Russian Original Vol. 4 No. 6, November-December, 1973

September, 1974

SJECAH 4(6) 467-568 (1973)

THE SOVIET JOURNAL OF ECOLOGY

ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN

CONSULTANTS BUREAU, NEW YORK

EFFECT OF LOCAL ELIMINATION ON RODENT POPULATION AND POPULATION STRUCTURE IN FOREST BIOCOENOSES

V. N. Bol'shakov, V. N. Boikov,
F. I. Boikova, N. S. Gashev,
N. G. Evdokimov, and L. P. Sharova

UDC 591.52

The studies carried out on Yamal Peninsula, in the Il'men' Preserve, Bashkir ASSR, and in Orenburg province indicate that local elimination of a part of a small-rodent population in forest biocoenoses does not result in substantial changes in population structure. Nonselective removal on the boundary of a species' habitat may have a directed effect on the population, resulting in definite changes in its sex and age structure.

Studies of changes in animal population structures brought about by nonselective removal are related to the major problems of modern population ecology.

The present study aimed at investigating those possible changes in the small-mammal populations of forest biocoenoses which are brought about by a local partial extermination of a population (creation of an "ecological vacuum"). Apart from a theoretical, such studies are undoubtedly of a practical interest as well, since rodent control is at present being carried on almost exclusively on limited areas of forest biocoenoses.

The study was carried out according to a general plan in various regions of the Urals (Lower Ob River, Chelyabinsk province, Bashkir ASSR, and Orenburg province) in 1971-72. Rodents were almost completely removed from a test plot with the aid of snap traps, whereupon observations were made on the plot's recolonization (removal by snap traps and live traps). During the same periods, samples were taken from control plots which were identical to the test plot in terms of vegetation structure, relief, etc. The procedure varied slightly, however, from region to region, depending on the biological characteristics of local rodent species and on differences in biotopes.

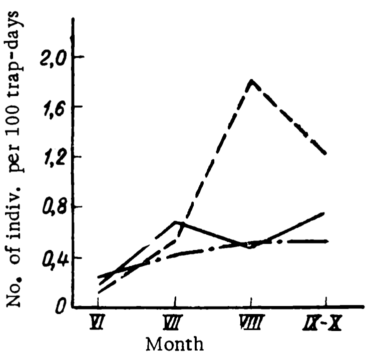

Fig. 1. Changes in small-mammal population numbers on the plot under study: ——) field vole; —·—·—·) bank vole; -----) shrews.

On Yamal Peninsula studies were carried out on the lower Polui River (right tributary of the Ob), 25 km to the south from the Arctic circle.

Seven plots about 1 ha each were designated in an island forest and a forest situated near the flood-plain. The main test plot, where rodents were trapped throughout the summer (June 17 to September 19, 1972), represented a narrow forest belt (birch, larch, and spruce) stretching along Great Gepnyurskii salt marsh (on the left bank of the Polui). The plot borders on the marsh on one side and is separated from large forest tracts by an extensive stretch of tundra on the other side. A chain of small lakes fringed with numerous willow bushes and a few larches and birches transects the tundra in one place only. It was along this belt that the

Institute of Plant and Animal Ecology, Ural Science Center, Academy of Sciences of the USSR. Salekhard Station, Ural Science Center, Academy of Sciences of the USSR. V. I. Lenin Il'men' State Preserve.
Translated from Ékologiya, Vol. 4, No. 6, pp. 57-65, November-December, 1973. Original article submitted May 28, 1973.

