapping sessions. Thus, the woodland rodents could inhabit both larger and smaller woodlots. *A. a.* was not recorded in all woodlots, a fact which could be attributed to the low numbers of this species. When analyzing the total numbers of rodents captured in each plot throughout the study period, *A. f.* and *C. g.* were not found to prefer the particular woodlots. The total number of

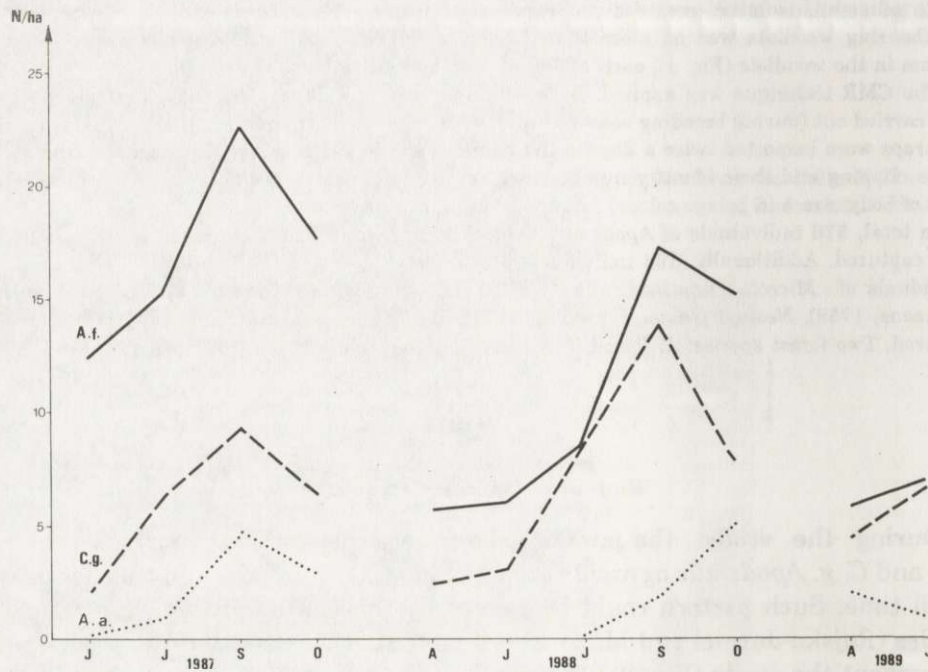


Fig. 2. Seasonal changes in density per ha of *Apodemus flavicollis*, *Clethrionomys glareolus* and *Apodemus agrarius*, as in woodlots.

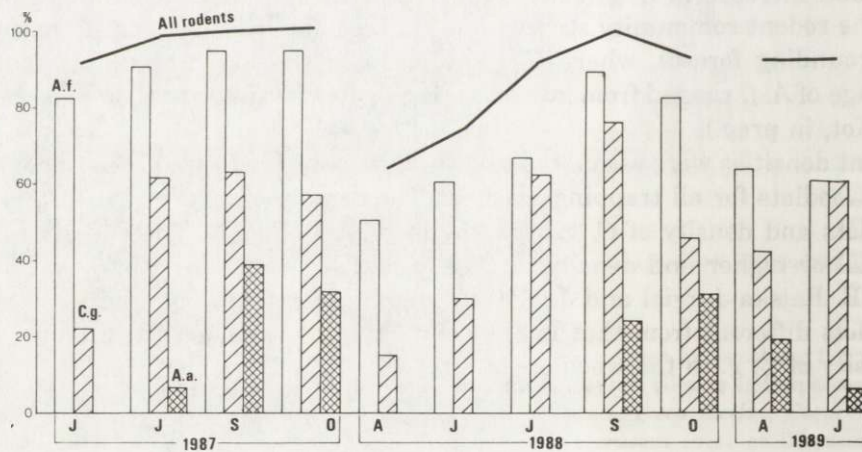


Fig. 3. Seasonal changes in space use expressed in percentages of trapping plots occupied.

individuals of *A. f.*, *C. g.* and *A. a.* per plot were  $23 \pm 5.1$ ,  $10.5 \pm 4.4$  and  $3.2 \pm 3.8$ , respectively. The trapping plots, with the total numbers of *A. f.* and *C. g.* close to the mean ( $\bar{x} \pm SD$ ) were 75% and 68% of all plots, respectively. *A. f.* inhabited



usually all woodlots. During low numbers (spring 1988 and 1989). *A. f.* occurred mainly in larger woodlots, *C. g.* was usually absent in small, isolated woodlots during spring. In autumn *C. g.* occurred in most woodlots, including small and isolated ones, except for plots with sparse herb and understorey cover. *A. a.* occurred in small numbers in each of woodlots occupied by this species.

