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## The Consequences of Small Mammal Censuses by Method of Irreversible Removal

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**Abstract**—Experiments were performed to estimate the effect of removal trapping with Gero trap lines on resident population density and dispersal rate of *Clethrionomys* voles and *Sorex* shrews. Parameters of animal density and dispersal were calculated based on the results of live-trap censuses taken before and immediately after the removal trapping. Resident population density in the latter case was accounted for not only by animals that escaped removal but also by those that moved in from surrounding areas during the next few days. Local reduction of animal numbers resulted in increased dispersal. Parameters of dispersal obtained by the method of long-term removal may be overestimated.

**Keywords:** small mammals, numbers, dispersal, individual marking, population density

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Dispersal is a major factor ensuring population viability in a heterogeneous environment. It is due to dispersal that animals redistribute over space and settle territories accessible to them. Dispersal is the mechanism underlying many demographic processes, and its analysis is an interdisciplinary problem for researchers in ecology, genetics, ethology, and evolution [1–3]. Logistical difficulties do not allow the dispersal of many species to be studied in detail, while unrealistic concepts of dispersal implemented in spatial population models may result in erroneous and expensive predictions [4]. Animal dispersal at the level of either individuals or a community as a whole is poorly known. This is largely due to difficulties in studying individual movements on the corresponding spatio-temporal scale and results in disconnection between direct analysis and theoretical understanding of dispersal [5]. It is difficult to evaluate dispersal quantitatively, and this process is often regarded as purely stochastic. Therefore, it remains uncertain how individual factors affect dispersal and what ecological consequences this may have [6]. Empirical findings tend to lag behind theoretical propositions, and too many theories remain without conclusive evidence [7].

The notion of dispersal is inevitably applied to a variety of events that may be differently manifested and have different results [8, 9]. Any study of dispersal is based on the concept of home range. Burt [10] defined home range as “...area traversed by the individual in its normal activities of food gathering, mating, and caring for young.” The animal that inhabits a home range is regarded as resident (settled). Dispersal

is usually defined as the movement of individuals from their birth site to their breeding site (natal dispersal) or from one breeding site to another (breeding dispersal) [11, 12]. On the other hand, there are several ambiguous types of closely related extra-home range movements, in particular nomadism, exploration (excursions), and home range shifting. Being clearly related to true dispersal, they are distinguishable from it and can be collectively called quasi-dispersal [1]. It is characteristic of animals displaying these behaviors that their visits to a certain point are unpredictable, unlike with resident individuals whose home ranges are confined to a certain territory. It was proposed that the former be collectively designated nonresidents [9, 13], as opposed to resident individuals remaining within their home ranges. Here, the term “nonresident” refers to any animal found beyond its home range, and the term “dispersal,” to animals searching for or changing their home range.

A widely used method to obtain data on dispersal involves depopulation followed by control over the vacant area [14–18]. Since population recovery after sudden collapse (caused by either natural or artificial factors) occurs on account of survivors or immigrants [19], it is supposed that individuals caught after the extermination of residents are incomers (dispersers). The timing of resident population recovery may vary considerably depending on species-specific features of social organization and the proportion of nonresidents in the population [9, 20, 21], with rapid recovery occurring primarily due to dispersal [20, 21]. However, there are several sources in this method, includ-

ing incomplete removal of residents, expansion of marginal home ranges, entrance of animals during excursions, and differences in the fate of animals colonizing vacant and unaffected areas [1, 8].

Studies of dispersal upon irreversible removal have been performed using test plot censuses [14–18, 22] and trap-line censuses [23–26]. Methods of quantitative analysis have been developed that allow the results of long-term irreversible removal of small mammals to be used for estimating the intensity of migration fluxes and the initial numbers of residents in the corresponding territory [23–27]. The idea of this approach is that the daily catch is regarded as the sum of catches of resident and nonresident animals, and its size after the removal of residents depends only on visits of nonresident animals to the vacant area. It has been shown in studies on the bank vole that the number of nonresidents does not increase in the course of removal trapping and that immigration is not initiated due to “social vacuum” [27].

In the majority of publications it is either directly stated or implied that dispersal in control and depopulated areas remains at the same level, although it has been shown in some cases that there are differences between the animals that settle in vacant and control plots [22, 28]. Studies in which dispersal has been evaluated before and after the removal of resident animals from a certain area are almost absent. Since the procedure of evaluating dispersal by the “empty space” method can itself have an effect on the rate of this process, it is necessary to have comparative data for similar control areas (not affected by removal trapping) or for the same area before and after trapping.