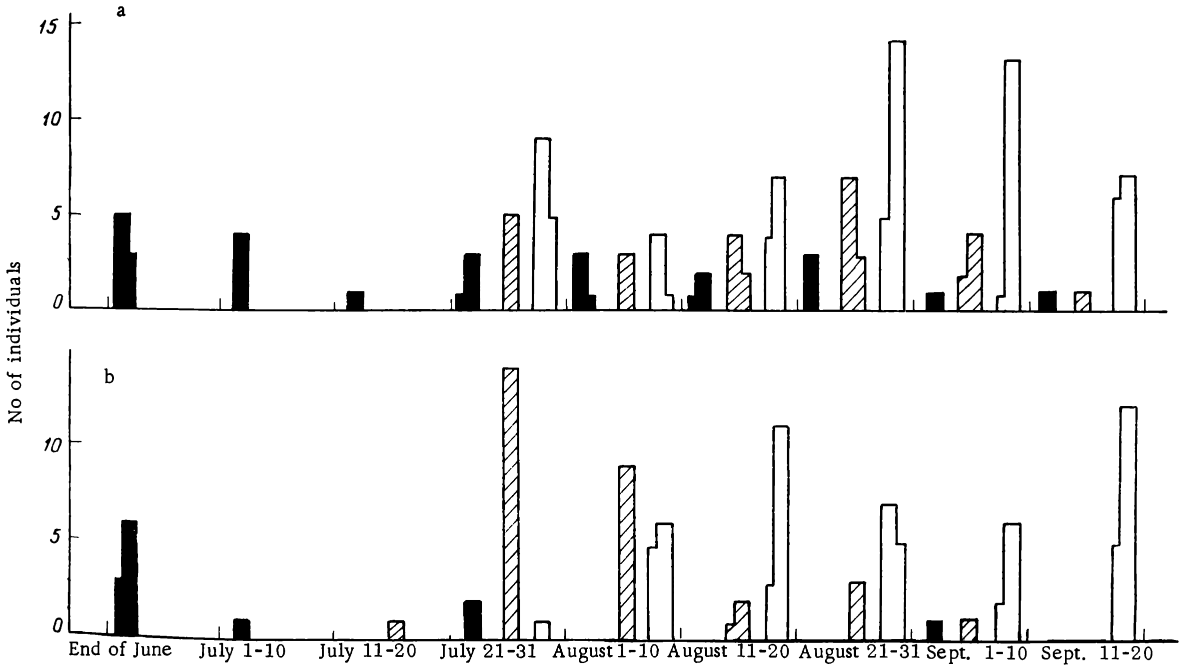

Fig. 2. Changes in the age and sex composition of redbacked vole on the test (a) and control (b) plots on Yamal Peninsula: filled columns, over-wintered animals; hatched columns, reproducing that year's brood; blank columns, sexually immature that year's brood; females on the left, males on the right of each column.

main stream of migrating rodents flowed. The test plots were situated for the most part in island forests, on the opposite side of the marsh.

Two lines of 500 "Gero" snap traps at 3-m intervals were laid out on the test plot. The traps remained there over the entire study period; they were checked daily and the bait was changed at regular time intervals. Subsequently, with the start of emigration of the young in mid-July, two additional lines of traps were laid out along the circumference of the plot.

In all, 239 northern red-backed voles, one Microtus oeconomus, and four shrews were trapped during the period of study.

The plots selected in the mountainous regions of South Urals (Mt. Kukshik, Bashkir ASSR) were situated on rocky alluvial fans running down mountain slopes. Such biotopes are dominated by the red-backed large-toothed vole. The clear-cut confinement of this species to alluvial fans and its absence in the adjacent forested areas (Bol'shakov, 1968) determined the fact that the test plot was settled by the voles in one direction only, namely, along the alluvial fan. Trapping was done on a 0.5-ha test plot in May, June, and September, 1971; concomitant trapping was done on control plots in June and September. The method of placing snap traps was similar to the one already described. The test plot yielded 230 rodents and the control plot, 94.