Distribution of rodents in woodlots was dynamic. The species did not always occupy the same places and local "extinctions" and "recolonizations" occurred. Mean probability of a plot to be occupied (the proportion of plots  $\times$  sessions occupied) was 0.8 for *A. f.*, 0.5 for *C. g.* and 0.15 for *A. a.* Probability of local extinction was similar for *A. f.* and much higher for *C. g.*, then that in surrounding forest (E. Rajska-Jurgiel and J. Kot, in prep.).

The co-occurrence of the species was studied by comparing spatial distribution of voles and mice in the woodlots in each trapping session. There was no correlation between the numbers of individuals of different species trapped in particular plots. Spatial separation between the species was not found even during low numbers. In spring 1988, almost half of the plots was occupied by *C. g.* together with *A. f.* Similarly, *A. a.* occurred in plots occupied by *A. f.* and *C. g.*

The total space occupied by *A. f.* (Fig. 3) changed with their numbers ( $r = 0.953$ ;  $p < 0.001$ ) and *C. g.* followed a similar pattern ( $r = 0.927$ ;  $p < 0.001$ ). The area occupied by *A. a.*, when present, also changed with the numbers ( $r = 0.596$ ;  $p < 0.05$ ).

#### Spatial activity

Movements of rodents were quantified by (1) the number of trapping plots visited and (2) the maximum distance moved by each individual separately for each trapping session. The analysis included individuals which were caught at least twice during a trapping sessions.

Most rodents were recorded in only one plot during short, five-day trapping sessions. Since distances between plots ranged from 30 to 100 meters (50 meters on average) so the movement range of most rodents was not large. However, some rodents were trapped in two or more plots. Males were more mobile than females, especially in spring. More males showed higher mobility in spring than in autumn. The differences in mobility of males and females and seasonal changes in male movement were very remarkable in *C. g.*, but less clear in *A. f.* (Table 1). The females most often visited the adjacent plots. The males traveled more extensively, visiting also some distant plots, separated by meadows. The observed movement range of females of *C. g.* and *A. f.* was up to 70 and 80 meters, respectively. The movement range of males of *C. g.* and *A. f.* was up to 180 and 270 meters, respectively.

The site tenacity of rodents over longer periods was estimated as an percentage of individuals trapped in successive trapping sessions in the same trapping plots. In the breeding seasons most rodents were captured in successive sessions in the same places (Table 2). The males showed less site tenacity in comparison with

Table 1. Mobility of rodents in woodlots, expressed as percentage of rodents visiting more than one trapping plot in 5-day periods (sample sizes in parentheses).

Season	<i>Apodemus flavicollis</i>		<i>Clethrionomys glareolus</i>	
	Females	Males	Females	Males
April – July	29 (130)	37 <sup>c, d</sup> (124)	14 <sup>a</sup> (114)	55 <sup>a, b, c</sup> (67)
Sept. – Oct.	21 (100)	23 <sup>d</sup> (123)	8.5 (94)	21 <sup>b</sup> (46)

<sup>a</sup> – <sup>a</sup>:  $\chi^2 = 34.6, p < 0.001$ ; <sup>b</sup> – <sup>b</sup>:  $\chi^2 = 12.6, p < 0.001$ ; <sup>c</sup> – <sup>c</sup>:  $\chi^2 = 5.9, p < 0.05$ ;  
<sup>d</sup> – <sup>d</sup>:  $\chi^2 = 6.05, p < 0.05$ .

Table 2. Site tenacity, during breeding season and through the winter, expressed as percentage of rodents captured in successive trapping session in the same trapping plots (sample sizes in parentheses).

Season	<i>Apodemus flavicollis</i>		<i>Clethrionomys glareolus</i>	
	Females	Males	Females	Males
Breeding season (April – Oct.)	67 <sup>c, d</sup> (109)	52 <sup>c</sup> (104)	84 <sup>a, b</sup> (74)	65 <sup>b</sup> (31)
Winter (Oct. – April)	48 <sup>d</sup> (39)	34 (24)	50 <sup>a</sup> (26)	44 (16)

<sup>a</sup> – <sup>a</sup>:  $\chi^2 = 11.7, p < 0.001$ ; <sup>b</sup> – <sup>b</sup>:  $\chi^2 = 4.8, p < 0.05$ ; <sup>c</sup> – <sup>c</sup>:  $\chi^2 = 5.1, p < 0.05$ ; <sup>d</sup> – <sup>d</sup>:  $\chi^2 = 4.2, p < 0.05$ .

