POLSKA AKADEMIA NAUK — ZAKŁAD BADANIA SSAKÓW
ACTA THERIOLOGICA
VOL. IX, 1. BIAŁOWIEŻA 30.V.1964

Jaroslav PELIKÁN, Jan ZEJDA & Věra HOLIŠOVÁ

On the Question of Investigating Small Mammal Populations by the Quadrate Method

Zagadnienie badania populacji małych ssaków metodą kwadratów

[With 6 Tables & 9 Figs.]

I. INTRODUCTION

The present paper, being of a mostly methodological character, contains a summary of our hitherto experience in applying the quadrate method in the investigation of small mammal populations, as well as a more detailed analysis of the results obtained during a period of three years. The observations of variations in population densities in different habitats will be published elsewhere. This paper is a continuation of our earlier study (Pelikán & Zejda, 1962) in which we endeavoured to analyze the efficiency of the quadrate from several viewpoints and, mainly, to check the values of population density obtained on the quadrate by means of the capture-recapture method.

Basis for the investigation of small mammal populations by means of snap traps laid in an area was given by B o l e (1939) in his classical paper on quadrates. Although later on, some ecologists proved and applied this method (S t i c k e l, 1946a; 1946b; T u r č e k, 1949; 1953; 1954; 1957), a great majority of authors applied live-traps in their studies. A summary of the knowledge on the quadrate methods, a survey of the present literature and experiance as well as valuable remarks were submitted by T u r č e k (1958) to whose paper we draw the reader's attention.

In applying snap-traps was soon believed that from the catch in these traps, laid either over an area or in lines, it is possible to obtain a rather accurate idea of the r e l a t i v e density of small mammals (D i c e, 1931; 1938). This method has been currently used especially in trap-lines although some doubts were expressed for the accuracy of the results thus obtained (F o w l e & E d w a r d s, 1954; T a n a k a, 1960). Notwithstanding the fact, that based on the catch in any quadrate or line of traps, the relative density can be expressed using the index "catch per cent of trap-nights", the opinion has been arrived at later on, that even this method has to be standardized (C a l h o u n ex B r a n t, 1962).

On the other hand, live-trapping and studies on marked populations brought knowledge both on population densities and, above all, on the movements of individuals in the population and on the general character of vagility of small mammals in a habitat. Finaly, the experience with the marked populations support the endeavour to evolve the snap-trapping quadrate method so that even this method could help to obtain an idea of the a b s o l u t e population density (P e l i k á n & Z e j d a, 1962), although this possibility is regarded with many skepticism (W i l l, 1962). On the other hand, however, we even find recent opinions (B r a n t, 1962), that with sufficient knowledge on the vagility of individuals in a population (naturally, in different time and space), it is possible to determine the absolute population density even by line-trapping. Endeavours to approach this final goal motivated the present study as well as our field work being in progress.

II. MATERIAL AND METHODS

As a standard trapping area we used a quadrate 50 by 50 m, covered with snap-traps laid in a 5 by 5 m grid, that is, 11 rows containing 11 traps each (a total of 121 traps, Fig. 1). All traps were baited with wicks soaked in fat and the bait was renewed if necessary. Traps remained in the quadrate for five days; they were inspected every morning, the catch removed and the traps reset. The catch was treated in the current ways.

On the whole, we plotted out 123 quadrates, all in forest habitats, of which 79 were in deciduous woods, 12 in mixed forests, and 32 in coniferous forests. Of the total number of quadrates, 8 did not yield any catch, and 9 were not evaluated as during the exposition the traps were either covered with snow or released by raindrops. Thus we evaluated a total of 106 quadrates, yielding a catch of 2451 small mammals, belonging to thirteen species. The representation of individual species in the catch is evident from Table 1.

Most of our quadrates were plotted off in the areas of our stationary investigations either in the environs of Hodonín (southern Moravia) in the period from October 1957 to August 1961 (80 quadrates), or in the environs of Opava (northern Moravia) from June 1958 to November 1960 (35 quadrates). Besides that, three quadrates were plotted out at Budišov near Třebíč (December 1957 and 1958), three in Orlické Mts. (October 1959) one at Brtnice near Jihlava (December 1957) and one at Sokolnice near Jihlava (December 1957) and one at Sokolnice near Brno (September 1961). The number of quadrates trapped in single months is seen in the following:

Month:	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	S
No. of Q.:	5	14	11	3	12	16	7	8	17	13	13	4	123

Table 1.

Total catch on quadrates in five successive days (106 quadrates evaluated).

Species		Day					S
		1	2	3	4	5*	
C. glareolus		509	261	148	100	85	1,103
A. flavicollis		388	176	107	82	65	818
A. silvaticus		83	42	42	34	22	223
S. araneus		40	39	40	29	18	166
M. arvalis		23	35	25	14	9	106
P. subterraneus		1	2	2	2	4	11
S. minutus		1	1	2	1	3	8
A. agrarius		2	2	1		2	7
C. suaveolens		1		1		1	3
D. nitedula		1		1			2
M. musculus				1		1	2
N. fodiens					1		1
M. agrestis					1		1
S		1,049	558	370	264	210	2,451
Avg. per 1 quadrate	n	9.90	5.26	3.49	2.49	2.19	23.33
	%	42.4	22.5	15.0	10.7	9.4	100.0

*) Only 96 quadrates were evaluated on the fifth day.

