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Contributions of Resident Populations and Nonresident Activities of Small Mammals to the Results of Censuses Performed Using the Permanent Removal Method

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Abstract—Population demography parameters of common small mammals have been obtained using two different census methods and intercompared. Resident population density and nonresident activity parameters were obtained on live-trap lines using the capture—mark—recapture method. Abundance parameters were obtained on break-back trap lines using the permanent removal (PR) method. Censuses performed using the PR method reflect the population dynamics of small mammals in general, but they may misrepresent the species ratio in the community. Multiple regression analysis shows that results obtained using the PR method are significantly affected both by the resident population density and nonresident activity of the species. Together, these factors explain 88.8% of the variance, while their individual contributions assessed on the basis of semipartial correlations in the multiple correlation model are as follows: $r = 0.39$ (resident population) and $r = 0.46$ (nonresident activities).

Keywords: small mammals, capture methods, censuses, capture—mark—recapture method, population density, dispersal

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INTRODUCTION

Relative census methods are broadly used in environmental studies to assess the population status of small mammals. Such methods make it possible to estimate their abundance, biotopical distribution, and sex—age structure. The trap-line method with Gero traps (steel spring traps) still remains widely accepted (Karaseva et al., 2008; Sheftel, 2018); the kill-trap method is used worldwide, although with some limitations (Sikes, 2016). In the course of censuses performed using the permanent-removal method, the specific catch (i.e., the number of caught individuals per catching effort unit) is assessed. This relative method is well suited for approximate estimations of changes in the abundance of a particular species. Significant disadvantages of this method making it ineffective for precise studies of the nature and degree of changes in the abundance of mouselike rodents originate from the fact that changes in the numbers of caught animals per 100 trap—days are not directly proportional to the changes in the species abundance (Smirnov, 1964; Hansson, 1967; Zhigal'skii, 1985; Pleshak, 1990; Bernshtein et al., 1995). In addition, individuals of various species react differently to various catching equipment and to the same bait, feature different mobility, and have home ranges of different sizes. As a result, catch indexes of various species differ significantly (Kucheruk, 1963; Smirnov, 1964; Hansson, 1967; Williams and Braun, 1983; Bury and Corn, 1987; Shchipanov, Litvinov et al., 2008). Many authors note that shrews are rarely caught in break-back traps, despite their relatively high abundance in nature; still, the trap-line method was broadly used for analyzing this group (Kupriyanova, 1976; 1994; Ivanter and Makarov, 2001; Bobretsov, 2016). Numerous attempts to compare census methods involving break-back traps and various true census methods had been made (Nikitina, 1961; Okulova, 1975; Zhigal'skii, 1985; Pleshak, 1990; Bernshtein et al., 1995; Prokop'ev, 2011; Shchipanov and Lyapina, 2011; Dobrinskii, 2017); in some cases, coefficients making it possible to recalculate relative abundance parameters into population density have been identified. The majority of such studies have been performed on voles.

A significant limitation of the trap-line method originates from the impossibility (without special methodologies) to differentially assess the abundance of resident animals and those occasionally visiting the area. Populations can be divided into open (whose size changes not only due to the combination of reproduction and mortality, but due to emigration and immigration as well) and closed (the size remains constant throughout the study period) ones (Southwood and Henderson, 2000). Aside from resident individuals, real populations almost always include immigrants, whose numbers sometimes may be significant (Rall', 1936; Naumov, 1955; Petrusewicz, 1983; Lukyanov and Lukyanova, 2002; Shchipanov and Kuptsov, 2004). Unlike resident individuals whose home ranges have fixed locations, the migratory part of the population visits various space points unpredictably. It was suggested to introduce a general term for such animals: nonresidents (Shchipanov and Kuptsov, 2004; Shchipanov, Kuptsov et al., 2008). Expansion is a key factor ensuring the viability of a population living in a heterogeneous environment (Lidicker, 1985; Lidicker and Stenseth, 1992; Krebs, 1999). The share of nonresidents increases as the unpredictability of living conditions goes up (Hanski, 1999) and under pessimal conditions (Lukyanov and Lukyanova, 1996). Therefore, various small mammalian species feature different ratios between residents and nonresidents, depending on the species specificity and environmental conditions; as a result, their populations have different sustainability in extreme situations (Shchipanov, 2002).

