Estimation of Absolute Abundance in Small Mammals. Let a Line Has an Area.

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Research Article

Abstract

Small mammals play an important role in ecosystems. Changes in their numbers make it possible to monitor environmental changes, and robust estimates of population density is crucial. Capture-mark-recapture (CMR) on grid, an established method for estimating small mammal population density, is costly and labor-intensive. The cost of the survey can be reduced by reducing observation time, as well as by increasing sample size by arranging traps in a line. Using our 9-yers data obtained on grid we test whether relative abundance indices calculated over shorter time periods correctly reflect population density. We also propose a method for calculating population density using data obtained by CMR on lines (since the grid can be viewed as a series of independent lines) by estimating the spatial activity of animals. It was found that all the indexes calculated for grid and lines were in good agreement with population density on greed, and the scale of both interspecies and inter-annual differences in indexes and density was similar. Although indexes significantly correlated with population density since 3rd day, reliability of the indexes increased over the time of observations (R^2 > 0.79 since 7th day). The population density calculated from the lines using the proposed method was in good agreement with the actual density recorded on the grid (R^2 > 0.9). We could recommend using the indexes to estimate inter-annual changes in population abundance and community structure at the same area under invariant trapping protocol with invariant time of the trapping sessions. Density calculated on lines requires long-term study, but it is a universal estimate, and could be used when rough assessment of absolute abundance is needed.

Introduction

Ever-increasing direct and indirect anthropogenic impacts are significantly altering natural ecosystems (Sage 2020). Given that ecosystems provide functions and services vital to human well-being, understanding their current state and prospects is a pressing applied problem (Sekercioglu 2010; Mori et al. 2017; Cardinale et al. 2012). The ability of ecosystems to maintain their key functions and services is closely linked to biodiversity (Díaz et al., 2006; Tilman et al. 2014; Isbell et al. 2015a, b; Berlinches de Gea et al. 2023). Large-scale monitoring of biodiversity using indicator species or groups of species provides the basis for decision making to manage different types of ecosystems in support desired services (Loreau et al. 2001; Hautier et al. 2015; Gao et al. 2015; Mori et al. 2017). Due to their abundance, small mammals constitute an important part of animal diversity in various habitats and are used as an indicator of the state of an ecosystem (Hayward and Phillipson 1979; Barrett and Peles 1999; Pearce and Venier 2005; Overmars et al. 2014; Gao et al. 2015; Torre et al. 2016, 2023; Parsons et al. 2023). Being small in size, these animals are sensitive to ambient temperature, food supply, available shelters, soil cover, and many other environmental factors (Merritt 2010; Hilmers et al. 2018; Paniccia et al. 2022). Depending on the species composition and abundance, small mammals can become a vital ecosystem component (e.g. Sieg 1987; Dickman 1999), or important reservoirs of emerging human diseases and severe pests (e.g. Cox 1979; Mills 1999; Singleton et al. 1999; Aplin and Singleton 2003; Torre and Balčiauskas 2023).

On the perspective of ecosystem monitoring the absolute size of wildlife populations is the most reliable estimate (Pollock et al., 2002). According to contemporary ethical standards live-trapping with following mark of animals is more preferable for the study (Sikes 2016). For small mammals, data on absolute abundance can be obtained by capture-mark-recapture (CMR) of animals in an area (Gurnell, Flowerdew 2006). However, this method requires a large number of trapping days, and a uniform grid, which is common in CMR studies, produces less accurate data than a random distribution of traps (Rees et al. 2011). So, widespread use of costly CMR is limited due to its high labor intensity while methods which can provide robust information at low-cost are more suitable for large-scale monitoring (Jones 2011). Labor intensity could be reduced if monitoring of small mammals is based on indexes of relative abundance, however, given that different small mammals vary in their ability to be detected, such estimate may be insufficient for understanding of a species resilience, interactions of animals in community and their role in ecosystems. Thus, testing the correlation, predictive ability, consistency, and calibration of relative estimates to actual population size is an urgent task (Parsons et al. 2023).

We use original CMR protocol developed for studying shrews, which turned out to be suitable for almost all small mammals dwelling in the taiga forests (Shchipanov et al. 2005, 2008, 2010, 2012; Kalinin, 2012, 2023). According to our technique, the daily operation time of traps (open – closed) made 1.5 - 3 hours per day. This substantially reduced the labor intensity, and permitted us to observe several habitats simultaneously. In our studies we widely place traps on a line. Note that a line crossing animal habitats in a random direction and at a random location. Also linear placing of traps increases the survey area compared to a grid of the same number of traps (Shchipanov, Kalinin, 2024). Since 2014 we have been monitored small mammals on the grid with fairly diverse species assemblage.

The purpose of this study was to evaluate whether we could use some simple indexes of relative abundance for short capture session, and could we obtain estimate of absolute abundance using data obtained on trap-lines. We used the grid data to assess the correspondence of relative abundance indexes obtained over different times (days of trapping) with the actual population density identified using CMR. Also we suggest a way to calculate population density for linear data using parametric estimate of spatial activity. Since the grid could be regarded as a number of lines, we assess the agreement of population density obtained on grid with population density calculated for the lines on the grid.

MATERIAL AND METHODS

Area under the study

The study was conducted in the central part of European Russia: in the vicinity of the Bakanovo village, the Staritsa Region of Tver Oblast (N 56°18'; E 34°53') on the southern edge of the coniferous forest bordering the deciduous forest zone. We monitored small mammals in the former household area went out of use and completely abandoned in the beginning of 2000s, when the village became almost depopulated. During the studied period 2014–2022 there has been no human activity at the site. The old-growth lindens (*Tilia cordata*) with wild-growing descendants of linden, seedlings of oak (*Quercus robur*), red elderberry (*Sambucus racemose*), young birches (*Betula pendula*), alders (*Alnus incana*), aspens (*Populus tremula*), occasional trees of goat willows (*Salix caprea*), various willow (*Salix spp.*) bushes and a few pines (*Pinus sylvestris*) grown in the area. Patches of sod grasses have remained between tall thickets of nettles (*Urtica dioica*), willowherb (*Chamaenerion angustifolium*) and creeping thistles (*Cirsium arvense*), with raspberry (*Rubus idaeus*) clusters and large burdocks (*Arctium lappa*). Because of the configuration of the available site the traps were installed as fore lines of 18 and one of 15 traps. The distance between traps in a line was 7.5 meters, and the distance between lines was 10 meters. As a result, the grid covered 0.65 hectares (see scheme Fig. 1).

Trapping protocol and animals.