In the V. I. Lenin Il'men' State Preserve the study was largely done on an 11.83-ha permanent test plot encompassing biotopes typical of the preserve (80.8% of the area is covered by forest and 19.2% by meadows and shrubs). A 2.15-ha plot was used as control. Ten lines of traps, each consisting of 100 snap traps and 11 live traps, were laid out on the permanent test plot. The snap traps were placed at 3-m intervals; the lines were 35 m apart; nine lines were parallel to each other, and one line was at right angles to the rest (at their starting points). In 1971, rodents were trapped daily from June 2 to August 22 and from October 6 to October 16; on the control plot the trapping was done from October 8 to October 16. In 1972, rodents were trapped for 3-4 days at the beginning of each month from May to October. Live traps were also used several times; trapped animals were marked by cutting off their digits. The control plot was processed in May and October. In all, 2347 animals were trapped.

In the Orenburg province the experiments were carried out on the boundary of the bank vole's habitat. Two isolated plots representing broad-leaved groves (oak, birch, aspen, linden, and bird cherry)

TABLE 1. Ratio of Species on Test and Control Plots

Plot	Season	Wood mouse	Yellow-necked mouse	Bank vole	Others	Total No. of individuals
Test.	summer	37 / 40,6	14 / 15,4	35 / 38,5	5 / 5,5	91
Control.		58 / 48,7	31 / 26,1	15 / 12,6	15 / 12,6	119
Test.	autumn	46 / 54,1	23 / 27,1	5 / 5,9	11 / 12,9	85
Control.		40 / 50,6	21 / 26,6	9 / 11,4	9 / 11,4	79

Note. Numerator, of trapped individuals; denominator, same, %.

and separated by a stretch of steppe 70-80 m wide were used. The area of the test plot measured 0.5-0.6 ha and that of the control plot, about 2 ha.

During two weeks in June a total catch was carried out on the test plot (no rodents were trapped for five days following this operation) with the aid of 300 snap traps arranged in lines. A partial catch was done on the control plot, and the animals caught by live traps were marked. The same procedure was repeated in October. Both catches yielded 374 animals (176 on the test plot and 198 on the control plot).

The studies carried out on the alluvial fans of the South Urals showed that for one week the catch of rodents and insectivores was close to total, especially prior to the migration of the young. Polish zoologists (Andrzejewski and Wroclawek, 1962) have found this procedure to yield about 95% of local residents.

In May, the bulk of the small-mammal population of the test plot on Mt. Kukshik was composed of large-toothed red-gray-backed voles (59.6% of total catch) and shrews (38.3%), the bank-vole population making up 2.1%. The catches did not result in any noticeable shift in the species structure of alluvial-fan populations. Thus, in July the percentage ratio of species on the test plot was as follows: red-gray-backed voles, 43%; shrews, 39%; bank voles, 17%; other rodent species, 1%; on the control plot the figures were 46, 40, 13, and 1%, respectively. The corresponding figures for September were 49, 21, 11, 19% and 46 26, 13, and 15%. The local thinning out of the population produced no changes in the age and sex structure of the red-gray-backed vole, the dominant species of the alluvial fans. The individuals of this species trapped in May were all represented by overwintered animals. In July, the voles representing that year's brood comprised 92.1% on the test plot and 92.3% on the control plot (age groups were determined on the basis of molar tooth root development). In September, the animals trapped on both plots were all from the young brood of spring and summer generations. The sex ratio was close to 1:1 in all catches. The two plots showed no difference in female fertility.

Thus, the local thinning out of rodent populations on small plots had no appreciable effect on population structure in this territory.

The phenomena accompanying the formation of a "vacuum," the sequence of events and times of its filling were followed in detail in the Il'men' Preserve. The dominant species on the permanent test plot were the field vole (30% of total catch) and bank vole (22%). Intensive use of snap traps had no substantial effect on rodent population numbers on this plot. Figure 1 gives an idea about the numbers and species percentages of animals trapped during the individual months of 1971. The smallest catch was in June for all species. The bank vole continued to increase in numbers between June and October despite continuous trapping. So did the number of trapped field voles following a rise in July and a slight drop in August. The influx of animals to the plot during the operation turned out to be so great that it was more than enough to compensate for the number of removed animals. In addition to the migrating young (by the end of July it already comprised 95% of that year's brood among the trapped field voles), a contributing factor was the mass migration of adult animals brought about by abundant rainfall in July. Marking enabled us to establish that there were many more migrants than residents on the test plot during all study periods (over 74%). Being constantly on the move, they cross the territory in all directions, often covering long distances in short periods of time. Rall' (1936) calls this a normal migration.