The nonresident activity of animals is essential for understanding the population structure dynamics of small mammals (Shchipanov, 2002). The ability to expand reduces competition and enables them to search for new home ranges and, ultimately, gain benefits from the colonization of optimal habitats (Ronce, 2007). The nonresident activity level determines, for instance, the intensity of water obstacle crossing by small mammals (Kalinin and Kupriyanova, 2015) and their role in the feeding of predatory fishes (Kalinin and Kupriyanova, 2016). Expansion may significantly affect many population biology aspects, including the genetic differentiation degree, population extinction/colonization rates, and habitat area enlargement (Zera and Brisson, 2012).

Some analysis methods make it possible to assess the migration flow intensity and initial abundance of resident small mammals in a specific area based on the results of their multiple-day trapping using the permanent removal method (Lukyanov, 1989; 1991; Shchipanov, 1990; Shchipanov and Lyapina, 2011). Such computations are based on the following idea: it is suggested to consider the daily catch the sum of catches of resident and nonresident individuals. The resident population abundance is assessed based on the catch index reduction dynamics: it is assumed that, after the capture of all resident animals occurring in the trapline coverage zone, the catch value levels off and is determined only by visits of nonresident individuals to that space. According to the above studies, nonresidents may constitute a significant portion of the catch in break-back traps. It is necessary to keep in mind that the nonresident activity may increase with a local population decline (Kalinin, 2019), while values of nonresidence parameters obtained using the long-term removal method may be overestimated. In censuses performed using live traps, resident animals constitute the basis of the catch, while nonresidents are caught relatively rarely, even though they are always present in the catches. Shares of nonresidents in populations of various species do not always depend on the resident population densities of these species; in some cases, the dynamics of these parameters are inconsistent (Krebs et al., 1976; Zhigal'skii and Belan, 1995; Lukyanov and Lukyanova, 2002; Ims and Andreassen, 2005; Kalinin, 2012; Kupriyanova and Kalinin, 2015). A positive-correlation effect between the population density and expansion intensity was registered in 50% of studies involving small mammals (Matthysen, 2005).

The purpose of this study was to quantitatively assess the contributions of resident and migratory parts of small mammalian populations of various species to the results of relative censuses performed using break-back traps. The objectives of the study were as follows:

(i) compare resident population density and nonresident activity parameters of common small mammalian species obtained on live-trap lines using the capture–mark–recapture method with census data collected on break-back trap lines;

(ii) assess specific features of censuses performed using the permanent removal method for voles and common shrews;

(iii) quantitatively assess the contributions of resident populations and nonresident activities to the results of censuses of common small mammalian species performed using the permanent-removal method.

MATERIALS AND METHODS

The materials were collected in August 2015–2017 on the upper reaches of the Ilych River in the Pechora-Ilych State Nature Biosphere Reserve in an area located between the influxes of the Bol'shaya Lyaga and Uk'yu tributaries (62.6° N, 58.9° E). The census lines were laid in a windfall area formed 15–17 years ago, formerly covered by a spruce forest with the participation of fir and Siberian pine and having a well-developed grass–dwarf-shrub cover and currently overgrowing with spruce–fir and birch undergrowth. Small steel spring traps (Gero traps) with ramps were used for catching with removal and dark bread with unrefined vegetable oil was used as the bait; the traps were checked once per day. The relative abundance (individuals per 100 trap–days) was assessed for each species. The population density and nonresident activity was assessed on live-trap lines. Springless live traps with ramps were used; they made it possible to catch the entire complex of small mammalian species, including insectivores (Shchipanov, 1986). Gerkules oat flakes moistened with unrefined vegetable oil were used as the bait. The live traps were installed in line (Shchipanov et al., 2000); the resident population density parameters (individuals per ha) and nonresident activity level parameters (individuals per 1 check per 100 traps) were calculated at the time of the marking on live-trap lines according to the methodology described in (Kalinin, 2012). The principle of the methodology is as follows: the probability of the presence of an individual in its home range is approximated by a bivariate normal distribution if the home ranges are randomly distributed in space. The use of a normal distribution for modeling of an individual's home range makes it possible to statistically compute the expected number of registrations depending on the distance between the animal's center of activity and the registration line and calculate the resident population density, while the deviation of the actual distribution from the expected one makes it possible to calculate the number of nonresident individuals on the registration line. In the presence of a purely resident population, individuals caught sporadically in excess of the expected number of captures were considered nonresidents (Kalinin, 2012; Kalinin et al., 2018). In each session, calculations were performed for each species taking in account the sex–age structure.