We used a live trap of an original design: a special feature of the trap is a wire trigger platform that does not frighten animals and is pressure sensitive, the trap is triggered by pressing the platform weighing 1.5-2 g. The chart of the trap is given in Shchipanov *et al.* (2005). The trap catches any animal that visited it, in our case ranging from the smallest pygmy shrew (*Sorex minutus*) with minimal weight near 2 g, to the largest root voles (*Microtus oeconomus*) with maximal weights of about 70 g. The dimensions and material of the trap are not so important; at least we did not find difference in capture success between aluminum and wooden traps, and traps 7x7x18 cm with traps 4x4.5x12 cm.

Oat flakes dipped in unrefined sunflower oil were used for bait. Each trap had its permanent position. The traps were checked once a day (early morning or evening), 1.5 h after daily activation. During the inspection, the locations of the animals were recorded, they were examined, weighed and released at the place of capture; all traps (both with animals and empty) were deactivated (turned over) and remained in their places, accessible to visitors, inactive and without bait. As a result, animals were able to move freely more than 90% of the daytime, so, a capture reflected the frequency of an individual's presence near a trap. Such a regimen minimizes mortality of shrews in traps to less than 1% of the animals

(Shchipanov et al. 2005). Animals were individually marked with ongoing numeration by toe clipping (we minimize the harm by using ID which require a minimal number of the toe), which did not affect survival (Shchipanov et al. 2005).

In this study, we used data obtained during two-week (14 trapping days) sessions in late July - early August 2014−2022. On total we caught 927 individuals of 12 species, of those 609 animals were recaptured (Table 1).

Table 1
Animals caught in 2014−2022 within two-week trapping sessions

Species	Total		Of those recaptured	
	Animals	Captures	Animals	Captures
Apodemus agrarius (Pallas, 1771)	11	20	3	12
Microtus agrestis (Linnaeus, 1761)	79	293	51	265
Microtus arvalis (Pallas, 1778)	14	43	9	38
Microtus oeconomus (Pallas, 1776)	131	578	88	535
Myodes glareolus (Schreber, 1780)	210	961	143	894
Neomys fodiens (Pennant 1771)	20	51	10	41
Sorex araneus (Linnaues 1758)	368	1710	272	1614
Sorex caecutiens (Laxmann 1788)*	4	7	2	5
Sorex isodon (Turov, 1924)*	3	4	1	2
Sorex minutus (Linnaeus 1766)	74	125	26	77
Sylvaemus flavicollis (Melchior, 1834)*	3	4	1	2
Sylvaemus uralensis (Pallas, 1811)	10	16	3	9
TOTAL	927	3812	609	3494
* - omitted from this study				

Residents.

The specificity of the animal component of the ecosystem is their mobility. In the same area we can observe both animals that live permanently and those that visit it temporarily. Most of the studies used Burt (1943) definition of home range as an area "traversed by the individual in its normal activities", while the "occasional sallies <…> should not be considered as a part of home range" (p. 351). Since possession of a home range presupposes preferential movement within a limited area, the repeated revealing of an individual at the area of home range is expected. In the case of a CMR study, animals with a home range, which we call "residents," can be distinguished as repeatedly captured individuals.

With respect to the duration of a study, we believed that individuals of a species could be reliably distinguished as resident if the maximal time required to recapture (T_r) in the average representative of the species did not exceed the duration of a trapping session (14 days in our case). This time was calculated as:

$T_r = I_m + 1.96 Sd$

where I_m is average interval (days) between captures of resident (recaptured) individuals, and Sd is standard deviation of the intervals between subsequent captures − I, calculated for the full set of intervals. As a result, we found, that

individuals of all the species can be reliably detected as residents during one trapping session (14 days) both on grid, and on the lines (Table 2).

Table 2
Maximum time (days) required to detect residence (recapture) in individuals. Details in text. Sq is for grid, L − for lines.

Species	Mean interval, I_m		Standard deviation of particular intervals, Sd		Maximal time, T_r	
	Sq	L	Sq	L	Sq	L
Apodemus agrarius	1.7	0.7	1.8	1.0	3.1	3.8
Microtus agrestis	1.8	1.5	2.6	2.0	4.7	6.5
Microtus arvalis	1.8	1.5	2.1	1.6	4.8	5.4
Microtus oeconomus	1.7	1.4	2.4	1.9	4.6	6.1
Myodes glareolus	1.9	1.5	2.6	2.0	4.8	6.5
Neomys fodiens	1.9	1.3	2.4	1.9	4.5	6.1
Sorex araneus	2.3	1.9	3.0	2.2	6.0	7.3
Sorex minutus	3.4	2.5	4.0	2.6	8.2	9.2
Sylvaemus uralensis	3.5	3.9	4.7	3.8	11.1	12.1

Indexes

To characterize population density several simple indexes of relative abundance can be proposed. The general idea of an index is that the catch is referred to a unit of trapping effort. usually 100 trap-days. For the live trapping, indices may be based on the number of captures and the number of individuals, either all animals or only local residents (Table 3). Index of catchability − I_c and total catch − I_{ID} are equal on lines and grid as were estimated for the same number of animals and the same trapping effort, while indexes attributed to residents (I_R and I_{IDR}) are different because of the different number of residents identifying on grid and lines (see scheme on Fig. 1). Therefore, the last two indexes were studied for both the grid and the line.

Table 3
Indexes of relative abundance used for the study

Index	Calculation
Total catchability I_C	$I_C = 100 C/(t.w)$; where C − total number of captures, t − number of traps, and w − number of workdays (checks in our case)
Resident catchability I_R	$I_R = 100 C_R/(t.w)$; where C_R − total number of captures of residents, t − number of traps, and w − number of workdays (checks in our case)
Total catch I_{ID}	$I_{ID} = 100 N/(t.w)$; where N − total number of individuals, t − number of traps, and w − number of workdays (checks in our case)
Resident catch I_{IDR}	$I_{IDR} = 100 N_R/(t.w)$; where N_R − number of resident individuals, t − number of traps, and w − number of workdays (checks in our case)

Spatial activity estimate

To estimate the spatial distribution of activity in residents we used the circular bivariate normal model of Calhoun and Casby (1958). By aligning a set of home ranges by activity centers (the average coordinates x and y of all captures), we

can obtain a "composed home range," which tends to be a circle and can be thought of as a range of average individual in a given species (Fig. 2a).