III. CATCH ON QUADRATE WITHIN FIVE SUCCESSIVE DAYS

1. Total catch curve

An evaluation of the catch of small mammals in a total of 106 quadrates within five successive days is gathered up in Table 1. From the table as well as from Fig. 2 it appears that within five days of trapping, the average catch curve on a quadrate gradually descends from 42.4% on the first day to 9.4% on the fifth day, taking the five-day catch for 100%. Taking the catch on the first day for 100% we may expect, on the same quadrate, the averages of 53.0, 35.4, 25.2 and 22.2 per cent of the catch or roughly a half, a third, a fourth and a fifth part of the catch on the first day.

Our results are in agreement with the catch curve obtained by B o l e (1939: 58, Fig. 2) in quadrates of the same size. The average sizes of his daily catch, derived from the diagram mentioned, were roughly 14.2, 6.8, 4.8, 4.2 and 4.0 individuals in five successive days (total 34.0), making up 41.8, 20.0, 14.1, 12.3 and 11.8% (total 100%) which is practically the same

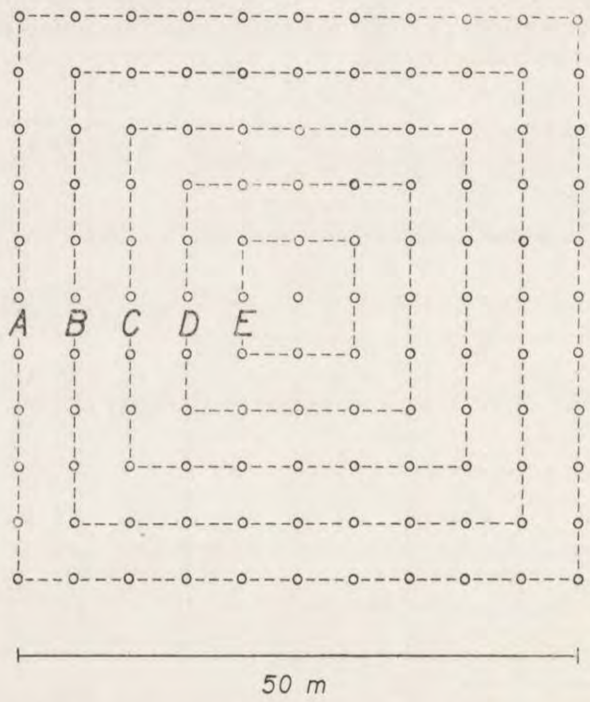

Fig. 1. Size of the standard quadrate used; traps in a 5×5 m grid. Interrupted lines connect the traps on individual squares A to E.

as in our experiments (cf. Table 1, bottom line). The similarity of results is rather striking with respect to the fact that B o l e, in his quadrates, disturbed the litter and set his traps (using about the same number of traps as we did) directly in the burrows or in other suitable sites, keeping to no fixed grid. B o l e's way of trapping would stimulate an opinion that the removal of individuals from the population would be quicker and, thence, the catch curve steeper. It appears from the above comparison that the course of the catch curve depends, above all, on the size of quadrate (as has been proved by B o l e) and not on the way of trapping, assuming that there is a sufficient number of traps present in a given area (cf. A n d r z e j e w s k i & G ł o g o w s k a, 1962).

As appears from Fig. 2, the catch curve obtained in quadrate trapping shows the most abrupt decrease within the first three days. In these days, the effectiveness of the quadrate is very high (P e l i k á n & Z e j d a, 1962), depending on the momentary vagility of individuals in the population. Within those three days, individuals resident in the quadrate are practically removed. In latter days, in our case starting from the fourth day, the catch curve shows a course more or less parallel with the abscissa and the catch consists of individuals gradually invading the quadrate from greater distances (S t i c k e l, 1946b; P e l i k á n & Z e j d a, 1962). Thus, in those further days of trapping, the catch size is conditioned by the pressure within the population and is rather an index of expansibility of individuals, invading, as suspected by A n d r z e j e w s k i & W r o c ł a w e k (1962), from greater distances from the quadrate.

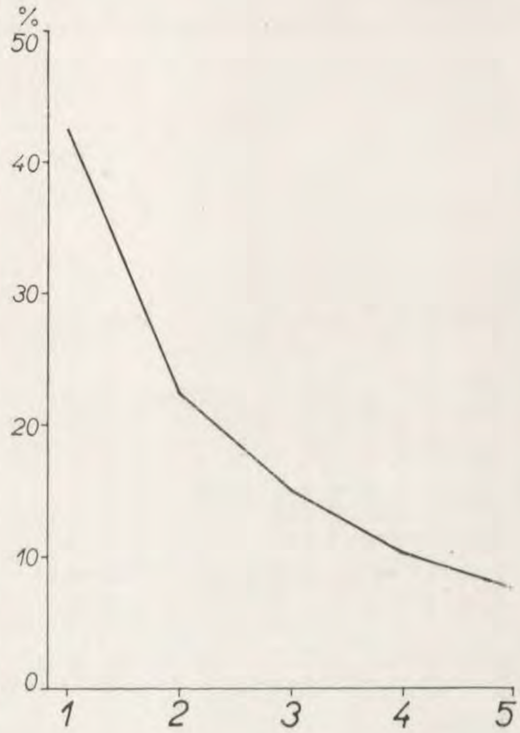

Fig. 2. Catch curve of all species captured in five successive days. Total catch of five days equals 100%.

2. Catch curves of different species

The catch curves were evaluated only in these species, where material was sufficiently numerous, viz., *Clethrionomys glareolus* (S c h r e b e r, 1780), *Apodemus flavicollis* (M e l c h i o r, 1834), *Apodemus sylvaticus* (L i n n a e u s, 1758), *Sorex araneus* L i n n a e u s, 1758 and *Microtus arvalis* (P a l l a s, 1779) (in the following text only abbreviations of these scientific names are used). The results are apparent from Tab. 2 and the course of catch curves are seen in Fig. 3.