Table 3. The rate of population change per week.

Species	Year	Apr. – June	June – July	July – Sept.	Sept. – Oct.
<i>Apodemus flavicollis</i>	1987		0.039	0.070	–0.033
	1988	0.013	0.048	0.146	–0.014
	1989	0.025			
<i>Clethrionomys glareolus</i>	1987		0.337	0.073	–0.050
	1988	0.036	0.320	0.077	–0.066
	1989	0.077			

females. Differences between males and females were greater in *C. g.* than in *A. f.* Most rodents surviving winter in the woodlots were found in spring at different plots than in previous autumn (Table 2). The dispersal distance ranged from 40 to 300 meters in both, *A. f.* and *C. g.*

The range of movement of males in *A. f.* and *C. g.* was probably affected by habitat configuration. In spring the number of *A. f.*, even in the largest woodlots, did not exceed 15 individuals and the number of *C. g.* – 10 individuals, which forced males to travel between the woodlots in search of receptive females. In autumn, when the numbers were highest, not more than 25 *A. f.* and 20 *C. g.* were observed in the largest woodlots. It seems that the park area cannot be



treated as a sum of isolated patches but as a patchy habitat, in which rodents move among woodlots.

#### Seasonal changes in population numbers, residency and recruitment

In the two years the numbers of *A. f.* and *C. g.* in woodlots increased constantly between spring and early autumn. The population peaks were synchronous; the highest numbers of rodents lived in the woodlots in September, although in the forests *C. g.* numbers peaked in July (E. Rajska-Jurgiel and J. Kot, in prep.). The decrease in numbers in both species occurred in late autumn (Fig. 2).

There were different patterns of changes in numbers of *A. f.* and *C. g.* The highest rate of increase in *A. f.* occurred in late summer, while in *C. g.* in early summer (Table 3). The rate of increase of both species was at first lower, and then higher than that in the forest. The population increase was delayed in comparison with that in forests (E. Rajska-Jurgiel and J. Kot, in prep.).

The overwinter mortality of rodents was similar in both years: in *A. f.* 78% in 1987 and 75% in 1988, and in *C. g.* 77% and 70%, respectively. All overwinterers captured in April were those from autumn litters. Few unmarked rodents also captured were probably autumn born. Spring was a critical season for forest rodents living in the woodlots. In June 1987 there were 6 adult females of *C. g.* captured in all woodlots together and no adult male. In June 1988 only 2 adult males of *A. f.* were captured

Since winter in 1988/89 was mild and without snow, an additional trapping session was carried out at the end of February. None of rodents was sexually active and their weights were significantly lower than those in autumn. Untypical weather conditions did not trigger winter breeding. In 1989 the vegetation season began 2 – 3 weeks earlier than usual (K. Falińska, pers. com.). It was found that in April most females of *C. g.* were lactating for first litters. Even single juveniles were trapped. Thus spring breeding of *C. g.* began about 3 weeks earlier than in other years.

The time of residency of each individual in the study area was analyzed, except for rodents caught for the first time in the last trapping session. Between June and September about 60% of captured rodents were recorded in one trapping session only (Fig. 4). Time of their residence in the woodlots was thus not longer than 6 weeks after leaving nest or immigration to the study area. Less than 5% of captured rodents failed to be detected during a trapping session in the interval between their first and their last capture. Most of such cases were found in early spring and concerned mainly females in both species.

Early spring was the period of highest proportion of residents in the study area, (when there were only overwinterers in the woodlots, remained there since autumn) and autumn after the end of breeding (Fig. 4). Only 40% of females, 33% males in *A. f.* and 37% of females and 22% males in *C. g.* were found to stay in the study area throughout several successive trapping sessions. There were no males captured in more than 2 trapping sessions. The females of both species were