This study deals with the consequences of local reduction of animal numbers using snap-trap lines in small mammal settlements of the forest zone. Resident population density and nonresident activity were estimated before and after removal trapping. Animal numbers in depopulated areas are rapidly restored due to dispersal, which is a part of overall nonresident activity. The null hypothesis was that dispersal is uniform over the entire population space and does not depend on local reduction of animal density.

## MATERIAL AND METHODS

The material was collected in the upper reaches of the Ilych River between the mouths of its tributaries, the Bolshaya Lyaga and Ukyu (62.6° N, 58.9° E) in August 2015–2017. Trap lines were arranged along a windfall area formed 15–17 year ago in spruce forest with an admixture of fir and Siberian pine and well-developed herb–dwarf shrub layer, which has been overgrown by young coppice forest of spruce, fir, and birch. Removal trapping was performed with small metal snap traps (Gero traps) baited with pieces of rye bread with unrefined sunflower seed oil. Population density and nonresident activity were evaluated using

trap-line censuses with springless live traps for catching all small mammal species, including shrews [29], which were baited with oat flakes moistened with unrefined sunflower seed oil. Parameters of resident population density (ind./ha) and nonresident activity (ind./100 traps per inspection) were calculated from the results of marking and recapture in live trap lines [30].

Calculations were based on approximating the probability for an animal to stay within its home range by bivariate normal distribution, assuming random spatial arrangement of home ranges. Single captures above the level expected in the presence of only resident population were regarded as nonresidents. Our previous studies provided evidence for the correspondence of calculated parameters of animal density with the results of direct censuses in the marking plot [31], and for highly significant correlation between the dynamics of nonresident activity calculated from the results of live trap-line censuses and the data on non-residence estimated in other ways [30]. Since the sizes of home ranges differ between species and sex–age groups, calculations were performed for each of them separately, and parameters for each species were summed up.

The design of the experiment was as follows:

(1) Live-trap-line census. Live traps were arranged in two lines, 50 traps each, at 7.5-m intervals; the distance between the lines was 30 m. The traps were inspected twice in the daytime, at a 1.5-hour interval, and then left unset until the next day to allow the animals to get accustomed to their presence. The census was conducted for 6–8 days.

(2) Snap-trap-line census (removal trapping). Snap traps were set along the same lines as live traps, at 5-m intervals (two lines, 75 traps each). The census was conducted for 2 days.

(3) Repeated live-trap-line census started on the next day after snap-trap census and conducted for 4–7 days.

Three experiments were performed during 3 years at the seasonal peak of animal abundance, and a total of 614 small mammals of eight species were trapped. Four species—northern red-backed vole (*Clethrionomys rutilus* Pallas, 1779), bank vole (*Clethrionomys glareolus* Schreber, 1780), common shrew (*Sorex araneus* L., 1758), and Laxmann’s shrew (*Sorex caecutiens* Laxmann, 1788)—were recorded in all census sessions and accounted for 97.6% of captures. Sufficient statistical material was collected for these species, which were therefore included in analysis. Thus, the data on four species from three census sessions (12 points) were used to compare the average parameters of resident population density and nonresident activity over the study period regardless of animal species ( $N = 12$ ) and for voles and shrews separately ( $N = 6$ ).

All samples were tested for normality of distribution (Shapiro–Wilk’s  $W$  test) and homogeneity of variances (Levene’s test). The distributions in all cases

**Table 1.** Results of trap-line censuses

Species	Year	Session 1: Live-trap-line census			Session 2: Snap-trap-line census			Session 3: Live-trap-line census			
		total catch, ind.	density*	nonresidence**	total catch, ind.	animal numbers***	animals marked during session 1, %	total catch, ind.	density*	nonresidence**	animals marked during session 1, %
<i>C. rutilus</i>	2015	25	5.04	0.50	34	11.3	88.0	18	1.44	1.63	5.5
	2016	30	6.01	1.00	36	12.0	56.7	21	2.87	1.30	19.0
	2017	47	9.28	1.00	58	19.3	80.9	12	0.96	0.71	0.0
<i>C. glareolus</i>	2015	10	2.84	0.06	10	3.3	60.0	6	0.15	0.75	33.3
	2016	9	0.95	0.50	26	8.7	77.8	6	0.23	0.60	0.0
	2017	7	1.89	0.01	6	2.0	57.1	3	0.47	0.14	0.0
<i>S. araneus</i>	2015	16	1.93	0.69	13	4.3	31.3	14	1.93	1.25	21.4
	2016	24	3.54	0.58	24	8.0	62.5	15	1.61	1.20	6.7
	2017	30	2.95	1.21	27	9.0	50.0	31	2.54	1.36	19.3
<i>S. caecutiens</i>	2015	6	1.41	0.06	5	1.7	50.0	2	0.15	0.13	50.0
	2016	4	0.94	0.17	9	3.0	0.0	7	0.94	0.50	14.3
	2017	3	0.23	0.07	3	1.0	33.3	2	0.15	0.14	0.0

\* Resident animals, ind./ha.