In both the forest species, *C.g.* and *A.f.*, the catch curves show a normal course. The observations on the character of residency and vagrancy, given above, hold true for the individuals of these species as well. The

Table 2.

Average catches of some species per 1 quadrate *).

Species		Day 1	2	3	4	5	S
C. glareolus	n	509	261	148	100	85	1,103
	$\bar{x}$	4.80	2.46	1.40	0.94	0.88	10.48
	%	45.7	23.3	13.2	8.8	9.0	100.0
A. flavicollis	n	388	176	107	82	65	818
	$\bar{x}$	3.66	1.66	1.01	0.77	0.68	7.78
	%	47.0	21.3	13.0	9.9	8.8	100.0
A. sylvaticus	n	83	42	42	34	22	223
	$\bar{x}$	0.78	0.40	0.40	0.32	0.21	2.11
	%	37.2	18.8	18.8	15.3	9.9	100.0
S. araneus	n	40	39	40	29	18	166
	$\bar{x}$	0.38	0.37	0.38	0.27	0.17	1.57
	%	24.1	23.5	24.1	17.5	10.8	100.0
M. arvalis	n	23	35	25	14	9	106
	$\bar{x}$	0.22	0.33	0.24	0.13	0.09	1.01
	%	21.8	32.7	23.7	12.9	8.9	100.0

*) 106 squares were evaluated but only 96 on the fifth day.

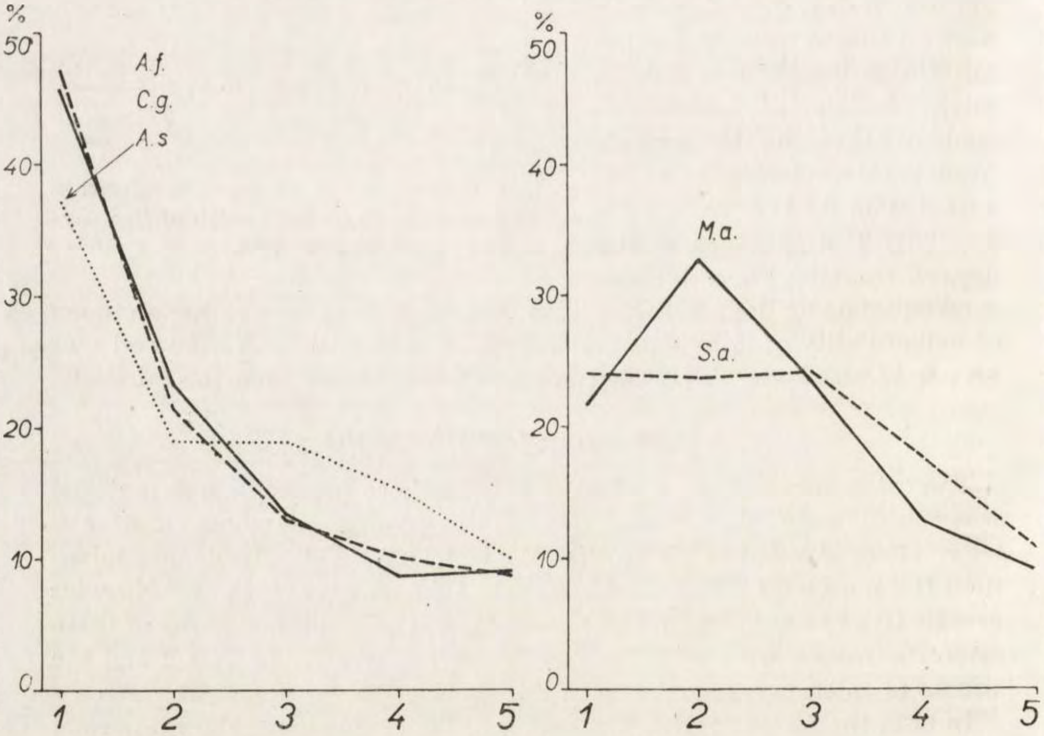

Fig. 3. Catch curves of different species. Total catch of five days equals 100%.

catch curve of *A.s.* resembles those of the two previous species but differs in its slower decline, being nearly parallel with the abscissa from the second day on. A possible explanation of this fact can be looked for in the circumstance that *A.s.* is not a typical forest species so that its populations, especially those of consistent forest stands of a uniform type of habitats, consist of a much greater number of vagrant individuals than in the two previous species.

The catch curves of *S.a.* and *M.a.* differ from those of the three above species substantially. Both of them lack in the steep decline during the first two days of trapping; on the contrary, they are more or less parallel to the abscissa already from the first day of trapping, which points at the more vagrant character of the populations of these species in the forest environment. The higher catches at least on the first trapping day, that is, a suggestion of the presence of a resident part of the population, are entirely absent. In *S.a.*, this can be explained by the circumstance that the individual shrews, perhaps save for lactating females, posses unusually large teritories, or that their roaming is not spatially limited at all, so that their possible immigration and capture in a quadrate is much the same in the successive days of trapping. Beyond doubt, even the individuals of *M.a.* posses a vagrant character in forest habitats, especially in continuous forest stands, where our quadrates were plotted off. This field species immigrates in the forest mainly during the periods of overcrowding and as far as it settles down permanently, it inhabits, under conditions of our country, various clearings, glades and similar habitats where the continuous crown coverage is interrupted.