The position of the center of a home range is defined by central coordinates x, y (x is the number of trap in a line and y is the number of line) which were found for each of the individuals as:

$$x = \sum x_i / n$$

$$y = \sum y_i / n$$

where x_i and y_i are coordinates of particular captures and n – is a number of captures. We calculated distances from the central coordinate to the particular capture on the grid (d_{iSq}) in meters as:

$$d_{iSq} = \sqrt{[7.5(x_i - x)]^2 + [10(y_i - y)]^2}$$

and on the lines (d_{iL}) as:

$$d_{iL} = 7.5(x_i - x)$$

When the pool of distances (for a sample) from the central coordinate excluding outliers, is considered in units of standard deviation, the cumulated number of observed distances on the lines is as expected with a normal distribution (Fig. 2c). As an estimate of the spatial activity of an average individual of a species, we used the standard deviation of all distances from centers of activity in a sample of a given species/demographic group, Sd, and assumed that the probability of capture of the average individual could be expressed in terms of the normal distribution of activity in space.

Calculation of population density on lines

The distance from the center of activity at which an average animal can be detected as a resident by recapture depends on the general activity of the animal, measured by the number of captures. We assumed that the probability to fall into trap decreases with distance from the center, and is proportional to "remaining activity", $1 - \sum p$, where $\sum p$ is the probability to fall into trap (activity) accumulated on a transect at a distance in units of Sd under normal distribution. The distance from the center of activity at which an animal can be detected as resident was taken to be the distance at which an average individual can be caught two or more times. Since we assumed that activity in space, measured in number of captures, could be expressed in terms of the normal distribution, the number of captures at a distance from the center of activity in Sd units was calculated by multiplying the average number of captures of residents of the species in question by $1 - \sum p$, rounding the result to the nearest whole number. The distance. at which the animal could be recaptured (2 and more captures) in units of Sd was used as the coefficient k (detailed in Supplement 1). The swath width (along a transect line) at which an average animal could be detected as resident (W) was calculated for a given species/demographic group as doubled distance from the line (since deviations are equally probable in each direction):

$$W = 2kSd$$

where k is coefficient obtained for average captures of residents of a given species, and Sd is standard deviation of distances from central coordinate of all captures in this species. So, we calculated population density on a line (D_L) as number of resident individuals N_r detected on swath area. The swath area obtained as length of a line (L) multiplied by calculated width in meters with coefficient 10000 to estimate it in ind./hectare:

$$D_L = 10000 N_r / LW$$

Therefore, population density calculated for line-trapping represents the number of activity centers within the swath area. We calculated density on lines considering each of the short lines as independent part of generalized line of 87 traps (see example on Fig. 1).

The correctness of calculating population density on a line depends on the accuracy of calculating Sd of distances from the central coordinate. Using a jackknife procedure (1000 iterations), we found that the confidence interval became acceptable (less than 5% of the Sd value) when a sample exceeded 50 distances. So, when we did not have a sufficient data set, we additionally used the general set of distances obtained for a species in question over the entire study period (2014–2022). The Sd obtained for the whole period was called the average, Sd_a. In the cases, when we had data sets above 50 distances except for several years, we used also compiled Sd_c, that is, in years with the sample > 50, the calculation was carried out with natural Sd_n, while in the years with < 50 data, Sd_a was used. As a result, three variants of calculations were made: using natural Sd_n, average Sd_a, and compiled Sd_c.

Calculation of population density on grid

Since on the lines population density was calculated as a number of animals with activity centers located within an area, to obtain comparable population densities on a grid the animals whose centers of activity are located outside the territory bounded by lines should be excluded. We assume that the position of the activity center in resident animals caught only in border traps inside and outside the territory of the grid is equally likely if the radius of area where an animal could be recaptured (kSd in meters) is less than distance between traps. This radius was below 10 m in all the species, and we simply subtracted half of resident individuals recaptured solely in border traps from total number of residents. Grid population density, D_{sq}, was calculated by dividing the number of recaptured animals minus 0.5 of their number caught only in the border traps by the grid area, 0.65 ha (see example Fig. 1).

Analyses

Both population densities and indices were compared with the population densities in the grid determined over the 14-day sessions – D_{sq}. We used a regression model design with D_{sq} as a continuous predictor, treating the model's R^2 as a measure of the estimate's discrepancies with the actual data, the larger R^2, the smaller the discrepancies in estimates.

To study whether the scale of differences in indexes values reflects differences in absolute abundance we calculated average population density of species for all the studied years, and divided it by the average density of $S.$ $araneus$, as the most numerous species. This gives the scale of differences in absolute abundance. The same procedure was performed with each of the studied index. The scale of absolute abundance was used as continues predictor and plotted against scales of differences in the indexes of relative abundance. The agreement was estimated in simple regression model with the omitted digit 1 in $S.$ $araneus$ from the data sets.

Both regression models were performed in General Regression Models module of Statistica 7.

When analyzing changes in indicators during observation, the ratio of the indicator in question to its final value on the 14th day in individual species was assessed. The mean share to the day in question represents a mean value of proportions found in all the studied species for all the years to the day in question. The coefficient of variation (CV) for a given day shows the variability in the ratio of an index to its final value among species.

RESULTS

Indexes

The value of catch index, I_{ID}, diminished gradually with the increasing time of observation, more slowly after 7th day when majority of individuals have been already marked, whereas the value of catchability index, I_c, was almost independent on the duration of observations. The CV of both indexes decreased over time (Fig. 3a). Due to accumulation of number of captures in residents the index of catchability in residents, I_R, raised during all the time, slower after 10-th day, while CV has been decreasing all the time both on grid and on lines (Fig. 3b). Index of residents' catch, I_{IDR}, depends on identification of animals as residents, which happens more slow on lines. This resulted to gradual rising of index on lines, due to appearing of new detected residents (Fig. 3c). On the grid, where the resident population was determined faster, the index increased until the 5th day, then gradually decreased due to the accumulation of trapping efforts with a slowly increasing number of residents. CV for both indices has been decreasing all the time.

When we studied correspondence of indexes to actual population density on grid, we found that the entire set of data significantly correlated with all the indexes since the 3rd day both on the grid and on lines (Table 4). However, we have to note that the R^2 of the models increasing sharply after the 7th day (Fig. 4). In four most abundant species we had sufficient data to study correlation of annual index with population density on the grid. Although indexes in some species may significantly correlated with the density since the third day, reliable correlations of all indexes in all species were observed only from day 7 (see Table 4).

Table 4

Results of simple regression (adjusted R^2; beta coefficient – β) of indexes of relative abundance with actual density on the grid as predictor variable. I_C – catchability index, I_{ID} – catch index, I_R – catchability index of residents, I_{IDR} – residents' catch index; Sq is for grid, and L – for line data. Insignificant ($p > 0.05$) values are highlighted in bold.