Andrzejewski and Wroclawek (1962) noted while studying the post-trapping colonization of an area by rodents that the filling of a "vacuum" was done by migrating individuals rather than by animals residing

TABLE 2. Rodent Sex Composition on Test and Control Plots

Characteristics of population	Summer		Autumn	
	test plot	control plot	test plot	control plot
Wood mouse				
Males	25 (67,6)	34 (59,7)	23 (50. 0)	20 (50, 0)
Females	12 (32. 4)	23 (40. 3)	23 (50. 0)	20 (50. 0)
Females, pregnant or with pregnancy spots, %	50. 0	34. 3	13. 0	–
Average size of droppings	7. 0	6. 1	10. 3	–
Yellow-necked mouse				
Males	9 (64. 5)	22 (71. 0)	12 (52. 2)	9 (54. 3)
Females	5 (35. 7)	9 (29. 0)	11 (47. 8)	12 (45. 7)
Females, pregnant or with pregnancy spots, %	40. 0	11. 1	9. 1	16. 6
Average size of droppings (embryos)	6. 0	8. 0	5. 0	7. 5
Bank vole				
Males	18 (51. 4)	13 (86. 7)	2 (40. 0)	6 (66. 6)
Females	17 (48. 6)	2 (13. 3)	3 (60. 0)	3 (33. 4)
Females, pregnant or with pregnancy spots, %	47. 0	–	33. 3	–
Average size of droppings	7. 0	–	5. 0	–

on the area's periphery. We found the field voles to be less mobile than the bank voles, whose "individual" territories were more extensive and the distances covered greater than in the case of field voles. So is their speed of movement from one place to another. The maximal speed at which a field vole moved away from the site of original catch was 21.5 m per day, which we recorded in June, 1972. The vole covered a distance of 106 m along a straight line in five days. The bank vole is capable of moving almost three times as fast. In September of that year, for instance, one of the females marked on the test plot was caught eight days later on the control plot, 500 m from the site of marking. Its daily speed of movement along a straight line was thus 62.5 m. Additional evidence for the higher mobility of bank voles as compared to field voles is their higher heart index (males 5.92 ±0.11 and 4.94 ± 0.11‰ females, 5.90 ±0.32 and 4.97 ±0.32 ‰).

The individual territories of bank voles also differ greatly in size. In the Il'men' Preserve they reach 1 ha in size, while for field voles the figure is not over 0.1 ha. The individual territories are overlapping not only for the individuals of the same species but also for those of different species. There was no displacement of one dominant species by another during the two years of study on the permanent plot. The absence of an effect of partial population removal on species ratios and preferred habitat has also been noted in the state of New York, USA (Romansky, 1970).

A slightly different picture is found when a population is thinned out locally on the periphery of a species' habitat, as exemplified by the redbacked vole (northern boundary) and bank vole (southern boundary of habitat), where these species are confined to flood plains and island forests.

The graph shown in Fig. 2 gives the results of trapping on the test plot and one of the control plots for 10-day periods during a study season on Yamal Peninsula. Only two red-backed voles were caught on the test plot, an overwintered male and a young male, during the July 1-20 period. This indicates that the catch of overwintered animals had been close to absolute on the test plot. The test and control plots did not differ in the number of overwintered animals. Substantial differences were found between the two plots in terms of distribution according to sex and age composition of the populations. Following elimination, virtually no overwintered animals were caught on the test plot throughout the summer (apart from two individuals), while on the control plot they were being trapped throughout the season.