3. Catch curve with different population densities

We compared the total catch curves obtained on quadrates with low population density (selecting those quadrates in which the total catch was at most 5 small mammals within the first three days) with those obtained on quadrates with high population density (quadrates with at least 30 small mammals trapped within the first three days). The results of this comparison are given in Tab. 3 and shown in Fig. 4.

Both the total catch curves are seen to differ quite substantially. With high population densities (Fig. 4, curve b), the catch curve has an altogether normal course, that is, a moderate decline of the catch size till the third day of trapping and a straightened part thenceforth. With low population densities (Fig 4, curve a), the curve shows a rapid decline; starting from the second day on, the catches are already very small, slightly increasing in the last days of trapping.

The steep course of the catch curve with low population densities can be explained by the circumstance, that the resident component there is

Table 3.

Variation of catch size with different population densities.

Density*			Day 1	2	3	4	5
0 - 5:	Catch size		52	17	10	16	18
	No. of quadrates		26	26	26	26	22
	Catch per 1 quadrate	$\bar{x}$	2.00	0.65	0.38	0.61	0.82
		%	44.8	14.6	8.5	13.7	18.4
30 and more:	Catch size		545	272	184	127	92
	No. of quadrates		18	18	18	18	16
	Catch per 1 quadrate	$\bar{x}$	30.3	15.1	10.2	7.1	5.7
		%	44.1	22.3	15.3	10.2	8.2

*) As an index of the population density the capture in the first three days is assumed.

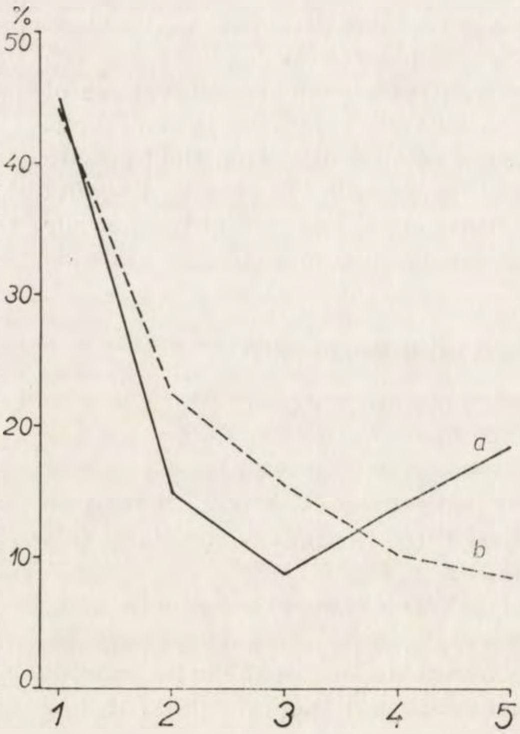

Fig. 4. Catch curve of all species on biotops with low (a) and high (b) population density. Total catch of five days equals 100%.

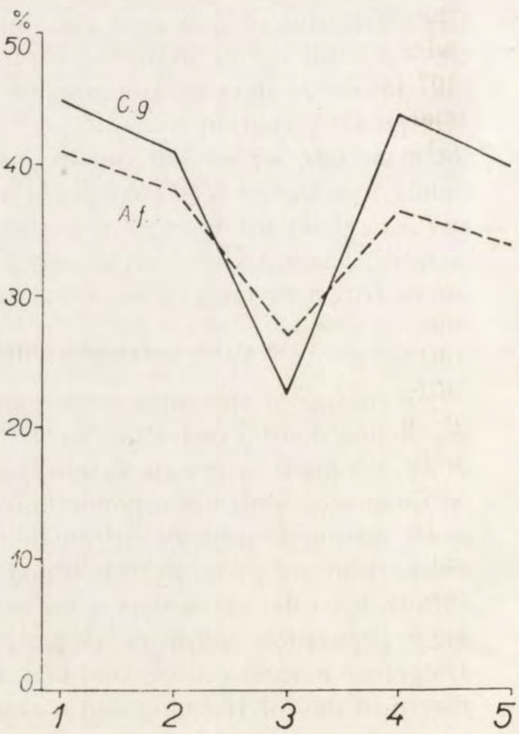

Fig. 5. Percentage of sexually active individuals in the daily catch of *C. glareolus* and *A. flavicollis*. Every-day catch equals 100%

rather small both in its absolute value and related to the number of traps laid, so that it is removed very quickly. On the contrary, the catch size on the fourth and fifth day indicates the size of the vagrant component which, apparently, constitutes the major part of the catch already by the second and third trapping day. This explanation may also be corroborated by the circumstance, that we most frequently meet with a low population density of small mammals in less suitable habitats (not considering populations being in depression), which are merely passed by most of the individuals.

IV. CHANGES IN CATCH STRUCTURE

1. Sex ratio

With respect to certain relations, discussed below, we endeavoured to analyze our material as far as the sex ratio in the catch is concerned. In the total catches of the five most frequent species (cf. Tab. 1), the following were the numbers of males: *C.g.* 606 (54.9%), *A.f.* 455 (55.6%), *A.s* 107 (48.0%), *S.a.* 89 (53.6%) and *M.a.* 50 (47.2%). The predominance of males was highly significant only in *C.g.* ($\chi^2=10.77$, $P<0.01$) and *A.f.* ($\chi^2=10.35$, $P<0.01$). In the remaining species, the difference of sex ratio from 1 : 1 was insignificant. Further analyses were possible only in *C.g.* and *A.f.* with respect to sufficiently numerous material.