Sample	Indexes	Day of the study											
		3		5		7		10		12		14	
		R^2	β	R^2	β	R^2	β	R^2	β	R^2	β	R^2	β
All data	I_C	0.81	0.90	0.87	0.94	0.89	0.95	0.91	0.96	0.93	0.96	0.93	0.97
	I_{ID}	0.84	0.92	0.90	0.96	0.94	0.97	0.95	0.98	0.96	0.98	0.96	0.98
	I_R Sq	0.52	0.73	0.77	0.88	0.86	0.93	0.89	0.95	0.91	0.96	0.92	0.96
	I_{IDR} Sq	0.58	0.77	0.84	0.92	0.92	0.96	0.96	0.98	0.99	0.99	1.00	1.00
	I_R L	0.38	0.62	0.61	0.79	0.79	0.89	0.85	0.92	0.88	0.94	0.89	0.95
	I_{IDR} L	0.39	0.64	0.63	0.80	0.84	0.92	0.90	0.95	0.93	0.96	0.94	0.97
Microtus agrestis	I_C	**0.31**	**0.67**	**0.54**	**0.80**	0.79	0.91	0.87	0.95	0.85	0.94	0.90	0.96
	I_{ID}	**0.35**	**0.69**	**0.53**	**0.79**	0.81	0.92	0.80	0.92	0.78	0.91	0.92	0.97
	I_R Sq	**0.23**	**0.62**	**0.49**	**0.77**	0.66	0.85	0.94	0.98	0.89	0.95	0.90	0.96
	I_{IDR} Sq	**0.10**	**0.53**	**0.32**	**0.68**	0.57	0.81	0.92	0.97	0.85	0.94	1.00	1.00
	I_R L	**0.21**	**0.61**	**0.53**	**0.79**	0.81	0.92	0.95	0.98	0.80	0.92	0.87	0.95
	I_{IDR} L	**0.21**	**0.61**	**0.47**	**0.76**	0.78	0.91	0.80	0.91	0.61	0.83	0.85	0.94
Microtus oeconomus	I_C	0.67	0.85	0.90	0.96	0.93	0.97	0.94	0.97	0.96	0.98	0.93	0.97
	I_{ID} Sq	0.77	0.90	0.94	0.97	0.98	0.99	0.97	0.99	0.96	0.98	0.96	0.98
	I_R Sq	**0.16**	**0.53**	0.73	0.88	0.81	0.91	0.85	0.93	0.90	0.96	0.87	0.94
	I_{IDR} Sq	**0.32**	**0.64**	0.87	0.94	0.89	0.95	0.99	1.00	0.99	0.99	1.00	1.00
	I_R L	**0.15**	**0.52**	0.71	0.87	0.80	0.91	0.81	0.92	0.88	0.95	0.86	0.94
	I_{IDR} L	**0.15**	**0.52**	0.75	0.88	0.81	0.91	0.83	0.92	0.93	0.97	0.95	0.98
Myodes glareolus	I_C	**-0.04**	**0.33**	0.54	0.78	0.81	0.91	0.85	0.94	0.89	0.95	0.92	0.96
	I_{ID}	**0.28**	**0.62**	0.82	0.92	0.88	0.95	0.87	0.94	0.90	0.95	0.92	0.97
	I_R Sq	**-0.15**	**0.12**	**0.04**	**0.42**	0.65	0.83	0.69	0.86	0.80	0.91	0.84	0.93
	I_{IDR} Sq	**-0.02**	**0.35**	**0.35**	**0.67**	0.77	0.90	0.85	0.93	0.96	0.98	1.00	1.00
	I_R L	**-0.12**	**0.20**	**-0.10**	**0.24**	0.47	0.74	0.67	0.85	0.83	0.93	0.87	0.94
	I_{IDR} L	**-0.10**	**0.24**	**-0.02**	**0.36**	0.78	0.90	0.89	0.95	0.87	0.94	0.88	0.95

Sorex araneus	I_c	0.53	0.77	0.53	0.77	0.63	0.83	0.66	0.84	0.62	0.82	0.62	0.82
	I_{ID}	0.84	0.93	0.80	0.91	0.90	0.96	0.92	0.97	0.72	0.87	0.70	0.86
	I_R Sq	**-0.11**	**0.23**	**0.17**	**0.54**	0.48	0.74	0.62	0.82	0.59	0.81	0.60	0.81
	I_{IDR} Sq	**-0.08**	**0.28**	**0.26**	**0.61**	0.74	0.88	0.94	0.98	0.94	0.97	0.98	0.99
	I_R L	**-0.15**	**0.12**	**0.13**	**0.50**	0.45	0.72	0.62	0.82	0.61	0.81	0.61	0.82
	I_{IDR} L	**-0.15**	**0.13**	**0.09**	**0.47**	0.51	0.76	0.79	0.91	0.78	0.90	0.76	0.89

To check whether the indexes accurately reflect scale of differences in population density of the species we compared the average population density and the indexes in five more numerous species. As a result, we found that since the 7th day of the study all the indexes (except for I_{ID} on the 7th day with $p < 0.052$) corresponds well ($R^2 > 0.9$; ß >0.95; $p < 0.02$) with the scale of differences in population density on the grid (Fig. 5).

Population density.

Computed for lines population density correlated with actual density on the grid in the entire samples in all three variants of calculation. Fore species were observed as residents for more than 5 years, and in those species we estimated correspondence of annual calculated density on lines to actual density on grid (Table. 5). Across the entire sample (all resident species for all years), and in particular species the best fit was found for densities calculated using the compiled Sd_c. Although the correspondence between the actual and calculated densities generally looks good (Fig. 6), it should be noted that the mismatch between calculated and actual density achieved on average near a quarter of the actual population density even in the best fitted models (see 'discrepancy' in Table 5).

Table 5

Results of simple regression of population density calculated on lines for natural (Sd_n), average (Sd_a), and compiled (Sd_c) standard deviation of distances from activity center with actual density on the grid as predictor variable. The discrepancy with the actual density (N) was assessed as % of the difference between the calculated density (n) and the actual one: (N-n)/N

Sample		Adjusted R^2	ß	p	Discrepancy %±Sd
All data	Sd_n	0.87	0.93	0.0000	41 ± 47
	Sd_a	0.90	0.95	0.0000	26 ± 21
	Sd_c	0.93	0.96	0.0000	25 ± 22
Microtus agrestis	Sd_n	-0.12	0.26	0.5666	48 ± 81
	Sd_a	0.50	0.76	0.0465	25 ± 17
	Sd_c	0.50	0.76	0.0465	25 ± 17
Microtus oeconomus	Sd_n	0.50	0.75	0.0201	68 ± 22
	Sd_a	0.89	0.95	0.0001	22 ± 16
	Sd_c	0.92	0.96	0.0004	21 ± 15
Myodes glareolus	Sd_n	0.81	0.92	0.0005	21 ± 15
	Sd_a	0.76	0.89	0.0014	25 ± 19
	Sd_c	0.91	0.96	0.0005	18 ± 14
Sorex araneus	Sd_n	0.74	0.88	0.0018	11 ± 8
	Sd_a	0.53	0.77	0.0153	17 ± 16
	Sd_c	0.75	0.88	0.0021	10 ± 8

DISCUSSION

Simple indexes.