With the onset of migration of the young (last 10-day period in July) there were clear-cut differences between the plots in terms of the sex and age composition of that year's brood. The animals trapped on the test plot during the third 10-day period of July were sexually mature males of that year's brood (82.2% ±9.26); on the control plot this group comprised 21.7% ±8.6, while the group of sexually immature males and females made up 61% ±10.2. During the next 10-day period, August 1-10, the share of that year's

TABLE 3. Percentage of Two Species of Mice on the Plots Studied, %

Site of trapping	Wood mouse	Yellow-necked mouse
Test plot		
Summer.	72.5 (37)	27.5 (14)
Autumn.	66.7 (46)	33.3 (23)
Control plot		
Summer.	64.8 (57)	35.2 (31)
Autumn.	65.6 (40)	34.4 (21)

Note. The number of trapped animals is given in parentheses.

sexually mature brood was 45% 11.1 on the test plot and 25% 12.5 on the control plot; sexually immature animals were for the most part represented by females.

The first sexually mature females appeared during the period of August 11-20 (on August 12). Only two females (one in August and one in September) were trapped on the test plot, while on the control plot they were caught till the end of the season. On the test plot the share of that year's sexually immature brood was 82.4% ±11.5, with a strong predominance of males (78.6% ±10.1, t = 3.67) during the second 10-day period of August. On the control plot during the same period, sexually immature young animals comprised 55% ±11.1, the sex ratio being close to normal (1:1). The percentage of that year's sexually mature males was 10 and that of females, 20%. During the last 10-day period of August, as during the preceding one, sexually immature young comprised 80% ± 10.3, but the sex ratio became equalized, so that females even became slightly more numerous than the males (58.3%). On the control plot, sexually immature brood comprised 59.4% ±8.7, but the sex ratio was out of balance, the males making up 73.6% ±10.1, t = 3.3. There were 31.3% ±8.2 sexually mature young, the share of females being 70% ±14.5, t = 1.95.

During the first and second 10-day periods of September the bulk of trapped animals was made up of that year's sexually immature brood on both plots: 89.4% ±5.81 on the test plot and 73% ±7.3 on the control plot. The sex ratio was unbalanced, the share of males being 72% ±8.97, t = 3.47 on the test plot and 74% ±8.45, t = 4.0 on the control plot.

Thus, during the study season we found considerable differences between the test and control plots in terms of the sex and age compositions of rodent populations. By the end of the reproductive season, however, the bulk of population consisted in both cases of that year's nonreproducing brood; even the sex ratio shifted in the same direction and to an equal extent on both plots, despite our intervention. Regardless of which plot they were trapped on, we found no differences between analogous vole groups in terms of morphophysiological indices.

According to our studies, the yellow-necked and wood mice and bank vole are the basic species inhabiting island forests in the low-hill region at the southern end of the Urals, which is being encroached upon by the steppe. The complete elimination of the small-mammal population of the test plot showed that subsequent recolonization was attended by a substantial shift in the ratio of the basic species (Table 1).

The percentage of the bank vole decreased sharply (reliability of difference, 5.3), while that of mice increased for both species. Taking into account the absence of large differences in fertility between mice and bank vole on the test plot in summer (Table 2), it may be assumed that the changes noted above were brought about by a more active recolonization of the trapped area by mice. As may be seen in Table 1, the ratio of the species under consideration remained unchanged (the differences being insignificant).

In order to study the recolonization of the test plot by the rodents, the latter were marked on the control plot during the summer (12 wood mice, 10 yellow-necked mice, and one bank vole). A line of snap traps was placed in the field separating both plots; two mice, one of them marked (an overwintered female weighing 22.27 g, 89 mm long) were trapped, which indicates that mice migrate even across biotopes which are untypical of them. Of the marked animals, one wood mouse was trapped on the test plot in the fall (a young male weighing 17.4 g, 85 mm long), which is indicative of migration on the part of young, sexually immature wood mice in the area of study. There was no significant change in the sex ratio (see Table 2), at least not in the both species of mice.

