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Estimate of the Number of Traps Visited by Small Mammals Based on a Probabilistic Model

[With 3 Tables & 3 Figs.]

The estimation of mean number of points visited by animals of particular population was performed for three species of small rodents: *Apodemus flavicollis*, *Apodemus agrarius* and *Clethrionomys glareolus*, basing on the assumption of the probabilistic model of sequence in visiting trapping points set out on the home range of individual specimens. The assumption of probabilistic model allowed to estimate the mean number of visiting points, basing merely on 2 or more captures of individuals. In result it was established that the mean number of visiting points does not change regularly in time of habitation on definite area, however the identity of points changes. It has been shown that the probabilistic model for visiting the trapping points is useful as a starting hypothesis for analysis of the course of visiting in small rodents.

I. INTRODUCTION

If we will establish the live-trap points or some other registering appliances in a certain defined pattern, covering particular home range of the individual of given small mammal species, the points may be visited by this individual according to one of the following ways:

(1) By chance, *i. e.*, the probability of the individual visiting each of all visited by it points is the same,

(2) Not by chance, and then the probability of visiting particular points by the individual is different, at which: (a) certain points preferred by this individual are visited more often, others more seldom; (b) the individual after visiting one particular point prefers to visit another new point the next time.

Of course, we could presuppose many other more complicated models concerning the sequence of visits made by the individual in its home range. Presented above three models as the simplest appear to be good basis for the analysis of this problem.

In given population the realization by chance sequence of points visiting by individuals allows for the statistical estimation of the number

of visited points even if the number of information concerning particular points is very limited. We can easily assume theoretically that the more mobile species will visit the points of registration differently than less mobile ones, and the individuals walking certain well defined paths otherwise than those moving at random on the whole home range etc.

Decisive influence on the way of visiting the points may have environmental conditions such as: microclimatic, nutritional, close neighbourhood of the individuals of the same or other species, the degree of coincidence in their home ranges or the place of particular individuals in the dominant structure of population, and such.

Finally, the method of trapping applied may be of the first importance for the sequence of visiting the points. For example strong psychological shocks connected with the registration at a particular point may frighten the animal and prevent its return, or otherwise the strong attraction of the bait will cause the animal to visit points nearest its nesting place repeatedly.

The individuals of given population will thus realize one of above mentioned models of visiting the points situated on their home range depending upon: 1) ecology of the particular species, 2) ecological situation of investigated population in the broad sense (environment, interpopulation relations) and 3) the method of registration.

Therefore establishing if the sequence of visited points occurs by chance or not by chance will provide not only the methodological pointer concerning the way of data elaboration, but as well will characterize the ecological situation of given population and its changes.

Various authors have tried to determine the size of the individual's home range taking into consideration the number of registration points visited. This method however has met with much criticism (Howard, 1949; Blair, 1951; Soldatova, 1963 and others). In the present paper we will not concern ourselves with this problem, but we will try to estimate the number of visiting points basing on limited number of registered visits by particular individuals. As well we will attempt to determine which one of described above three patterns of visiting sequence has been realized by particular populations of three species of small forest rodents: *Apodemus flavicollis* (Melchior, 1834), *Apodemus agrarius* (Pallas, 1771) and *Clethrionomys glareolus* (Schreber, 1780).

II. MATERIALS AND METHODS

Present investigation was carried out on rodents live-trapped continuously during 6 years (1955—1961) on the forest area of 3 ha. The traps were set checkerwise on

investigated area at 14×14 m intervals (10 rows of 15 traps each). Trapping was performed once weekly and the traps were checked twice in 24 hours. Each trapped rodent was marked with a particular number and then released.

During investigation period 3111 animals were captured and the total of registered visits has reached 10054. Only the results concerning specimens trapped more than once were used in the present elaboration.

More detailed description of methods and the analysis of trapping intensity, migrations and population dynamics for particular species were presented in the publication by Andrzejewski (1963).

III. RESULTS

If a given individual was captured for the first time at a given point, it has indicated the first of all visited by it points. The second registration may have occurred at a different point, that the first one and thus the individual revealed the second of visited by it points, or the second capture happened at the same point, and no new point was revealed.