\*\* Nonresident activity index, ind./100 traps per inspection.

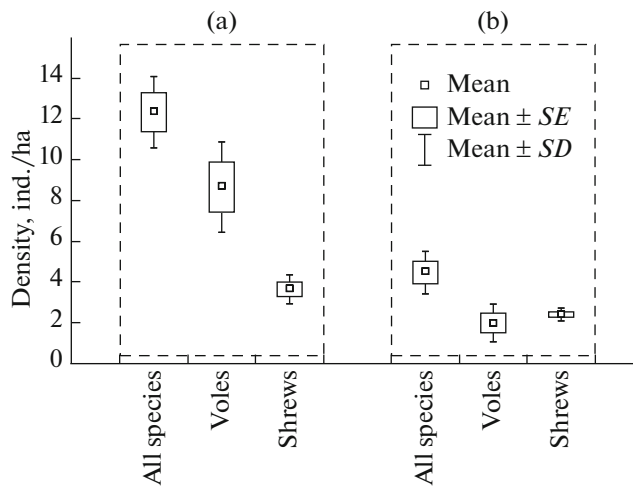
\*\*\* Catch per 100 trap–days, ind.

were normal ( $p > 0.05$ ) but had a right skew, and variances in some samples were unequal ( $p < 0.05$ ). Since sample sizes were small, pairwise comparisons were made by Wilcoxon matched pair test. Fisher exact was used for frequency comparisons. The null or alternative hypothesis was accepted at  $p = 0.05$  in all statistical tests. Mean values are presented with standard deviations ( $M \pm SD$ ).

## RESULTS AND DISCUSSION

During the period of the experiment, basic parameters such as resident population density, nonresident activity index, and catching rate per 100 trap–days changed by a factor of no more than two. The main results of censuses are summarized in Table 1. As averaged over 3 years, the overall resident population density of all species before the removal trapping was  $12.3 \pm 1.7$  ind./ha; nonresident activity index,  $1.9 \pm 0.6$  ind./100 traps per inspection; and snap-trap catching rate,  $27.9 \pm 6.3$  ind./100 trap–days. *Clethrionomys rutilus* was previously found to dominate in all biotopes of the study region: according to the results of snap-trapping in August averaged over 11 seasons, the proportion of this species in catches reached 58%. The proportions of shrews in catches were significantly lower than those of voles, with *S. araneus* always prevailing over *S. caecutiens* [33].

Snap-trap censuses resulted in the removal of a major part of animals marked during the first live-trap census session (on average, 63% in all experiments). These were mainly resident animals remaining within the marking area. Nonresidents live-trapped only once moved out within a short time and did not fall into snap traps. Catches in snap traps consisted of 47% of unmarked animals, i.e., mainly of nonresidents that visited the marking area during the census period. Changes in resident population density after snap-trap censuses are illustrated in Fig. 1. As averaged over 3 years, the resident population density of all the four species decreased from  $12.3 \pm 1.7$  to  $4.5 \pm 1.0$  ind./ha (Wilcoxon test:  $N = 12$ ;  $Z = 2.8$ ,  $p = 0.005$ ). This decrease occurred mainly on account of voles ( $8.7 \pm 2.2$  vs.  $2.0 \pm 0.9$  ind./ha,  $N = 6$ ;  $Z = 2.2$ ,  $p = 0.03$ ), while change in the resident population density of shrews lacked statistical significance ( $3.7 \pm 0.7$  vs.  $2.4 \pm 0.3$  ind./ha,  $N = 6$ ;  $Z = 1.57$ ,  $p = 0.11$ ). Such uneven reduction of animal density may be explained by the selectivity of trapping gear for different species. Thus, the proportion of marked animals during snap-trap censuses was higher among voles than among shrews: 73.4 vs. 47%, with the difference approaching statistical significance (Fisher exact test,  $p = 0.065$ ). Snap traps are not specially adapted to catch shrews, especially small ones, and the proportion of these species is usually underestimated during censuses [32, 34].