An indispensable condition from perspective of ecosystem monitoring is the reliability of the assessment of changes in the population size of target species and in their share in the community. Despite the criticism, simple relative abundance indices continue to be used due to lower research costs or when long-term studies are not possible (McKelvey and Pearson 2001, Gomes et al. 2011; Gentili et al. 2014). The use of simple indices to study biodiversity is possible if the indices correctly reflect the scale of differences in population sizes. We found that estimates of relative abundance obtained over a fairly short period of time (3 days) acceptably corresponded to actual population densities. However, when using these indices to estimate inter-annual population densities, we found that for individual species, significant agreement between actual population densities and indices only emerged from day 7 onwards. Even the simplest catchability index (counter number of captures) from the 7th day correctly reflected the scale of differences, both interspecific and inter-annual, in population density under our trapping protocol. The catch index, which counted number of individuals, is the most alike to catchability under removal trapping. The latter index a bit more accurately reflected

population density, but its value notably changed with the longevity of the study, while the index, which counted number of captures, remained almost similar over all time of the observations.

Estimation of a resource flow, mediated by biomass, is a relevant component in some ecosystem studies (Vandewalle et al., 2010; Wilman et al. 2014; Barnes et al. 2016; Suárez-Castro et al. 2022). The possession of a home range is crucial for the survival of small mammals (Fleming 1979; Krebs and Davies 2009). Assaying resource flows in individual habitats we have to know whether population in a plot is local, or represented by animals casually visited an area. We believed that local animals were closely related to the resources of the area where they lived, that is, they had in this territory their home ranges in terms of Burt (1943). Kie et al. (2010) considered "a home range as the area an animal knows and maintains in its memory because the area has some value" (p. 2228). Similar is understanding home range as a "part of an animal's cognitive map of its environment that it chooses to keep updated" (Powell and Mitchell 2012). Given that the important area requires repeated visits, we could estimate significance of the area by the repeated captures. Using mean interval between the repeated captures we found that most of the observed species could be reliably distinguished as residents under our protocol of trapping. This was the reason to study indexes specifically related to resident animals.

Indexes of both catchability (number of captures) and catch (number of individuals) of residents depend on the number of animals identified as resident, and one could expected that longer observation is required to get indexes corresponded with actual abundance. Interestingly. in our study resident catchability and catch indexes, although they were based on different number of residents detected for a period, hence had different values, significantly corresponded to population density since the 3rd day in the general sample. Nonetheless, the reliability of these indexes increased markedly after 7th day of the study. Similar to the general indexes, significant agreement between the inter-annual population density and resident indices emerged from day 7 onwards.

Note, the value of indexes related to count of individuals, and residents in particular, were critically dependent on the arrangement of traps and the longevity of the study. As a result, the indexes are comparable only when traps of an invariant type are used under the same arrangement in space and with invariant number of trapping days.

Based on the results of this study. we can conclude that the use of simple indices is acceptable in research when it is necessary to monitor changes in population density and community structure in a specific area. Clearly, using of such indexes required application of invariant trapping protocol. However, even in this case the indexes should be used with caution, as it is known that the probability of capture could vary among sites and seasons, thus the indexes may vary irrespectively of invariant protocol (Slade and Blair 2000; Parsons et al. 2023). Our study was conducted at a permanent site during similar seasons for species with roughly similar home range sizes, and we have no idea whether we will find an agreement between interspecific differences in absolute abundance with other species or between different habitats or seasons.

Population density.

Absolute abundance of individuals is commonly estimated as the population density, i.e. a number of individuals permanently living on some unit of area, usually a hectare. This assessment involves counting the animals that permanently lived on the studied plot during the study period. Typically, population density can be estimated using CMR at live trap grids. Establishing of a grid is a time consuming, observations on a grid is also take a large time, and as a result, the study is commonly attached to some constant, relatively small area. All these circumstances limit the ability to directly estimate population density using CMR at a large scale. Arranging traps in a line significantly increases the surveyed area, allows for an integrative assessment of the population in the habitat, and the line can be easily established in a new site. Therefore, we try to find way to estimate population density using line data. There have been suggested two ways of calculation of population density using line data (Kalinin 2012; Shchipanov 2020). In both calculations we based on Calhoun and Casby (1958) model of parametric distribution of spatial activity of animals at

their home ranges. The criticism of the model is related to the configuration of the home range area, which is fare from the ideal circle. Indeed, each particular home range has a complex structure and configuration, with a number of foci of various "normal" activities (Kie et al. 2010; Powell and Mitchell 2012). However, when aligned along central coordinates, the distribution of activity of many individuals in space tends to a regular circle. This may be regarded as home range of an average individual of a species. Since the distribution of activity in such a home range could be predicted based on the normal distribution, we could calculate the distance from the line at which the animal can be detected as a resident. It should be emphasized that we used Sd of distances from the central coordinate as a measure of spatial activity of the average individual of a species, but not as an accurate estimate of home range. It is clear that we are not actually observing a distribution of activity that perfectly matches what would be expected from a normal distribution, but if the error is not too large, we might consider the estimate based on Sd of distances from activity center to be appropriate.

In our previous calculations we tried to assess the accurate number of animals lived within some zone encompassed the probability of capture of a resident animal (Kalinin 2012; Shchipanov 2020). There were rather complex and equivocal calculations. Here we tested more simple calculation based on full revealing of residents with correction of the width of observed (along the line) swath in accordance to the current activity of animals. The accuracy of this estimate depends on the correct determination of the number of residents. We verified that virtually all small mammals living on the site could be reliably identified as resident within a 14-day trapping session. Also, the estimate is sensitive to the correctness of calculation Sd of distances from activity center. We suggest to use standard deviations for the set of data accumulated for all the years of a study, the average Sd, for the classes when < 50 distances could be taken for analyses. However, keeping in mind, that home ranges may vary according to the direct and indirect influences of weather, food store, and population density (McNab 1963), we should note that the average Sd may produce larger errors, than Sd calculated for a given year. The best results were obtained when we used the "average" Sd calculated from all data obtained in all study years for the cases with fewer than 50 distances in a sample, and the actual Sd in years when we had more.