Experimental procedure:

1. Census performed on live-trap lines. The live traps were installed in two lines consisting of 50 traps each. The distance between the lines was 30 m and the distance between traps was 7.5 m. Checks were performed in daylight hours with an interval of 1.5 h, twice in succession. Then the traps were left disarmed and available for animal visits until the next day. The census duration was 6–8 days.

2. Census performed using the permanent-removal method on break-back trap lines. Break-back trap lines were installed on the last day of the live-trap census on the same lines; the distance between traps was 5 m; two lines consisting of 75 traps each were installed. The census duration was 2 days.

3. Repeated census performed on live-trap lines. The census began on the next day after the end of the census with break-back traps. The census duration was 4–7 days.

Three experiments were carried out for 3 years during the seasonal maximum population periods. In total, 641 small mammals were caught belonging to 8 species: northern red-backed vole (*Clethrionomys rutilus* Pallas, 1779), common red-backed vole (*Clethrionomys glareolus* Schreber, 1780), grey red-backed vole (*Clethrionomys rufocanus* Sundevall, 1846), tundra vole (*Microtus oeconomus* Pallas, 1776), wood lemming (*Myopus schisticolor* Lilljeborg, 1844), common shrew (*Sorex araneus* L.,1758), masked shrew (*Sorex caecutiens* Laxmann, 1788), and even-toothed shrew (*Sorex isodon* Turuv, 1924). Four species out of the eight (northern red-backed vole, common red-backed vole, common shrew, and masked shrew) were caught in all census sessions and constituted in total 97.6% of all captures. The amount of collected statistical data is sufficient only for these four species, and this study is dedicated to them.

All samplings (resident population densities and nonresident activities of all species in all sessions prior to the beginning of the trapping and after its end and catch indexes for break-back traps in the course of the trapping with removal) were compared with a normal distribution using the Shapiro–Wilk *W* test and checked for equality (homogeneity) of variances using Levene's test. If the normality and homogeneity conditions were met, the two dependent groups were compared using the Student's *t*-test for dependent samples. Interrelations between variables were assessed using Spearman's Rank correlation coefficient (*Rs*).

The Kruskal–Wallis test was used for comparison of several groups if the normal distribution condition was not met in all cases due to small sizes of the groups; if the differences between groups were significant, then post hoc comparisons were performed using Dunn's test.

The frequency analysis was perform using the Fisher's exact test.

The analysis of correlation relationships between population density and nonresident activity on the one hand and results of censuses performed on break-back trap lines on the other hand was performed using the multiple linear regression method. Distributions in the samplings were not different from a normal distribution (Shapiro–Wilk *W* test: $p > 0.05$) but beveled to the right, and an inequality of variances was noted (Levene's test: $p < 0.001$). Because the regression analysis is sensitive to such deviations from a normal distribution, a Box–Cox transformation was performed. The model was assessed on the basis of the determination coefficient (R^2); the model adequacy was tested through the analysis of residuals, while individual contributions of independent variables were assessed on the basis of semipartial correlations.

Mean values are provided with standard deviations ($M \pm SD$).

In all statistical tests, the null hypothesis or an alternative one was accepted at the significance level: $p = 0.05$.