Similar situation will occur when given individual will be trapped for the third time. Then four possibilities will have to be taken under consideration. If the individual in the first two registrations has revealed two points then: (1) at the third one it may have registered at a new third point and so has revealed three of all visited by it points, or (2) the individual has registered at one of the two points disclosed previously, and the number of revealed by it points remains two. However if the individual after first two captures, revealed only one point there will develop two eventualities: (3) the individual at the third visit has been captured at a new point in relation to the point where it was caught two times previously (quantitatively we have an analogous situation to the (2), after three visits two points revealed) and at last (4) the individual visited for the third time the same point and after three visits it still has only one point revealed.

Similar computation may be made for the fourth, fifth and so on registered visits. As an example table 1 and 2 show the distribution of the number of points revealed by individuals of *Apodemus agrarius* up to and including successive captures with division into sexes.

At the applied method of trapping the frequency of captures for particular species is more or less constant and the length of residency of individuals on investigated area has an exponential distribution (Andrzejewski & Wierzbowska, 1961; Andrzejewski, 1963). Therefore the number of individuals with the high number of registered visits decreases along with increasing number of trappings.

Presently the mean number of revealed points after 2, 3, 4, etc. captures by animals of determined sex and species (Table 3) were computed. If we assume that the animals visit the points at random then,

Table 1.

Distribution of number of traps »revealed« by females *A. agrarius*
n — number of captures of the rodent; *N_n* — number of rodents,

s \ n	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
1	40	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2	291	72	15	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
3		152	80	31	12	7	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
4			77	72	34	20	12	7	9	2	2	1	-	-	-	-	-	-	-	-	-	
5				38	53	33	14	12	9	4	4	1	1	1	1	-	-	-	-	-	-	
6					19	34	29	16	10	10	4	5	2	2	1	1	1	1	1	-	-	
7						8	18	27	20	14	9	5	7	6	4	2	1	1	1	2	2	
8							3	7	15	14	12	7	4	2	2	4	3	2	-	-	-	
9								2	4	7	10	10	10	7	5	2	2	1	1	-	-	
10									2	3	4	4	7	8	7	6	6	5	3	2		
11										1	3	3	3	3	5	1	2	3	4	3		
12												2	1	1	1	4	3	3	3	1		
13														1	-	-	-	-	-	1	3	
14															1	1	1	-	-	-	-	
15																		1	-	-	-	
16																				1	1	1
<i>N_n</i>	331	229	172	144	120	102	79	71	61	53	45	36	33	30	26	23	19	17	15	14	12	

basing on above mean, we can estimate the mean number of points (size of the pool) which there are inside area and changes in this number with successive captures. The estimation was achieved as follows:

Let the random variable X_n represent the number of different points which the animal visited up to and including the n captures, r — the number of points which there are inside area of animal. Assuming that the animal visits each of the r points with equal probability $p = \frac{1}{r}$. Then the probability that the rodent will reveal after n captures s different points [$s = \min(r, n)$] equals:

$$P_{n,s} = \binom{r}{s} \cdot \frac{1}{r^n} \cdot (-1)^s \cdot \sum_{v=1}^s (-1)^v \cdot \binom{s}{v} \cdot v^n \dots \dots \dots (1)$$

Mean value of this distribution is expressed by:

$$E(X_n) = r \cdot \left[1 - \left(\frac{r-1}{r} \right)^n \right] \dots \dots \dots (2)$$

Accepting in equation (2) empirically obtained mean number of points (\bar{S}_n) »revealed« by rodents up to and including the n capture as an estimation of average value $E(X_n)$, the number of points which there are inside area (r) was estimated.

from amongst all the traps present on the home range.
 captured at least n times; S — number of traps »revealed«.

23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	-	-	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-
4	5	5	4	3	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	-	-	1	-	-	1	2	1	1	1	1	1	1	1	1	1	1	1	-	-
2	2	1	-	2	2	1	1	2	2	1	1	1	-	-	-	-	-	-	1	-
-	-	1	1	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1
-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-
1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	10	8	7	7	6	6	5	5	5	3	2	2	1	1	1	1	1	1	1	1

The usage of tables elaborated by Wierzbowska (1969) made it possible to omit the complicated and time absorbing calculations connected with the multiple estimation of the number of points (\hat{r}) for numerous means corresponding with particular successive captures of rodents. From these tables it is possible to read out directly the value \hat{r} for the particular defined mean number of points visited by rodents.