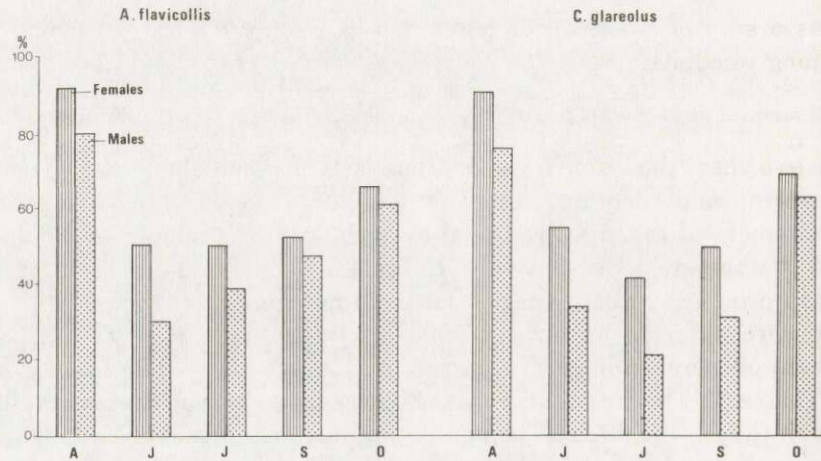


Fig. 4. Seasonal changes in percentage of residents; years combined.

Table 4. Seasonality of recruitment in woodlot populations expressed as number of recruits per breeding female in the previous trapping session.

Species	Year	Apr. – June	June – July	July – Sept.	Sept. – Oct.
<i>Apodemus flavicollis</i>	1987		2.4	3.1	1.8
	1988	1.3	2.7	5.0	1.8
	1989	1.4			
<i>Clethrionomys glareolus</i>	1987		4.3	2.3	1.4
	1988	1.4	5.1	2.8	0.6
	1989	1.9			

more resident than the males, especially in *C. g.* ( $\chi^2 = 7$ ,  $p < 0.05$ ). The lowest number of residents was found in males of *C. g.* ( $\chi^2 = 4.8$ ,  $p < 0.05$  for comparison with *A. f.* males).

The seasonal changes in recruitment were estimated by calculation of the number of new (unmarked) individuals per breeding female captured in the previous trapping session. The intervals between successive sessions were sufficient for gestation and weaning of one litter.

The highest recruitment in *A. f.* was recorded between July and September, and in *C. g.* between June and July (Table 4), that coincided with the period of the highest rate of increase in these species (see Table 3). Observed rates of recruitment indicate high immigration from outside the study area during rapid increase in the numbers, i. e. for *A. f.* in late summer, and *C. g.* in early summer.

#### Sex ratio, maturity, age structure

When analyzing sex ratio in all rodents trapped throughout the study period, a surplus of males was found in *A. f.* and in *C. g.* – surplus of females. Male/female



ratios were 1.23 and 0.75 respectively and they were significantly different from 1:1 ratio ( $\chi^2_{Af} = 6.1, p < 0.05, \chi^2_{Cg} = 6.6, p < 0.05$ ). The numbers of males and females captured in each trapping sessions showed that the sex ratio in *A. f.* changed seasonally: females prevailed in spring and males in autumn. In *C. g.*, females were more numerous than males over breeding season (Table 5). In spite of different numbers seasonal sex ratio change in *A. f.* appeared in both years as well as there was surplus of females in *C. g.* in all trapping sessions.

In the breeding season most individuals of *A. f.* and *C. g.* were mature. Only during peak numbers in September, a considerable number of sexually inactive rodents was observed, about 40% of *A. f.* and 50% of *C. g.* (Fig. 5). In April, in most females advanced pregnancies were noted.

Table 5. Seasonal changes in sex ratio.

Month	Numbers	M : F ratio				
		Total	Mature	Immature	Adults	Young
<i>Apodemus flavicollis</i>						
April	70	0.59*	0.59*		0.59*	
June	151	0.91	0.64*	1.88*	0.49**	1.84*
July	143	1.05	0.91	1.83	0.82	1.54
Sept.	236	1.40**	1.39	1.42	1.59**	1.10
Oct.	195	1.29			1.42*	0.96
<i>Clethrionomys glareolus</i>						
April	40	0.43*	0.43*		0.43*	
June	71	0.73	0.59*	2.70	0.30***	2.10*
July	93	0.70	0.53**	1.86	0.39**	1.44
Sept.	141	0.78	0.55*	1.10	1.55*	1.05
Oct.	82	0.64*			0.65	0.61

Deviations in 1:1 ratio statistically significant,  $\chi^2$  test; \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ .

The operational sex ratio is a significant factor in the population development. It was found among mature *A. f.* that females prevailed in spring and males in autumn. There was a higher number of mature females than males in *C. g.* throughout the study (Table 5, Fig. 5). There was a surplus of males in immature rodents in both species, especially in spring. A small number of immatures makes these deviations statistically insignificant.