In the catch of *C.g.* during the period of its reproduction (III to IX, $n=714$) there were 57.3% of males ($\chi^2=15.20$, $P<0.01$); in the winter non-breeding period (X to II, $n=389$) there were only 50.6% of males (difference insignificant). Thus the sex ratio was rather balanced. The difference between both sex ratios is highly significant ($\chi^2=19.48$, $P<0.01$), so that we may infer that, during the breeding period, the percentage of males in the catch increases (in our case by some 7%), obviously due to their greater vagrancy at that period.

In the successive days of trapping during the winter period, the sex ratio in the catch is rather balanced. During the breeding period, males predominate in all days of trapping, their percentages showing considerable variations in the successive days (53.8, 60.2, 58.3, 56.1 and 68.3%). Considering only the catches of sexually active individuals in the successive days of trapping in that period ($n=151$, 68, 19, 29, 23), we can observe a very conspicuous, increasing predominance of males in the catch (53.6, 70.6, 63.2, 75.9 and 82.6%). Although we have at our disposal only a rather small material, the predominance of males is significant in all days with the exception of the first and third day. Thus it appears that the quadrate area vacated by the removal is later on occupied by sexually active males in a far greater extent than by females, owing to the greater vagrancy of the former as mentioned above.

This fact is still more apparent from a comparison of catches of sexually active and inactive individuals during the reproduction period. Among the total catch of active individuals during the first three days (n=238) there are 58.8% of males; on the contrary, during the last two days (n=53), the predominance of males increases to 77.4% or, practically, by 80% (χ^2=54.14, P<0.01). On the other hand, the sex ratio of sexually inactive individuals is rather balanced. During the first three days, there are 54.6% of males in the cath (n=350); during the last two days, only 50.6% of males (n=7 and 3), the difference between these two ratios being insignificant. These observations indicate, that the greater influx of sexually active males to the vacated area is in fact stimulated by the greater vagrancy due to sexual activity. Moreover, they testify that the catches obtained on the fourth and fifth day bias the idea of the actual sex ratio in the population of *C.g.*

In the catches of *A.f.*, males predominate both in the breeding period (n=605, males 55.4%, χ^2=6.93, P<0.01) and the non-breeding period (n=213, males 56.3%, χ^2=3.42, P≐0.07), no significant difference existing between both these ratios. During the breeding period, males predominate in the catch over all five days of trapping (n=279, 132, 81, 63 and 50) but, contrary to the previous species, their predominance in the catch gradually decreases (56.3, 56.1, 55.6, 55.0 and 52.0%) although this decrease is very small. In the catches of sexually active individuals during the first three days (n=186) and the last two days (n=40) of trapping in the breeding period, the predominance of males is weak (53.2 and 55.0%); the difference between these two values is insignificant. In the catch of sexually inactive individuals in the same period, the predominance of males is higher during the first three days (n=306, males 57.8%); during the last two days, the sex ratio is balanced, the males making up only 50.6% (n=73). The difference between these two values is almost significant (χ^2=7.73, P=0.05).

Thus, the relations observed in *A.f.* are different from those in *C.g.*; so far, we lack in an explanation of these differences. We are inclined to believe that for *A.f.*, occupying far larger home ranges and being far more vagrant than *C.g.* the quadrate of 50 × 50 m is very likely still too small to reveal certain relations clearly observed in *C.g.*

2. Ratio of active and inactive individuals in the catch

There is a question whether it is possible to find out a difference in the influx of sexually active or inactive individuals to the quadrate in the later days of trapping. Again, the evaluation has been done only in *C.g.* and *A.f.*, considering only their reproduction periods (March to September), as in winter nearly all individuals are sexually inactive.

In the total catch of *C.g.* in the reproduction period, less than half of the individuals were sexually active (40.8%, difference insignificant); however, in the catches on successive days (n=338, 166, 84, 66 and 60), the percentage of sexually active individuals shows a rapid decline down to the third day when it attains the lowest value (44.7, 41.0, 22.6, 43.9 and 40.0%), becoming balanced again during the two last days. The difference in percentages of the two components are significant in all days except for the last two ones (cf. Fig. 5).

A similar variation is observed in the catches of *A.f.* in the same period when in the catches on successive days (n=279, 132, 81, 63 and 50), the percentage of active individuals decreases again down to the third day, whereupon the curve becomes rather balanced again (40.9, 37.9, 27.2, 36.5 and 34.0%).

The similar course of the catch curves of both species (cf. Fig. 5) indicates that within the first three days, most of the sexually active individuals are removed both from the quadrate and its closest vicinity and that on those days, the influx consists mostly of sexually inactive individuals. On the fourth and fifth day again, the vacated area of the quadrate is invaded by sexually active individuals from greater distances, their percentage in the catch increasing and the ratio becoming balanced again.

The component of sexually inactive individuals contains surely a certain part of juvenile, just weaned animals (weighing about 8—13 g), which leave the nest after the eventual mother's death in traps. In fact, these young animals belong to the resident component of population. Their proportion in the catch of all sexually inactive individuals is: in *C.g.*, 5.8, 13.9, 27.3, 25.8, and 14.8%; in *A.f.*, 20.2, 17.5, 28.0, 30.8 and 23.8% in five successive trapping days. As can be seen, the catch of these youngest animals is greatest on the third and fourth trapping day, but in general, their proportion in the sexually inactive component of catch is rather low.

This observations provide another evidence of the fact that in trapping quadrates of our type, three days of trapping are the most satisfactory span to obtain the population samples least biased.

V. CHANGES IN THE INDEX "CATCH PER CENT OF TRAP-NIGHTS" WITHIN FIVE DAYS

To afford a comparison of the results of trapping in various trap-lines or quadrates with any number of traps laid, the catch is expressed as a percentage of the traps laid, whereby a relative value, called the "catch per cent of trap-nights" is obtained.