RESULTS

Estimated values of resident population densities, nonresident activities, and catch indexes on break-back trap lines for four common small mammalian species are provided in Table 1. For each species, the above parameters varied insignificantly in different years. The total average resident population density of all species over the course of three years was 12.3 ± 1.7 individuals per ha; the average nonresident activity was 1.9 ± 0.6 individuals per 1 check per 100 traps, while the average catch index in break-back traps was 27.9 ± 6.3 individuals per 100 trap–days. Figure 1 (A, B, and C) shows the dynamics of these parameters. Average resident

Table 1. Results of censuses on experimental lines

Year	Species	Session 1. Census on live-trap lines			Session 2. Census on break-back trap lines			Session 3. Census on live-trap lines		
		density*	nonresidence**	individuals	catch index***	individuals	marked during session 1 (%)	density*	individuals	marked during session 1 (%)
2015	*Cl.rutilus*	5.04	0.50	25	11.3	34	88.0	1.44	18	5.5
2016		6.01	1.00	30	12.0	36	56.7	2.87	21	19.0
2017		9.28	1.00	47	19.3	58	80.9	0.96	12	0.0
Average		6.78	0.83	34.0	14.2	42.7	75.5	1.76	17.0	9.8
2015	*Cl.glareolus*	2.84	0.06	10	3.3	10	60.0	0.15	6	33.3
2016		0.95	0.50	9	8.7	26	77.8	0.23	6	0.0
2017		1.89	0.01	7	2.0	6	57.1	0.47	3	0.0
Average		1.89	0.19	8.7	4.7	14.0	65.4	0.28	5.0	13.3
2015	*S.araneus*	1.93	0.69	16	4.3	13	31.3	1.93	14	21.4
2016		3.54	0.58	24	8.0	24	62.5	1.61	15	6.7
2017		2.95	1.21	30	9.0	27	50.0	2.54	31	19.3
Average		2.81	0.83	23.3	7.1	21.3	50.0	2.03	20.0	16.7
2015	*S.caecutiens*	1.41	0.06	6	1.7	5	50.0	0.15	2	50.0
2016		0.94	0.17	4	3.0	9	0.0	0.94	7	14.3
2017		0.23	0.07	3	1.0	3	33.3	0.15	2	0.0
Average		0.86	0.10	4.3	1.9	5.7	30.8	0.41	3.7	18.2

* Density of residents (individuals per ha).

** Nonresident activity index (individuals per 1 check per 100 traps).

*** Results of censuses performed using break-back traps (individuals per 100 trap–days).

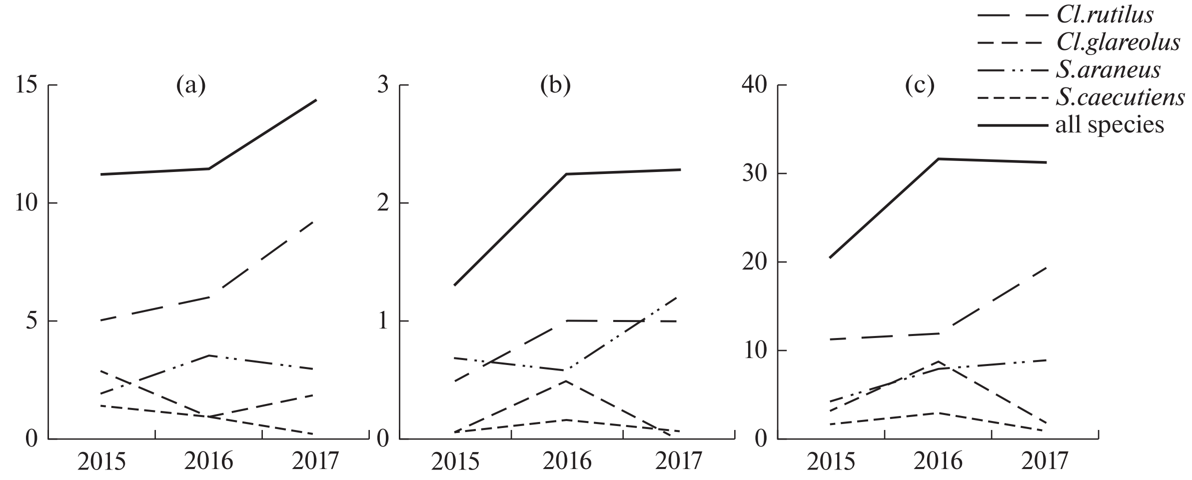

Fig. 1. Dynamics of demographic parameters on experimental lines: (A) resident population (individuals per ha), (B) nonresident activity (individuals per 1 check per 100 traps), and (C) results of censuses performed using break-back traps (individuals per 100 trap–days) on experimental lines.