The estimated number of points visited by rodents carries two kinds of error: (1) Due to nonuniformity of population in relation to the number of points which there are inside area of animal, (2) the error as a function of n and N_n (N_n — the number of animals with n captures). The detailed description of these errors in estimation is given in the tables (Wierzbowska, 1969).

Thus assuming random visiting of the points we can estimate the number (pool) of points which there are inside area (r) on the basis of at least two or more registration visits, on condition that the number of individuals with that number of visits will be high enough.

On this basis the number of points \hat{r} by each of investigated species has been estimated, taking under consideration first two captures, first three captures, first four captures and so on up to the number which is still represented by large enough number of animals (Fig. 1).

Table 3.

Empirical mean number of traps »revealed« and its standard deviation.
 n — number of captures of the rodent; S_n — mean number of traps »revealed«
 up to, and including the n capture; σ_{S_n} — standard deviation for the mean S_n .

n	Cl. glareolus			A. agrarius			A. flavicollis		
	Σn	δ/S_n	δ/S_n	Σn	δ/S_n	δ/S_n	Σn	δ/S_n	δ/S_n
2	1.9056	0.0154	0.0131	1.87915	0.0179	0.0081	1.93684	0.0176	0.0136
3	2.68928	0.0298	0.02403	2.64192	0.0345	0.0278	2.82482	0.0341	0.0347
4	3.40969	0.0455	0.0392	3.36046	0.0485	0.0446	3.54635	0.0659	0.0592
5	4.09474	0.0601	0.0492	4.00694	0.0625	0.0645	4.36619	0.0874	0.0755
6	4.67722	0.0792	0.0670	4.62500	0.0842	0.0787	4.98039	0.1255	0.1066
7	5.23664	0.1029	0.0878	5.15686	0.1035	0.1001	5.76923	0.1794	0.1396
8	5.77669	0.1266	0.1047	5.70896	0.1341	0.1481	6.48387	0.2181	0.1719
9	6.30435	0.1504	0.1312	6.29577	0.1455	0.1584	7.24483	0.2181	0.2301
10	6.82908	0.1696	0.1560	6.52239	0.1783	0.1715	8.00000	0.2181	0.2885
11	7.34944	0.2011	0.1837	7.18868	0.1907	0.2134	8.80000	0.2181	0.2885
12	7.8603	0.2311	0.2215	7.60000	0.2402	0.2349	9.60000	0.2181	0.2885
13	8.36833	0.2545	0.2545	8.13889	0.2809	0.3057	10.40000	0.2181	0.2885
14	8.875814	0.3359	0.2799	8.63636	0.2964	0.3287	11.20000	0.2181	0.2885
15	9.37179	0.3611	0.3238	9.13333	0.3391	0.3867	12.00000	0.2181	0.2885
16	9.87143	0.3919	0.3722	9.63636	0.3769	0.3700	12.80000	0.2181	0.2885
17	10.3714	0.4662	0.4128	10.13333	0.3769	0.3700	13.60000	0.2181	0.2885
18	10.87175	0.5631	0.4915	10.63636	0.3769	0.3700	14.40000	0.2181	0.2885
19	11.375000	0.6703	0.5240	11.13333	0.3769	0.3700	15.20000	0.2181	0.2885

Results of computations show that for *Clethrionomys glareolus* and *Apodemus agrarius* the estimated number of visited points increases along with successive captures. In *Apodemus flavicollis* the estimated number of visited points is high at the beginning and then decreases up to 3—4th capture, to increase again as in two described above species. In all three species the estimated number of visited points in males is higher than in females in the whole analysed capture sequence.