If the traps are exposed for several successive nights, both the catches and the numbers of traps are summed up and the index is determined from the sum of catches, traps and trap-nights. T u r č e k (1957) subjected this method to statistical analyses and found that it is possible to express the indices from any number of trap-nights. It is true that the index is the highest on the first day and then decreases gradually but with traps exposed for five days, the differences are statistically insignificant, so that it is possible to express the index from an arbitrary number of trap-nights.

The evaluation of our material (Tab. 4, Fig. 6) brings results similar to those obtained by T u r č e k (1957). The index is 8.18 for the first night, 6.26 for the first and second night, further values are 5.14, 4.37 and 3.90 (for the first to fifth night). Thus, the value of the index decreases but the decrease is statistically insignificant ($\chi^2 = 3.19$, $P \doteq 0.55$).

Table 4.
Index "catch per 100 trap-nights" evaluated from 106 quadrates (only 96 on the fifth day).

		Day				
		1	2	3	4	5
Catch:	n	1,049	558	370	264	210
	summation	1,049	1,607	1,977	2,241	2,451
Traps:	n	12,826	12,826	12,826	12,826	11,616
	summation	12,826	25,652	38,478	51,304	62,920
Index		8.178	6.264	5.138	4.368	3.895

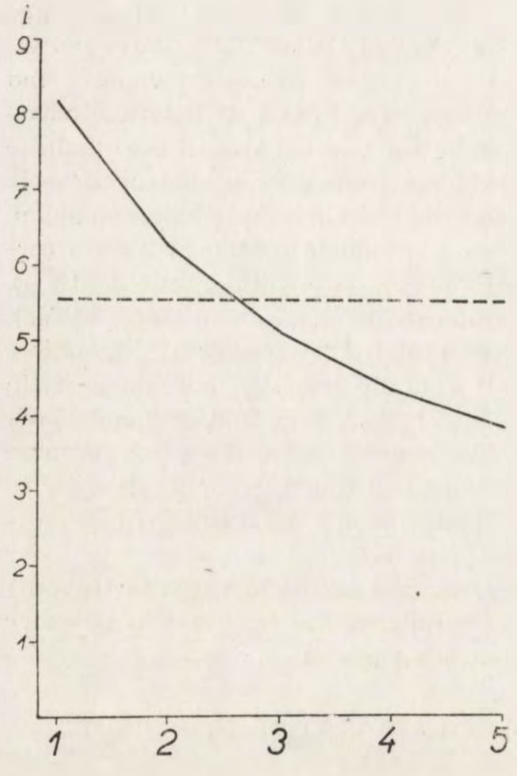

Fig. 6. Decrease of the index "catch per cent of trap-nights" (full) compared with the five-day average of index (interrupted).

Although it is thus possible to express the index from an arbitrary number of trap-nights, we take it for most satisfactory to evaluate only the first three days of trapping in quadrates of our type, with respect to the effectiveness of the quadrate, the general character of the catch curve and the structure of the catch, as discussed in the previous chapters. Nevertheless in expressing the index from catches obtained in quadrates or trap-lines of any type, it is necessary to state the number of trap-nights used for the evaluation.

VI. CATCH ON THE MARGINS AND INSIDE OF QUADRATE

If we consider the traps lying on the margin of a quadrate to form a square A, then there are further squares B to E inside the quadrate (cf. Fig. 1); the central trap is included in square E. The catches on different squares of traps on a total of 106 quadrates are given in Tab. 5.

Table 5.
Catch sizes in individual squares of traps of a quadrate *).

Day		Catch on square:					
		A	B	C	D	E	S
1.	n	438	274	170	127	40	1,049
	%	41.8	26.1	16.2	12.1	3.8	100.0
2.	n	267	138	75	53	25	558
	%	47.9	24.7	13.4	9.5	4.5	100.0
3.	n	160	89	55	44	22	370
	%	43.2	24.1	14.9	11.9	5.9	100.0
4.	n	136	57	39	22	10	264
	%	51.5	21.6	14.8	8.3	3.8	100.0
5.	n	97	53	32	21	7	210
	%	46.2	25.3	15.2	10.0	3.3	100.0
S	n	1,098	611	371	267	104	2,451
	%	44.9	24.9	15.1	10.9	4.2	100.0
Traps on square		40	32	24	16	9	121
Traps, total		20,800	16,640	12,480	8,320	4,680	62,920
Catch per 100 trap-nights	n	5,279	3,672	2,973	3,209	2,222	17,355
	%	30.4	21.2	17.1	18.5	12.8	100.0

*) A total of 106 quadrates were evaluated but only 96 quadrates were evaluated on the fifth day.

It appears from Tab. 5 as well as from Fig. 7 that the greatest part of the total catch (44.9%) was trapped on square A; towards the centre of the quadrate, the catch sizes decrease, making up only 4.2% on square E. The course of the catch curve remains the same on individual squares in successive days, irrespective of the fact that the total catch on the quadrate decreases gradually in successive days. Thus, even on the fourth and fifth day, when the greatest part of the catch consists of invading individuals, the frequency of catches on squares does not differ from that on the first three days when, on the contrary, the individuals resident in the quadrate and its closest neighbourhood are removed. This indicates that on the last two trapping days the immigrants are not more frequently trapped on the outer squares as we might expect, but that they penetrate through the 5 × 5 m grid down to the centre of the quadrate.