population-density parameters over the course of 3 years were different for various species (the Kruskal–Wallis test: $H_{(3,\ N=12)} = 9.51, p = 0.023$); however, significant differences were noted in the post hoc test only between the northern red-backed vole and masked shrew (p = 0.019). Nonresident activity parameters were similarly different: $H_{(3,\ \mathrm{N}=12)} = 7.99$, $p = 0.046$; nonresident activities of the northern red-backed vole and common shrew were significantly higher in comparison with the common red-backed vole and masked shrew ($p < 0.05$). In the course of the subsequent census performed on the same lines using break-back traps, the abundance parameters (individuals per 100 trap–days) were changing in a similar way. Abundance parameters of various species were different: $H_{(3,\ N=12)} = 9.15, p = 0.027$; similarly with the resident population density, the catch index of the northern red-backed vole was significantly higher in comparison with the masked shrew ($p = 0.019$). Therefore, the results of the censuses performed using steel spring traps reflect the population status of all species in the community in general; however, the census results are affected not only by the resident population density, but by the nonresident activity level as well.

The species ratios were not significantly different in censuses performed using live traps and steel spring traps. Over the course of the entire study period, the share of shrews at the time of the marking in live traps was 39.3% of all marked individuals, while their share in censuses performed using steel spring traps was 32.3%; based on the Fisher's test, this difference is not significant (p = 0.12). Interestingly, in censuses performed using steel-spring traps, the share of earlier marked voles was slightly higher than that for shrews. In total, 73.4% of earlier marked voles and 47% of earlier marked shrews have been caught; based on the Fisher's exact test, the difference is close to significant ($p = 0.065$). These data are consistent with an opinion shared by many researchers that steel spring traps are nonspecific catching equipment for shrews, especially for small species, and the share of such species in censuses is normally underestimated (Smirnov, 1964; Shchipanov et al., 2000). In all the three experiments, the resident population density of all species had decreased after the catching with steel spring traps. In general (on average for the three years), the density of all species has dropped from 12.3 ± 1.7 to 4.5 ± 1.0 ind./ha. Annual average density levels of all the four species (N = 12) and density levels of red-backed voles and shrews taken separately were compared (N = 6). Based on the Student's test, the average annual parameters significantly decreased (3.1 ± 2.6 ind./ha before the catching and 1.16 ± 0.9 ind./ha after the catching, $N = 12$; $t = 2.9, p = 0.015$). This reduction of the resident population density due to the catching occurred at the cost of red-backed voles (4.3 ± 3.1 and 1.0 ± 1.0 ind./ha, $N = 6$; $t = 3.0, p = 0.029$), while the resident population density of shrews had not changed significantly (1.8 ± 1.2 and 1.2 ± 1.0 ind./ha, $N = 6$; $t = 1.9, p = 0.121$). Censuses performed using break-back traps reflect the population dynamics of small mammals in general but may misrepresent the species ratio in the community.

Various factors may affect the results of censuses performed using break-back traps, including the resident population density and nonresident activity level that are examined in this study. The analysis was performed disregarding species-specific features: the reaction of the entire small mammalian community was assessed. Any of our samplings can be characterized as small animals featuring a certain density of resident individuals, a certain nonresident activity level, and a certain catch index in steel spring traps. Correlation relationships have been noted between all variables (Fig. 2): Spearman's Rank correlation coeffi-