Next we have investigated the question if the probability of revisiting one of revealed points is the same in the complete trapping sequence of given individual. With this aim in view we have calculated how many mice should reveal after n captures s points, where $s = 1, 2, \dots, \min(r, n)$. The probability expressed by equation (1) was multiplied by the number of mice with n trappings. The value of corresponding probabilities was

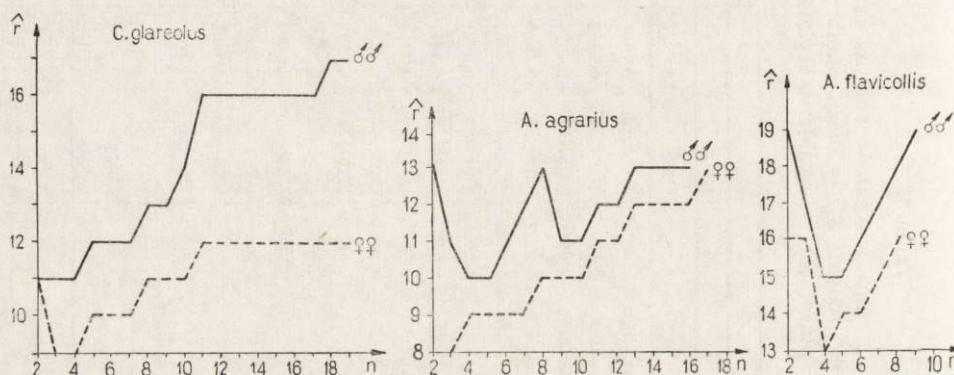


Fig. 1. Estimated number of traps present on the home range of the rodent. n — number of captures of the rodent, \hat{r} — estimator value of the number of traps (r) present on the rodent's home range.

read out from tables elaborated by Wierzbowska. Computed in this way number of mice was compared with the number obtained empirically by means of chi-square statistics of Pearson's. Verification was performed at the level of significance $\alpha = 0.05$.

It was established that equal probability of revisiting the points is limited only to the initial period of capture sequence and that it is different for definite species and sexes (Fig. 2).

Analyses described were performed on growing sequence of captures of individuals, analysing each time the sum of captures counting from the first capture of the individuals. Thus the number of revealed points in successive captures could have increased, and reach at its maximum the number of captures.

As it was said above the estimation of the number of visiting points is possible also on the basis of two successive captures or expressing it differently on the basis of the ratio of registered visits number realized by animals at the same point (h) to the number of visits realized at two different points (m): in given pairs series of successive captures.

Basing on this principle the changes in the number of visiting points in *Clethrionomys glareolus* were analysed in successive captures. It was

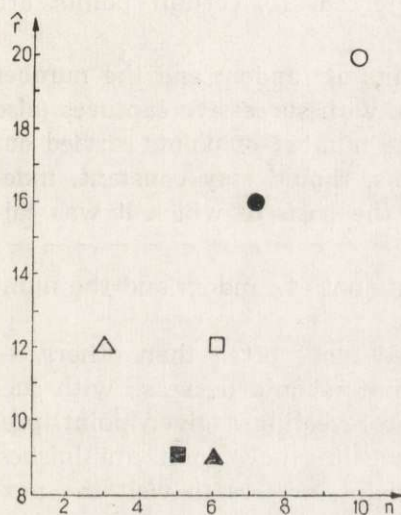


Fig. 2.

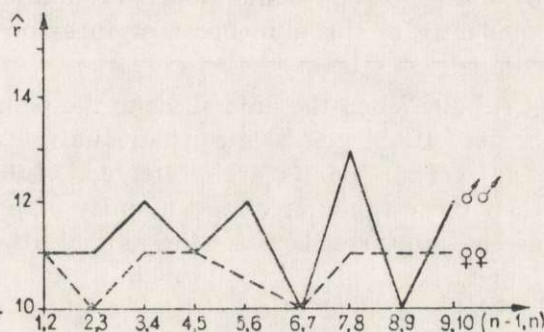


Fig. 3.

Fig. 2. Illustration of the manner of traps visiting by rodents.

n — number of captures realized in the period of rodent's by chance movements;
 \hat{r} — estimator value of the number of traps (r) present on the rodent's home range, for species and sexes.

Squares — *C. glareolus*, triangles — *A. agrarius*, circles — *A. flavicollis*, open — males, filled — females.

Fig. 3. Number of traps present on the home range, estimated by means of result for consecutive pair captures.

$(n, n-1)$ — successive captures of the rodent; \hat{r} — estimator value of the number of traps (r) present on the rodent's home range.

done in the following way: first the number of visited points was estimated basing on series of pairs of first and second captures in a given group of animals, then basing on series of pairs of second and third captures, then third and fourth and so on (Fig. 3).