All rodents captured in each trapping session were divided into two groups: young, under 2 months, weaned in the intervals between the trapping sessions and adults, older than 2 months.

Among adult *A. f.* females prevailed in spring and males in autumn. There was a surplus of females from spring till autumn among adult *C. g.* (Table 5). Males prevailed in the young of both species in first litters of the year. The male/female ratio in successive generations decreased between spring and autumn (Table 5).

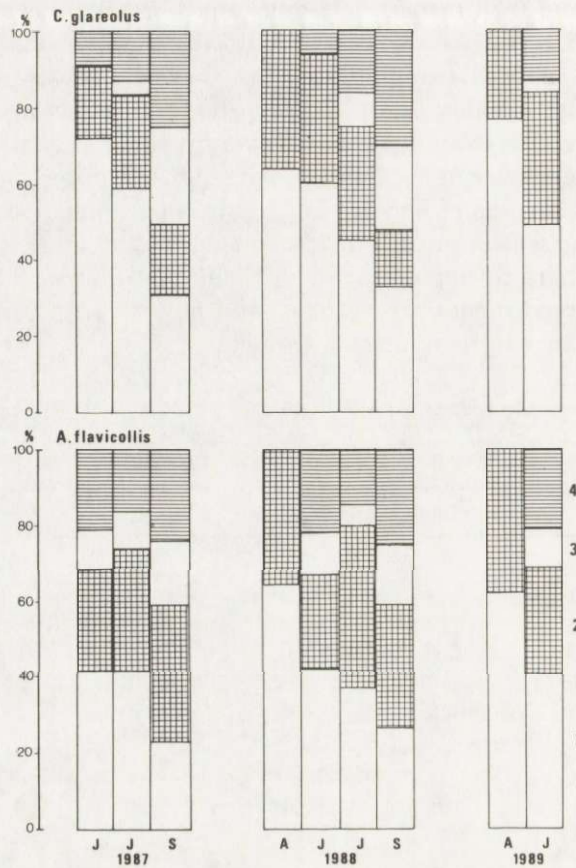


Fig. 5. Seasonal changes in percentage of mature and immature rodents. 1 – mature females, 2 – mature males, 3 – immature females, 4 – immature males.

Consequently, the age structure of males and females in species differed. Among female *A. f.*, adults, older than 2 months, prevailed throughout all the season. In June overwintered females prevailed and since July female yearlings, that were equal to overwinterers in respect of weight, size and maturity. Among males the young prevailed in June because of significant losses among male overwinterers; since July the fraction of adult males increased (Fig. 6). Overwinterers also prevailed among female *C. g.* in June. In July adult female yearlings, equal in size and weight replaced them. Only in September the young made up 50% of females. In male *C. g.* the young prevailed from June till September, although the fraction of adult males increased gradually (Fig. 6). The highest number of young was recorded in *A. f.* in June and in *C. g.* in September. The fraction of young *C. g.* was again small in October. In June 1989, because of early start of breeding there were more yearlings of *C. g.* than in previous years (Fig. 6).