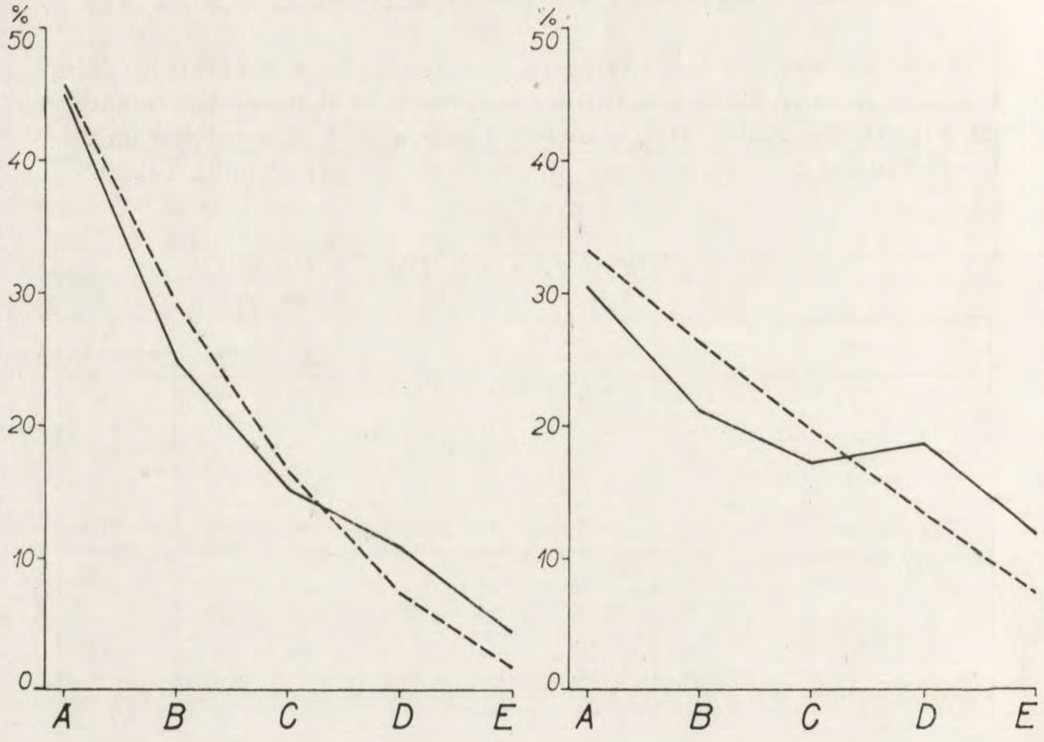

Fig. 7. Catch on individual squares A to E of the quadrate. — Left: absolute catch of all species (full) compared with decreasing surfaces of squares (interrupted). — Right: relative catch of all species (full) compared with decreasing circumferences of squares. Summe of individual values on all squares equales 100%.

This circumstance is of special practical importance as it shows to what extent a stripe of five rows of traps in a 5 × 5 m grid could possibly check the immigration of small mammals to an area requiring protection and isolation from the influx of rodents from the environs. As evident from the results, such protection would not be effective enough. The reasons is not only in the insufficient density of trap stripes but in the circumstance that small mammals frequently utilize subterranean, mainly mole, burrows, thus evading the traps laid on the soil surface. Thus if we intended to supply snap-traps to protect a particular area, we should have to surround it with a stripe with the litter and turf removed to such depth to destroy the system of subterranean burrows, which would increase the effectiveness of the traps against invading small mammals.