Estimated in this way number of visited points shows in successive captures small random deviations from a certain constant value. The difference in this value for females and males of investigated species is as noticeable as in previous analyses.

IV. DISCUSSION

Let us analyse the course of the diagram illustrating the number of points which there are inside area (r) in successive captures, estimated on the basis of the number of points revealed up to successive capture.

We shall consider following cases: (1) the sequence of points visiting occurs at random, (2) the sequence of visiting the points occurs not at random, and (a) certain points are preferred, (b) certain points are omitted at successive captures.

Ad (1). When the animal visits the points at random and the number and identity of the points does not change with successive captures (also with the time flow), then estimation of the number of points carried out by means of above mentioned calculations, should stay constant, independently of the number of captures on the basis of which it was calculated.

Ad (2). When the animal visits the points not at random and the number of visited points is constant and:

(a) certain points are preferred, visited more often than others, — then the estimation of the number of points should decrease with successive captures, because the animal after revealing a given point, prefers to revisit it — the probability of revealing new points diminishes.

(b) the animal after visiting a given point, prefers to visit the next time a different new point — then the estimation of the number of visited points should grow with farther captures, because the animal as it were strives to reveal the still unrevealed points — the probability of revealing new points is higher than revisiting the points already revealed.

The assumption concerning the stability of the number and identity of points which animal visits in the same interval of time and so connected to a degree with a definite period of animal's life does not have to be true. To the contrary the life »dynamics« of small mammals seems to indicate that the assumption is most probably false.

Let's examine now two farther alternatives of variations in estimating the number of points (r) with growing number of captures. We can distinguish two cases:

(1) When during successive captures the number of visiting points decreases then the number of estimated points (r) will also show the tendency to decrease. The distinction elaborated previously in 2a is nonspecific, as the decrease in the number of points (r) with successive captures may indicate the preference for certain points or the decrease in the number of points belonging to area. However both cases are univocal to a degree, because the preference for particular points may lead

the animal in extreme cases to not visiting other previously visited points.

(2) When during successive captures the animal increases the number of visiting points — (adds new visiting points or changes its home range) then the number of points (r) will grow along with successive captures. The situation is similar to 2b and so here also the above distinction is non specific.

The analysis of gathered materials has shown, that with growing number of captures of individuals the estimated number of points which there are inside area increases. We can present two interpretations of this phenomenon: (1) that the animals avoid revisiting already revealed points or that (2) with successive captures the number of visiting points increases. It appears that the first interpretation must be rejected. The high trappability of rodents at the applied method of trapping and numerous cases of revisiting the same point by given individual, established in two consecutive checkings of traps points to it. The second interpretation agrees with an observation that small mammals when occupying given area change their home range, so that the summation of visiting points established in prolonged period of time gives the overestimation of the home range (Soldatova, 1963).

From amongst the investigated species this phenomenon is best noticeable in *Apodemus agrarius*. In *A. flavicollis* in examined material there appeared certain regular changes in males as well as females, starting with the decreasing tendency of the number of visited points after first two or three captures of the individual, to the increasing tendency in the number of visited points after farther captures. It seems that for the first captures of this species, the interpretation of true decrease in the number of visited points should be accepted. However the highest number of visiting points is shown in the second capture. Therefore it appears that the animal revisits relatively rarely in the second capture the point that it has visited initially. As it concerns the first two captures we may suppose that in this species the place of first capture is often spatially different from the place of successive captures. It should be noticed that the number of points visited by *A. flavicollis* is much higher than in two remaining species.

Above conclusions were confirmed by testing how long the probability of visiting the pool of registration points by the animal remains the same. It was established that the probability oscillated in investigated material from 3 (*A. agrarius*) to 10 (*A. flavicollis*) captures. It is difficult to ascertain what is the reason for such differentiation in results.

Changes in the number of visited points during successive captures in case of the estimation of this number based on independent pairs will

occur analogically as in estimation done previously. However the analysis of material carried out, indicates in this case that in *Clethrionomys glareolus* as in *Apodemus agrarius* the number of visiting points does not change regularly with successive captures. Examined were only the pairs of successive captures in which the second capture occurred at the same point as previously or at another point. It is possible to assume then, that the probability of capturing the same individual twice at the same point in succession in investigated species and at the kind of trapping method applied, does not change regularly for this individual in successive captures.