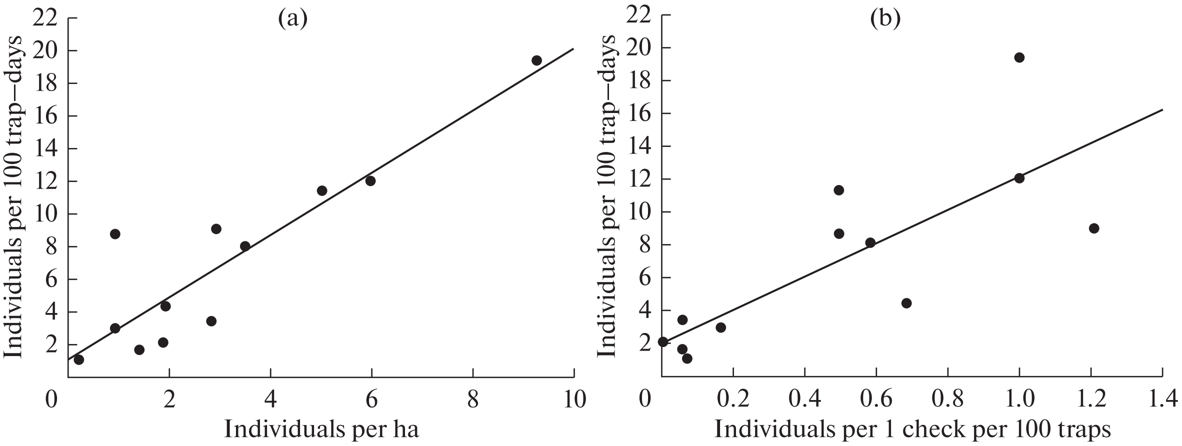

Fig. 2. Correlation relationships between the catch index in steel spring traps on trap lines the one hand and (A) the resident population density and (B) nonresident activity level on the other hand.

cient (*Rs*) between the resident density and catch index in steel spring traps was 0.84, $p < 0.001$; for the nonresident activity and abundance in steel spring traps, *Rs* was 0.80, $p = 0.002$. After the transformation, the resultants samplings were not different from a normal distribution (Shapiro–Wilk *W* test: $p = 0.99$, $p = 0.23$, and $p = 0.79$), sampling variances were not different (Levene's test: $p = 0.34$), and the analysis of the scatter diagrams did not identify any nonlinear relationships. The result of the census performed using steel-spring traps (individuals per 100 trap days) was the dependent variable; the independent variables were the resident population density on the live-trap line prior to the experiment (individuals per ha) and nonresident activity level (individuals per 1 check per 100 traps). The calculations have been performed for four species and 3 years ($N = 12$). The resultant regression explains some 90% of the variance in the dependent variable (determination coefficient: $R^2 = 0.89$). The model adequacy was tested through an analysis of residuals. The distribution of residuals corresponds to a normal distribution (Shapiro–Wilk *W* test: $p = 0.48$), the residuals are not correlated ($r = 0.35$ $p = 0.186$), and there are no autocorrelations (Durbin–Watson statistic: $DW = 1.95$), which indicates the adequacy of the model.

The individual contribution of the respective independent variable to the multiple regression coefficient was assessed on the basis of semipartial correlations. The contributions of the two independent variables are close to each other, although the density contribution ($r = 0.39$, $t_{(9)} = 3.46$, $p = 0.007$) is slightly lower than the nonresident activity level contribution ($r = 0.46$, $t_{(9)} = 4.14$, $p = 0.002$). Results of censuses performed on break-back trap lines using the permanent removal method are significantly affected by two factors: resident population density and nonresident activity of the species. Together, these factors explain 88.8% of the variance; in our case, the nonresident activity effect on the census results was slightly higher. It is necessary to keep in mind that these parameters may be different for a different species ratio in the community or for other abundance levels.