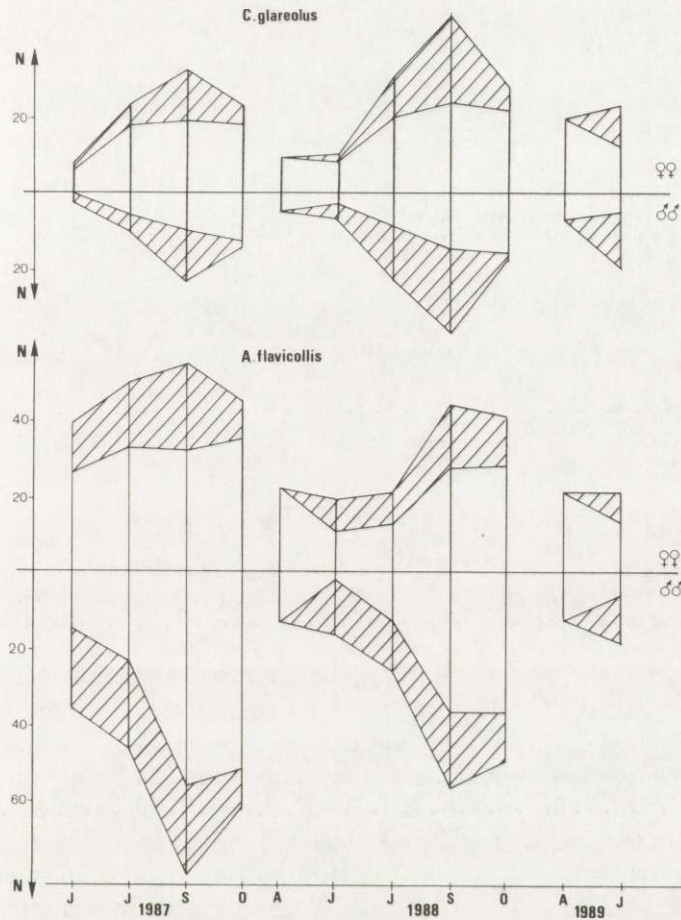


Fig. 6. Seasonal changes in total numbers across woodlots and in age structure in females and males. Open areas – individuals older than 2 months, shaded areas – the young, younger than 2 months.

Sex ratio and age structure in the population are affected not only by breeding and survival but also by dispersal. Among unmarked rodents captured in each trapping session there were not only the young but also adults, more than 2-month-old. All adults recruits were considered to be immigrants. The highest number of unmarked adult *C. g.* occurred in the woodlots in early summer, and most of *A. f.* – in late summer, i.e. in the periods of highest increase and highest recruitment in these species (Fig. 7). Males prevailed in unmarked adults of *A. f.* ( $\chi^2 = 6.5$ ,  $p < 0.05$ ) and females in *C. g.* ( $\chi^2 = 9.5$ ,  $p < 0.01$ ). There was low probability of capturing rodents marked previously in distant forest. However, several individuals of both species marked on the edge of the forest as well as within the forest (up to 3 km away from the woodlots) were trapped.

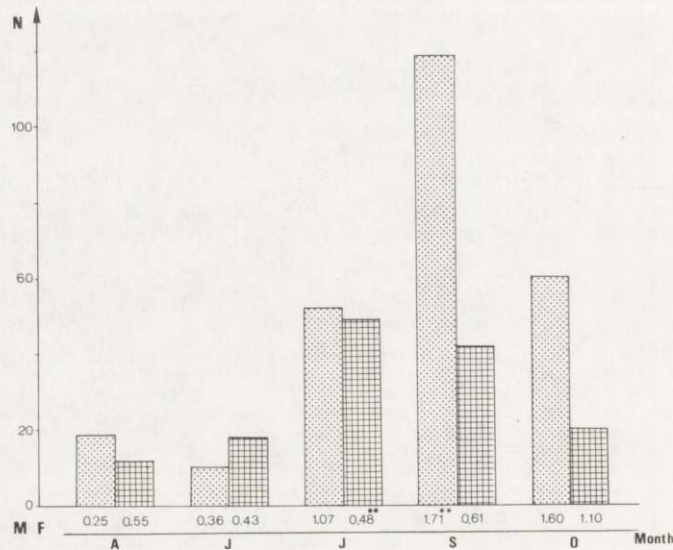


Fig. 7. Seasonal changes in numbers and sex ratio of immigrants; years combined. Dotted bars – *Apodemus flavicollis*, checkered bars – *Clethrionomys glareolus*.

Thus, the numbers, sex ratio and age structure in woodlot populations were affected by the influx of rodents from outside. In spite of different numbers in 1987 and 1988 the demography did not change significantly. Thus seasonal demographic changes can be outlined as follows: there were few rodents in the woodlots in early spring. Females prevailed in both species. The surplus of females in overwinterers increased in late spring, caused by rapid losses among males. Since males prevailed among the young from first spring litters, most of the females were overwinterers and most males were young yearlings. In summer, the woodlots were inhabited by single overwinterers. Adults born in first spring litters prevailed among females (in *C. g.*, a considerable number of these rodents were dispersers). The number of adult males increased (in *A. f.* a fraction of them were immigrants). In autumn, the number of adult males continued to increase (in *C. g.* slightly, in *A. f.* rapidly, which was mainly connected with immigration), (Fig. 6, 7). The synchronous peak of population numbers in both species was probably caused by different reasons: in *C. g.* by reproduction and in *A. f.* by immigration.

### Discussion

The species composition in woodlots was different from that in surrounding forests because of the high density of *A. f.* and the low density of *C. g.* caused by frequent local extinctions of the latter species. Also Geuse *et al.* (1985) always observed lower density of *C. g.* compared with the density of *Apodemus sylvaticus* (Linnaeus, 1758) in forest remnants in Belgium.