Comparing the conclusion that rodents along with successive captures increase the number of visiting points if we consider this number counting from the first capture each time, with the conclusion that the number of visiting points does not change regularly with successive captures, and if we estimate this number on the basis of pairs of successive captures then it is possible to describe the changes in the number of visiting points during inhabitation on a particular area in more detail. It could be presented as a simultaneous process of visiting new points along with increasing number of captures of individual (so to a degree along with the time of residency of the individual on a particular area) and discontinuation of visiting other, previously visited points. These changes do not lead however to regular decrease or increase in the number of visiting points along with repetition of captures (and thus also with the time of residency on given area).

Presented analysis does not allow for decisive conclusion, whether animals observed on a given area and at applied trapping method have preserved the at random sequence in visiting the points situated on area inhabited by them. This assumption however is not contrary to presented conclusions, and based on it model of points visiting fulfilling simple condition, may be considered as zero hypothesis for the analysis of the pattern of trapping points visiting.

The presupposition of by chance visiting of trapping points allows to estimate the mean number of visited points by individual from a particular group of animals on the basis of merely two captures of each individual.

Even if the estimation would be weighed with certain error, nevertheless it facilitates the elaboration of trapping materials from short periods of time and allows to analyse the variability of this number for the short periods of time in given population as well as changes occurring during the life-time of individuals.

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OCENA LICZBY PUŁAPEK ODWIEDZANYCH PRZEZ DROBNE SSAKI
NA PODSTAWIE PROBABILISTYCZNEGO MODELU ICH ODWIEDZANIA

Streszczenie

Na powierzchni leśnej wielkości 3 ha śledzono poruszanie się gryzoni na podstawie odłowu w żywołowne pułapki. Badaniom podlegały trzy gatunki: *Clethrionomys glareolus* (Schreber, 1780), *Apodemus agrarius* (Pallas, 1771) i *A. flavicollis* (Melchior, 1934). Metodą badań był intensywny połów zwierząt zamieszkujących badaną powierzchnię, znakowanie ich, wypuszczanie i poprzez dalsze połowy śledzenie dalszych ich losów. Zebrany w ten sposób materiał posłużył do oceny punktów połowu (r) znajdujących się w obrębie poszukiwanego areału. Oceny dokonano poprzez analizę rozkładu liczby różnych punktów w które gryzoń złowił się w ciągu n kolejnych złowień. Zakładamy, że areał ma wyraźne granice, oraz, że prawdopodobieństwo złowienia w każdy punkt połowu jest jednakowe i wynosi r . Wówczas funkcja rozkładu prawdopodobieństwa analizowanej zmiennej jest dana przy pomocy wzoru (1) ze średnią wg wzoru (2). Empiryczny rozkład liczby „ujawnionych” punktów do n -tego złowienia włącznie z podziałem na gatunki i płęć dane są w tablicach 1—3.

Przyjmując empirycznie otrzymaną średnią liczbę różnych punktów, które gryzoń „ujawnił” do n -tego złowienia, jako oszacowanie wartości przeciętnej z równania (2), otrzymujemy oszacowanie liczby pułapek (r), poprzez rozwiązanie równania (2) przy określonym n .

Dokonane wyliczenia wykazują, że jednakowe prawdopodobieństwo ponownego odwiedzenia punktów jest ograniczone do pierwszych kilku złowień, przy czym liczba złowień jest różna u różnych gatunków i płci (Ryc. 2). Ponadto, zarówno dla samic jak i samców u *Clethrionomys glareolus* jak i u *Apodemus agrarius* oszacowana liczba odwiedzanych punktów rośnie w miarę kolejnych złowień. U *A. flavicollis* oszacowana liczba odwiedzanych punktów ma początkowo wartość wysoką, następnie spada do złowienia 3—4, by następnie wzrastać podobnie jak u pozostałych gatunków (Ryc. 1). U wszystkich trzech gatunków oszacowana liczba odwiedzanych punktów jest wyższa u samców niż u samic na przestrzeni całego analizowanego okresu czasu.