As a result of the study, we found that the population density calculated in this way from linear data correlates well with the grid population density; the adjusted R^2 of the model turned out to be above 0.9. Although, the error of the estimate made on average a quarter to actual density, this high percentage resulted from relatively small number of animals lived on the grid. As, for example, 25% for 20 animals/ha made 5, i.e. if we found on the grid (0.65 ha) 13, the error will made ± 3 individual.

Therefore, we believe that the density calculated with this way on lines could be used as a rough measure of population density for purposes of estimation the magnitude of resource flow.

Declarations

Animal and Human Research at A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (which are in accordance with recommendations of US and EU ethical committees) (permission No. 30a issued on April 10, 2023), following all relevant laws and regulations. This article does not contain any experiments on human subjects performed by any of the coauthors. The capture method used does not affect animal welfare. No animal died in traps in the course of the study.

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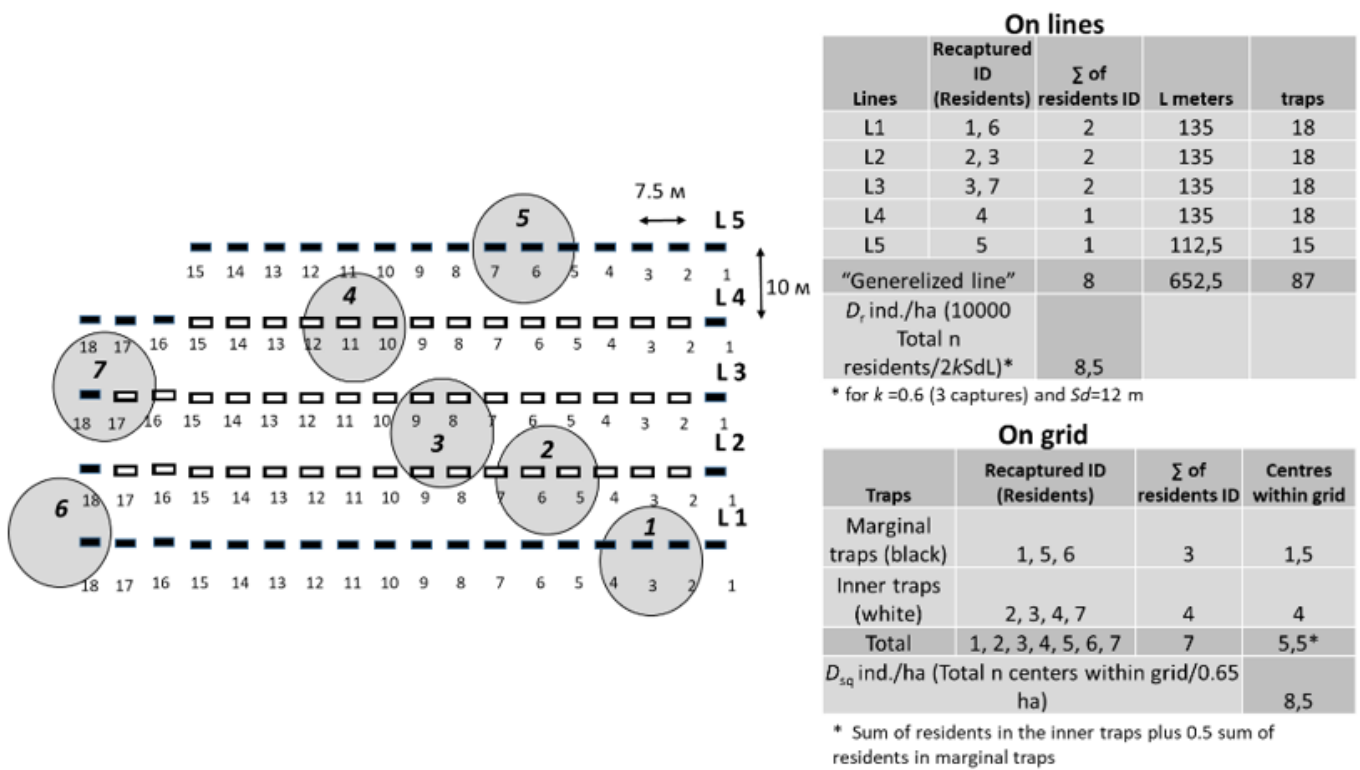
Figures

On lines

Lines	Recaptured ID (Residents)	Σ of residents ID	L meters	traps
L1	1, 6	2	135	18
L2	2, 3	2	135	18
L3	3, 7	2	135	18
L4	4	1	135	18
L5	5	1	112,5	15
"Generelized line"		8	652,5	87
D_r ind./ha (10000 Total n residents/$2kSdL$)*		8,5		

* for k =0.6 (3 captures) and Sd=12 m

On grid

Traps	Recaptured ID (Residents)	Σ of residents ID	Centres within grid
Marginal traps (black)	1, 5, 6	3	1,5
Inner traps (white)	2, 3, 4, 7	4	4
Total	1, 2, 3, 4, 5, 6, 7	7	5,5*
D_{sq} ind./ha (Total n centers within grid/0.65 ha)			8,5

* Sum of residents in the inner traps plus 0.5 sum of residents in marginal traps

Figure 1

The scheme of the grid and example of calculating population density on lines and on grid. The gray circles are the areas where the average individual can be caught two or more times (detected as resident) within 14 days of trapping; figures in italic in the circles show animals *ID*, L1-L5 mark line numbers; small rectangles show places of traps, ones colored black – marginal traps; smaller figures show trap numbers, doubled arrows – distances between traps in a line (7.5 m), and between lines (10 m). Details in the text.
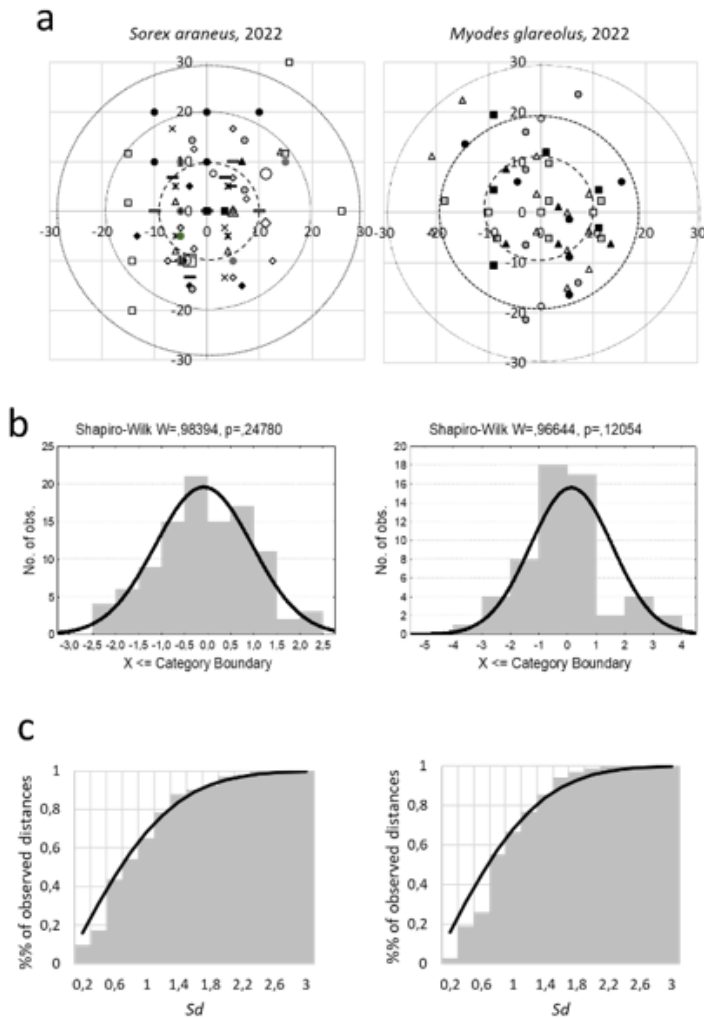
Figure 2