In the woodlands of Poland, the density of *A. f.* does not usually exceed 10 – 15/ha. Only in high crop years it can increase up to couple of dozens (Gębczyńska 1966, Mazurkiewicz and Rajska-Jurgiel 1987). Density of *C. g.* can reach similar figures every year.

*A. f.* is a species occurring in mature deciduous forests (Zejda 1976, Mazurkiewicz and Rajska-Jurgiel 1978, Mazurkiewicz 1984, Gurnell 1985). Yet, it is a species, known for its seasonal migrations in the search of food (Bergstedt 1965), appearing in autumn on the forest edges (Mazurkiewicz and Rajska-Jurgiel 1987, E. Rajska-Jurgiel and J. Kot, in prep.), visiting the small farm woodlots (Rajska-Jurgiel and Mazurkiewicz 1988) and inhabiting the forest steppes of Ukraine (H. Remmert, pers. com.). A relatively high density of *A. f.* in the woodlots resulted from the influx of rodents easily crossing crop fields. The low density of *C. g.* could be caused by low capacity of crossing habitat barriers (Bakowski and Kozakiewicz 1989, Kozakiewicz and Jurasińska 1989) or high mortality in the woodlots.

High turnover rate in population of *A. f.* is a feature of this species, resulting from high mobility and low residency (Bergstedt 1966, Montgomery 1980, Mazurkiewicz and Rajska-Jurgiel 1987). *C. g.* is a site-tenacious species, some observations indicate however low residency of this species in suboptimal habitats (Mazurkiewicz and Rajska-Jurgiel 1987, Gliwicz 1989). The low residency of *C. g.* results in low density (Andrzejewski 1963, Mazurkiewicz and Rajska-Jurgiel 1987), similarly as in *C. gapperi* (Bondrup-Nielsen 1986) and *Microtus californicus* (Ostfeld and Closterman 1986).

The highest proportion of resident was observed in the woodlots in early spring (the rodents which survived winter) and in late autumn. The decrease in movements and home range size were observed in autumn especially among males (Mazurkiewicz 1971, Green 1979, and others) After the end of breeding, the individual strategy changes, aiming now at surviving till next breeding season, which results in low mobility of rodents. The high proportion of residents during autumn were also observed in these two species by Mazurkiewicz and Rajska-Jurgiel (1987).

Rapid increase in movements and home range size of the males occurs in spring during low numbers (Bergstedt 1966, Crawley 1969, Mazurkiewicz 1971). High mobility in searching for females translates into high mortality of male *Apodemus* spp. (Randolph 1977, Green 1979, Montgomery 1980). In population of *Clethrionomys* spp. spring decline in number of males was also observed (Bujalska 1986, Kohn 1986, Kawata 1989).

The mosaic of fine patch woodlots and meadows creates specific living conditions for the rodents. If predation is an edge effect (Goszczyński 1985, Andren *et al.* 1985, Angelstam 1986), the risk of predation in the area is high. The rodents inhabiting woodlots, especially males moving in search of receptive females, use the entire area as a patchy habitat. If risk of predation depends on availability of prey (Goszczyński 1983, Jaksić 1986, 1989; Kotler 1984, Korpimäki and Sulkava 1987, Dörting and Cranford 1989) high mobility of males, especially in the open,



means more exposure to predation. A rapid decrease in the number of male overwinterers in spring was probably caused by their mortality. Consequently, a surplus of females was observed in both species.

In *A. f.* better antipredator adaptations such as large ears, big eyes, better locomotory abilities, active escape from predators, nocturnal activity, can possibly lessen the predation risk. The low density in *C. g.* forces males to travel intensively in search of females throughout the season. The high mobility and worse antipredator adaptations increase the risk of predation. Korpimäki (1985) proved that among small rodents it was males in *Microtus* spp. that were the most frequent prey for raptors studied. Among rodents inhabiting woodlots, the most available prey to predators (especially birds of prey, always occurring in the study area) are the males in *C. g.*, active during daytime, relatively slow, nevertheless most often moving between the woodlots.

The reproductive strategy of males, which includes taking risk of predation, caused the largest losses in male *C. g.* This high mortality of male *C. g.* resulted in a constant surplus of females in this species. The mortality of males in both species decreased after the end of breeding season.