It is of interest to note that the wood to yellow-necked mouse ratio always remains constant, even when the test plot is colonized (Table 3). It can hardly be said in this case that, being stronger and more aggressive, the yellow-necked mouse displaces the wood mouse.

TABLE 4. **Exterior and Interior Indices of Rodents** (Autumn)

Indices	Wood mouse		Yellow-necked mouse		Bank vole	
	test plot	control plot	test plot	control plot	test plot	control plot
Length, mm						
Body.	79,9±0,76	80,17±0,54	101,0±4,52	103,5±2,37	90,0±2,77	85,7±2,97
Tail.	79,8±0 81	74,7±0,90	101,7±5,40	106,8±2,78	43,8±1,39	42,8±2,01
Hind foot.	19,9±0,11	19,9±0,12	25,9±0,49	25,9±0,23	17,4±0,08	17,1±0,08
Height of ear, mm.	14,0+0,14	13,9±0,10	16,6±0,42	17,4±0,22	13,2±0,11	13,1±0,34
Body weight, g.	16,4±0,37	16,2±0,44	34,1±2,26	37,4±2,72	19,7±1,37	16,8±1,07
Weight index,‰						
Heart.	9,07±0,22	9,17±0,23	8,08±0,28	7,67±0,26	7,11±0,48	7,34±0,17
Kidney.	8,29±0,24	8,34±0,22	6,24±0,29	6,39±0,21	6,93±0,61	6,52±0,19
Liver.	53,47±1,05	56,46±1,21	61,92±2,08	59,07±1,49	65,09±3,75	59,06±2,05
Length index,%						
Cecum.	10,77±0,37	10,37±0,36	9,08±0,31	8,08±0,34	15,22±1,63	17,20±0,84
Intestine.	489,65±8,95	435,16±13,89	544,84±12,81	528,60±9,63	594,68±50,09	529,66±16,37
No. of individuals.	46	40	23	21	5	7

A different picture is found with respect to the bank vole. The male to female ratio was 1:1 on the test plot in summer (51.4 and 48.6%), while males were predominant on the control plot (87.6%). In the fall, females became predominant on the test plot, while on the control plot the males continued to dominate.

At the same time no significant changes were found in the age composition of bank vole on either plot: in the fall the populations of both plots consisted entirely of that year's brood, although it may be assumed on the basis of certain differences in body size and weight that the test plot was settled by individuals belonging to earlier generations (Table 4). Comparison of the species residing on different plots revealed no internal differences.

Thus, our studies of the small mammals inhabiting forest biocoenoses in various regions indicate that local elimination of part of a population does not result in significant changes in the population's structure. This is a graphic illustration of Shvarts' (1969) suggestion that "a population has a capacity for maintaining its composition at a relatively constant level in spite of drastic fluctuations in its numbers." The emergence of local vacuums under natural conditions may be assumed to be a widespread phenomenon (due to floods, anthropogenic factors, etc.); they are rapidly filled by individuals of the surviving part of a population without causing noticeable changes in its structure.

It should, however, be noted that in a number of cases nonselective elimination may produce a directed action upon a population's development by bringing about certain changes in the sex and age structures of some populations. Specifically, this is suggested by the changes we found in the course of vacuum filling in the island forests of Arctic and South Urals. For the most part, however, the constant random translocations of small mammals during periods of mass multiplication and migration of the young, reinforced by the influence of abiotic factors, actually exclude the possibility of a vacuum being created within a population by its local elimination, even if this population is relatively small. A population restores its numbers to a more or less constant level three to four weeks after its removal (Andrzejewski and Wroclawek, 1962) and often even sooner, as indicated by our studies in the Il'men' Preserve. This, in turn, suggests that elimination measures against small mammals in circumscribed areas of forest biocoenoses are without any prospects whatsoever.

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