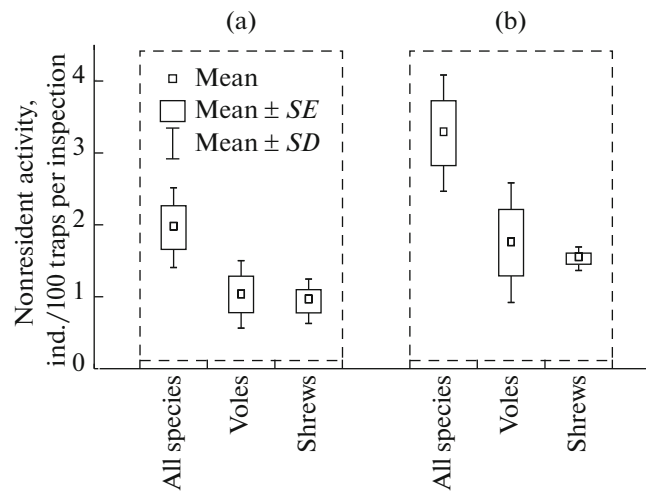


**Fig. 1.** Resident population density (a) before and (b) after removal trapping.

After the removal trapping, the total resident population included 47.5% of animals marked during the first census session, and the respective proportions in the resident populations of voles and shrews were 38.9 and 54.5%, with the difference between them lacking statistical significance (Fisher exact test,  $p = 0.36$ ). Thus, new individuals that could be classified as residents appeared after local reduction of animal numbers and comprised about half of the resident population. In other words, resident population density was accounted for not only by animals that escaped removal (residual density) but also by those that moved in from surrounding areas. It should be emphasized that new residents appeared already on the first few days after the removal trapping.

Our experiment demonstrated a very early onset of resident population recovery after local reduction of animal density. However, this process in different species may take different periods of time, sometimes very long [19, 21]. The rate of population recovery depends on the functional group to which the species belongs [20]. Depending on the proportion of nonresidents and recovery rate, the “recovery” and “control” types of population functioning have been distinguished [9]. Note that all three series of experiments were performed in August, at the peak of animal numbers and dispersal [35]. If removal trapping is performed in another season, the timing of resident population recovery in the same species may be markedly different.

The appearance of resident animals in vacant areas may be due to a shift or expansion of marginal home ranges or to dispersal. It was impossible to distinguish between these processes in our experiment, but the majority of studies dealing with repopulation of such areas provide evidence that this occurs mainly on account of long-distance immigrants rather than via shifts in marginal home ranges.



**Fig. 2.** Nonresident activity index (a) before and (b) after removal trapping.

The level of nonresident activity during live-trap censuses was estimated as the excess in the number of single captures above the level expected in the presence of only resident population. Comparisons were made between nonresident activity indices of small mammal species before and immediately after the removal trapping, which was conducted for 2 days; therefore, change in the natural level of dispersal over such a short period of time was negligible. Changes in nonresident activity resulting from snap trapping (average over 3 years) are shown in Fig. 2. The index of this activity for all species increased significantly after reduction of animal density: from  $1.9 \pm 0.6$  to  $3.3 \pm 0.8$  ind./100 traps per inspection ( $N = 12$ ; Wilcoxon test:  $Z = 2.59$ ,  $p = 0.01$ ); the increase in the index for shrews was also significant, from  $0.9 \pm 0.3$  to  $1.5 \pm 0.2$  ( $N = 6$ ;  $Z = 2.2$ ,  $p = 0.028$ ); and that in the index for voles—from  $1.0 \pm 0.5$  to  $1.7 \pm 0.8$ —approached statistical significance ( $N = 6$ ;  $Z = 1.83$ ,  $p = 0.068$ ). These results show that local reduction in the numbers of animals leads to enhancement of nonresident activity.

The null hypothesis that dispersal remains at the same level in depopulation experiments is rejected. The number of animals classified as nonresident increases after the removal of residents. This increase is probably explained by the accumulation of nonresidents in the site of local reduction in animal numbers rather than by general enhancement of nonresident activity throughout the surrounding territory. Nonresidents accumulate in such a site due to “social vacuum,” and some of them may settle down and switch to the resident mode of life.

The statement concerning the constancy of dispersal upon irreversible removal is usually not verified in real experiments. Based on practical verification of the results of trapping, the authors [27] conclude that immigration is constant across time rather than initi-

ated by irreversible removal. It should be noted that they compared the hypothesis of constant dispersal with the alternative hypothesis of the absence of dispersal prior to the onset of removal trapping, and the results were in favor of the former hypothesis. Here, the alternative hypothesis concerned quantitative change in the level of nonresident activity changes in sites of local reduction in animal density. Nonresident individuals are continuously present in the population, but their proportion in such a site increases above normal. Intensification of dispersal leads to rapid repopulation of vacant territory and recovery of resident population density.

The probability of increase in dispersal stimulated by local reduction of animal density indicates that parameters of dispersal obtained by the “empty space” method should be interpreted cautiously. In experiments involving long-term trapping in plots or trap lines, parameters of dispersal recorded in the study area during the period after its depopulation may be overestimated, compared to those in an intact area.

## COMPLIANCE WITH ETHICAL STANDARDS

### *Statement on the Welfare of Animals*

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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