Males prevailed in the first spring litters in both species. The surplus of males in spring litters and that of females in autumn ones were also reported by Goundie and Vassey (1986) for an isolated population of *Peromyscus leucopus*, inhabiting a small forest patch. A surplus of males in first litters, because of their rapid maturation, partly made up for the mortality of male overwinterers in the woodlots. Later in the season, immigration made up for male losses in *A. f.*, but not in *C. g.*

Dispersal rates are seasonally variable and regard also different categories of individuals (Lidicker 1975, Gliwicz 1988). According to Anderson (1989) young males are most numerous among dispersers, at least during early summer. This seems to be relevant to species with territorial males, such as *A. f.*, but not to species with territorial females, such as *C. g.* A surplus of male disperses in *Clethrionomys* was reported by Bondrup-Nielsen (1986), Hannson (1987) and Kozakiewicz (1976). During this study males prevailed in *A. f.* immigrants; among *C. g.* immigrants the females appeared in at least similar number. Although it might be caused, in part, by intensive losses among male *C. g.* immigrants in the woodlots, the same was reported by Gliwicz (1988).

If resident pressure is a driving force of rodent dispersal (Anderson 1989), high immigration in woodlots should be associated with a rapid increase in forest populations. Actually the increase in woodlot populations was delayed in comparison with that in the forests. The seasonal changes in recruitment showed that high immigration occurred in *A. f.* later than in *C. g.*, a fact which is consistent with the dynamics of these species in the forests (E. Rajska-Jurgiel and J. Kot, in prep.). According to Fahring and Merriam (1985), a low increase by reproduction



is a feature of isolated populations whereas their numbers increase owing to immigration, which was a case in the populations under study.

The adult and mature individuals prevalence during breeding season was an effect of immigration, quick maturing of early born young and relatively low juvenile recruitment. Although young rodents usually make up 50% of the population in breeding season (Pelikán 1967), Zejda 1961, Bergstedt 1965), a significant fraction of *C. g.* juveniles was only observed during peak numbers. In September 1987 and 1988 several weasels, probably attracted to the woodlots by appearing of numerous young rodents, were commonly captured in rodent traps. The low numbers of young *C. g.* and population decline in autumn were probably an effect of mortality due to weasel predation as well as low immigration, especially in *C. g.*, linked with seasonal changes in life strategy of the rodents.

In spite of differences in population numbers in 1987 and 1988, the demography presented above (residency, sex ratio, maturity, age structure) did not differ significantly between years. Low residency, relatively "old" age structure, low increase in numbers caused by reproduction and delayed rate of increase are features of population inhabiting patchy areas with sharp edges, suboptimal habitats and ecotone zones (see also Bondrup-Nielsen 1986, Mazurkiewicz and Rajska-Jurgiel 1987, Rajska-Jurgiel and Mazurkiewicz 1988, Viitala 1989, Krohne 1989).

The differences in mobility and residency of males and females in breeding season and female-biased spring sex-ratios were effects of different reproductive strategy in males and females. In risky habitat, the reproductive success and survival are lower and more variable in males than in females. Low mobility, high residency and selection of places providing secure cover resulted from seasonal changes in life strategy of rodents in autumn. The different sex ratios of *A. f.* and *C. g.* in summer and autumn resulted mainly from different dispersal rates of males and females in these two species.

Both, species composition and population size of a species in the woodlots resulted from different life strategies of species, *A. f.* more dependent upon food and less vulnerable to predation, willingly cover long distances. *C. g.*, a less food-selective species, being less mobile and more resident, hardly leaves the forest shelters. Avoiding passively the risk of predation, *C. g.* probably falls prey more often than *A. f.*, when crossing the fields, "a death trap" for dispersers. Thus the number of *A. f.* reaching the woodlots was higher in comparison with the number of *C. g.* although the proportions in those two species are completely reverse in adjacent forests.

Spatial structure of this small model of a patchy landscape, affecting the success of potential immigrants and the survival of residents, offered different chances to these species under study. Both the specific configuration of habitat, and the isolation of this area, offered *C. g.* lower probability of survival and colonization.

Animal spatial behaviour is the combined effect of food habits and predation risk affected by species morphology. Changing the landscape structure we offer to

forest-dwellers different chances of species survival, depending on life-history strategy adopted by a species. Site-tenacious and less mobile species, usually less food-selective and more vulnerable to predation, are the most affected by landscape fragmentation which restricts their dispersal. The food/habitat selective species owing to high mobility and frequent dispersal, can easier colonize small patches of suitable habitat in fragmented landscape. These species, preadapted to habitat fragmentation, are more likely to be affected by loss of preferred habitats, e. g. mature deciduous and mixed-deciduous forest. Is it the habitat fragmentation in man-dominated landscape that is the last step before the habitat loss?

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