Home ranges in the common shrews (*S. araneus*) and bank voles (*M. glareolus*) in 2022. a) All the distances of captures from activity centers of individuals on the grid (different individuals are shown by different markers; rings encompass areas of 1, 2, and 3 *Sd* in radius). Histograms below the home range charts of a corresponded species: b) Checking normality of distribution of distances from activity center on lines (generalized line); c) accumulated percentage of observation of distances from activity center in units of *Sd* on lines (generalized line). The bold line shows the expectation for a normal distribution.
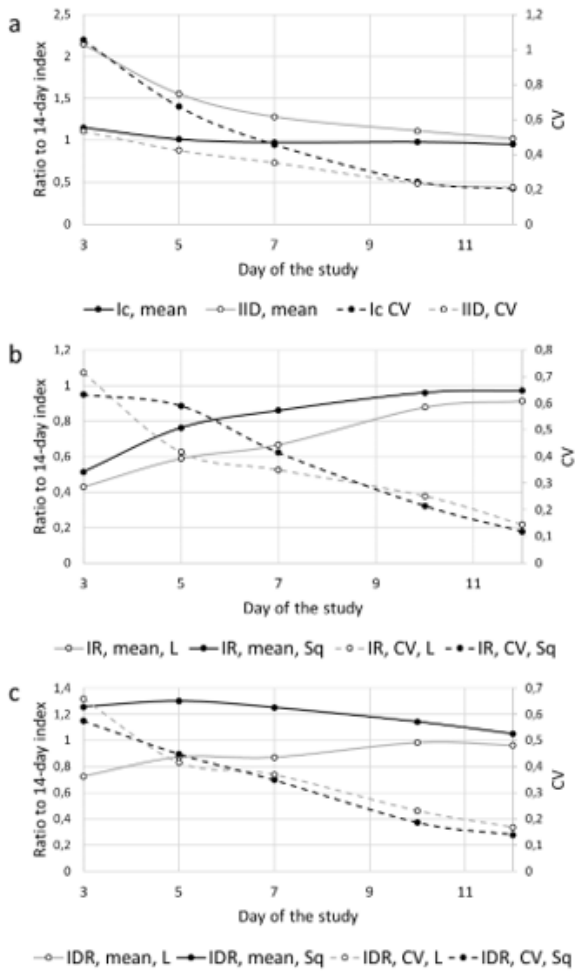
Figure 3

Changes of relative abundance indexes (mean deviation from the final 14-day value among the species, CV – coefficient of variation) with respect to time of the study. a) The indexes in the total sample: catchability – I_C, and of catch – I_{ID}; b) the indexes in residents: catchability of residents – I_R on lines – L, and on the grid – Sq, and c) the indexes of residents' catch – I_{IDR} on lines – L, and on the grid – Sq.
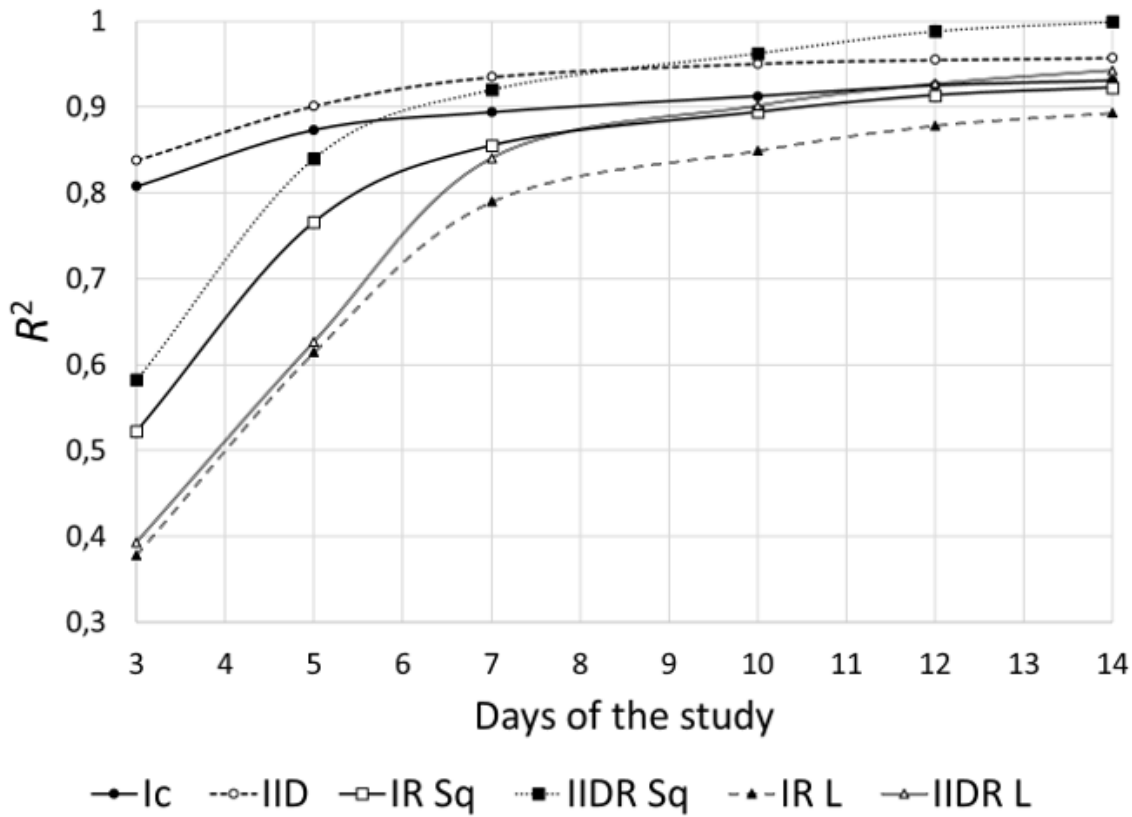
Figure 4