DISCUSSION

Overall, the abundance parameters of small mammals obtained through censuses on break-back trap lines reflect the general population dynamics well. It is necessary to note that the abundance of all species in north taiga throughout the three observation years was not high. The northern red-backed vole is a predominant species in all biotopes of the study area. Based on the steel-spring trapping data, in August, the share of northern red-backed voles in catches amounts to 58% on average throughout 14 seasons, while the share of common red-backed voles is only 11.8%, despite the fact that in some years the share of common red-backed voles had reached 40% in the study area. The share of common shrews in steel spring trap catches was always higher in comparison with masked shrews; concurrently, their abundance parameters were significantly lower in comparison with voles. In the course of the experiment, the maximum steel spring trap catch index was noted in 2016: 31.7% of catches for all species and 12% for the northern red-backed vole. With minor population fluctuations, a significant correlation between the density and nonresident activity of small mammals on the one hand and their catch index on steel spring trap lines on the other hand was identified. To gain insight into the population density on the basis of relative census data, some authors use a conversion coefficient: the ratio of the absolute abundance (individuals per hectare) to the relative abundance (individuals per 100 trap days) (Nikitina, 1961; Okulova, 1975; Bernshtein et al., 1995). We have calculated this coefficient as the ratio between the computed resident population density to the relative census results. Based on our data, the integral ratio for all species throughout all observation periods was 0.5 ± 0.3 on an average, and it slightly varied for some species: 0.5 ± 0.03 for the northern red-backed vole, 0.6 ± 0.5 for the common red-backed vole, 0.4 ± 0.07 for the common shrew, and 0.5 ± 0.3 for the masked shrew. Our calculated coefficients are significantly lower than those computed by other researchers. According to A.D. Bernshtein (Bernshtein et al., 1995), in optimal habitats, values of this coefficient vary for the common red-backed vole from 1.3 to 3.5 (the average value is 2.2) depending on the abundance level. The coefficients calculated for field mice vary from 2 to 2.9 (Nikitina, 1961). Other studies provide coefficients amounting to almost 4 both for the common red-backed vole (Dobrinskii, 2017) and northern red-backed vole (Okulova, 1975). In our opinion, such a difference between the computed coefficients may have two reasons. First, the ratio between absolute and relative abundance parameters varies nonlinearly and the coefficient value is higher at low abundance levels (Bernshtein et al., 1995; Nikitina, 1961), while the common red-backed vole abundance levels in optimal habitats at the lowest parameter values correspond to the maximum parameter values in our experiments. Second, the difference may originate from the absolute density calculation specificity. The calculations of density parameters on marking sites described in the above studies do not take into account the nonresident component of the animal population. All animals caught on the site throughout the entire study period are included in the calculation of the total density parameter. The results reflect the dynamic population density (Rall', 1945). As is known, abundance parameters obtained through the capture of animals on fenced (where the nonresident component is absent) and unfenced sites are significantly different. In all cases, the abundance of animals on unfenced sites is higher. With smaller unfenced sites and longer catching sessions, this difference increases due to animal visits from the outside (Kucheruk, 1963). The "edge effect" is of great importance in density calculations on marking sites; it has the maximum effect on smaller sites and was not taken into consideration in most studies. In our study, we calculate density as the number of resident individuals whose geometrical centers of home ranges are located within an area unit. The adequacy of our method used for calculation of the resident population density and nonresident activity at the time of the marking with subsequent recapture on live-trap lines (Kalinin, 2012) is confirmed by the comparison of the calculated data, with the results of direct censuses performed in an area 15.2 ha in size taking into consideration the edge areas (Kalinin et al., 2018).

CONCLUSIONS

The ratio between resident and nonresident individuals in natural populations may vary widely: from close (normally isolated) populations consisting only of resident individuals to areas with no permanent residents but high levels of nonresident activity. For instance, on stony beaches near the waterline, catch index values on trap lines may be pretty high (Kalinin and Kupriyanova, 2015). Our data show that both components contribute to results of censuses performed on break-back trap lines. The same catch indexes in break-back traps may be obtained for populations with completely different dynamic structures. It is impossible to distinguish the resident population from the nonresident component in the course of standard censuses performed within 1–3 days using the permanent removal method; this requires special studies (Lukyanov, 1989; 1991; Shchipanov, 1990; Shchipanov and Lyapina, 2011). The analysis of census results obtained on break-back trap lines must take into account that such data reflect not only the resident population density, but the mobility level in the population as well.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest

The authors declare that they have no conflict of interest.

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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