Changes of the adjusted R^2 in regression model of indexes with actual population density on the grid as predictor variable with respect to duration of the study. I_c – catchability index, I_{ID} – catch index, I_R – catchability index of residents, I_{IDR} – residents catch index; Sq is for grid, and L – for line data.
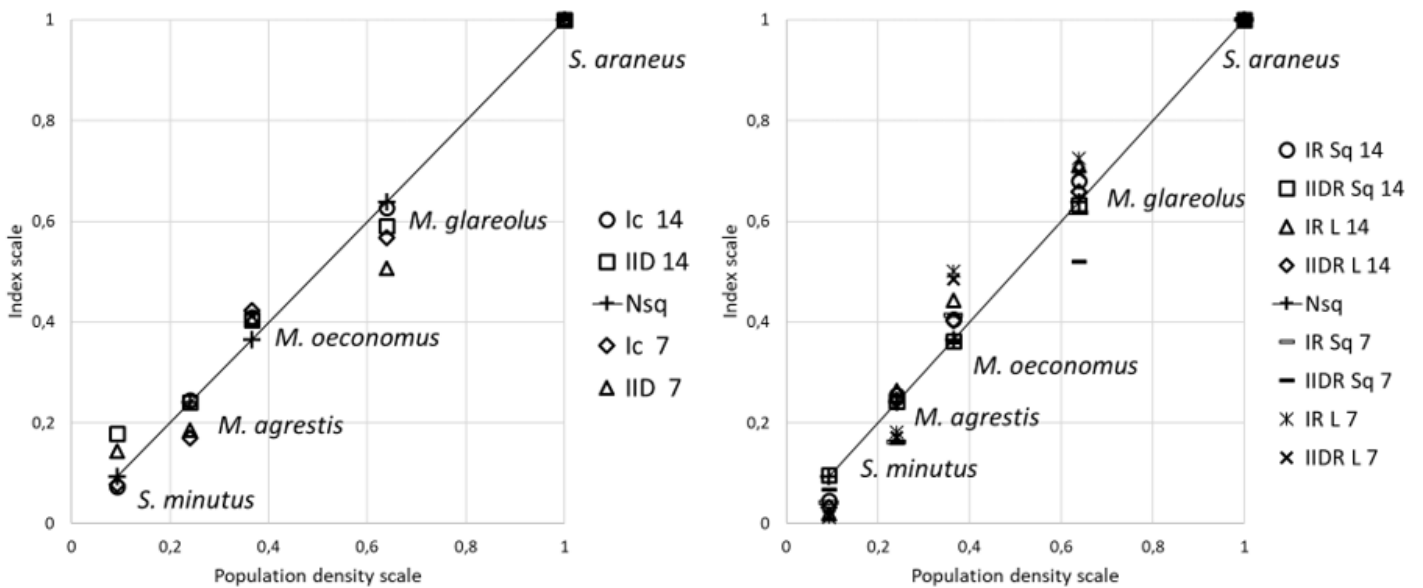

Figure 5

Scaling population abundance as ratio to most numerous *S. araneus* values. a) Indexes for the total sample: I_C – captivity index, I_{ID} – catch index; b) Indexes for resident sample: I_R – index captivity of residents, I_{IDR} – catch index of residents, Sq – calculated for grid data, L – calculated for lines. The numbers to the right of the index in the legend indicate the number of trapping days used to calculate the index. The actual population density on grid - N_{sq} (number of residents/ha for 14 trapping days) is shown as line with the cross as the marker.
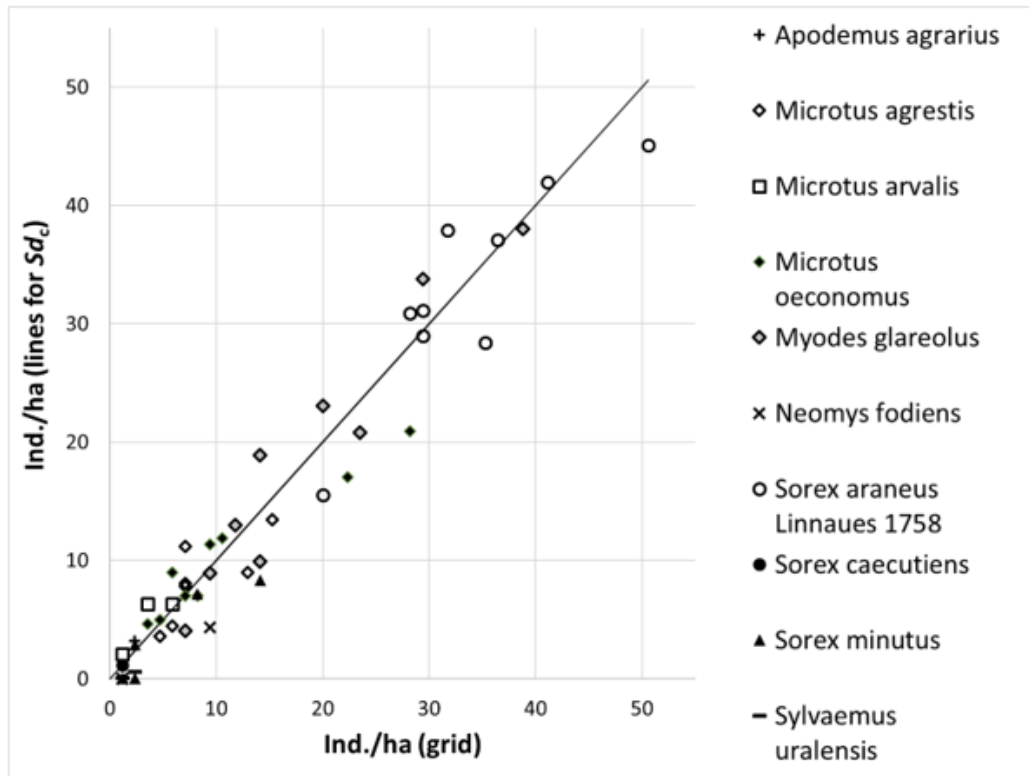

Figure 6

Correlation of population density on grid with population density calculated on lines with using compiled standard deviation of distances from activity center (Sd_c).

Supplementary Files

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- Supplement1.docx