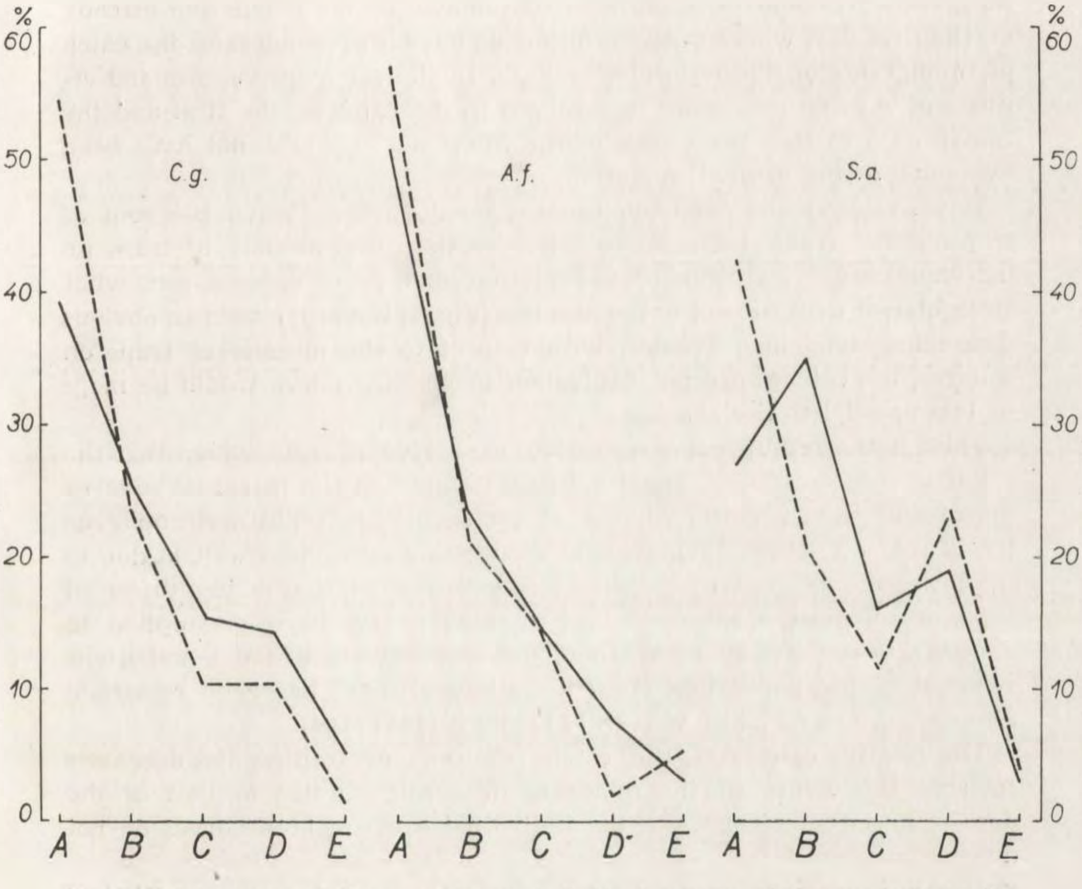

Fig. 8. Catch curves of three species on individual squares of the quadrate on the first (full) and fourth (interrupted) day. One-day catch on all squares equale 100%.

Although the catch frequency on the squares remains rather unchanged during the five days of trapping, the influx of individuals to the quadrate is still apparent from the relative size of the catch on the outermost square. It is evident from Tab. 5 that on square A is the relative part of the catch the smallest directly on the first day (41.8%), the percentage increasing on the subsequent days even if the increase is not gradual (47.9, 43.2, 51.5, 46.2%). In fact, the difference between the catch on the first and that on the fourth day (9.7%) is statistically significant ($\chi^2=8.50$, $P \doteq 0.015$).

In evaluating the catches of *C.g.*, *A.f.* and *S.a.* on individual squares of traps (Fig. 8) we observe that their catch frequencies show a course much the same as that of the total catch on the squares. The difference between the first and the fourth day is most distinct in *C.g.*, probably due to its greatest residence causing a rapid removal of the population already on the first day, where upon on following days it preponderates the catch of immigrants on the outermost square. In the far more vagrant individuals of *A.f.*, no difference is observed in the catch on the first and the fourth day. In *S.a.*, the course of the catch curve could not have been evaluated owing to small material.

If we express the catch on squares by the index "catch per cent of trap-nights" (thus taking into consideration the number of traps on individual squares, cf. Tab. 5), the relative catch curve becomes somewhat straightened with respect to the abscissa (Fig. 7) but still shows an obvious descending tendency. Thence, with respect to the number of traps on squares, the catches are not equivalent or else the curve would be more or less parallel to the abscissa.

Thus, gathering up our observation, we arrive at a conclusion that the catch is both absolutely and relatively greater on the marginal squares than inside the quadrate, witch is at variance with the hitherto opinions (cf. Turček, 1953 : 333). Beyond doubt, this different result is due to the lower number of traps applied to the same area, that is, to a different type of quadrate used by Turček (1953). His 36 traps applied to a quadrate of 50 × 50 m are obviously too few to afford a sufficient removal of the population from the study area, as has been remarked already by Obraztsov & Stilmark (1957 : 104).

The relative catch (i.e., the catch per cent of trap-nights) decreases towards the centre of the quadrate in a rate similar to that of the decreasing circumferences of the individual squares, both curves do not differ significantly from each other (Fig. 7). The absolute catch on squares decreases towards the centre of the quadrate in a rate similar to that of the decreasing surfaces of squares. Of course, this is a purely speculative comparison.

VII. CATCH SIZES OF SMALL MAMMALS ON QUADRATES

In our previous paper (Pelikán & Zejda, 1962), we based the estimation of hectare numbers of smal mammals on a catch obtained on the first three days of trapping, transforming them to the quadrate area

Table 6.

Catch sizes on quadrates in the first three nights.

Catch size	No. of quadrates with the respective catch of all species	C. glareolus	A. flavicollis	A. sylvaticus	S. araneus	M. arvalis	A. agrarius
1	3	9	18	27	20	1	3
2	6	10	14	15	10	5	1
3	6	7	10	7	6	4	
4	9	10	5	1	4	1	
5	2	4	5	5	1	1	
6	3	4	6	1	2	1	
7	6	10	4	1			
8	3	2	2	1	1		
9	4	1	5		2	2	
10	1	3	1				
11	3	1	2				
12	6	4	2	1			
13	5	3	3			1	
14	5		3			1	
15	2	3	1				
16	3	2	1				
17	3	1	2				
18	4	2					
19		1					
20	3	1					
21	1						
22	2	1					
23	3						
24	1	1		1			
25	1						
26			2				
27	1	1					
28	2						
29		1					
30	1						
31	1	1					
34	2						
35	1						
36		3					
38			1				
39	1						
40			1				
41	1						
42		1					
44	1						
47	1						
49	1		1				
50	1		1				
52		1					
53	1						
57	1	1					
66	1						
85	1						
98	1						
99	1						
109	1						

enlarged by a marginal stripe of certain width. However, the width of this marginal stripe is both specific in different species, varying in dependence of the type of habitat, population density and of the general vagancy of individuals of a given population. As we still know little about these relations we here compare the simple catch sizes on the first three days. As far as estimations of hectare density are stated they be taken with some cosideration.

The frequencies of sizes of the three-day catches are given in Tab. 6. Of the total of 123 quadrates, 114 were suitable for evaluation. Of these 8 (7.0%) did not yield any catch; 74 (65.0%) yielded a catch of 1 to 18 individuals of various species; 20 (17.5%) a catch of 19 to 39 individuals; 7 (6.1%) a catch of 40 to 60 individuals; and only 5 (4.4%) a catch greater than 60 individuals of all species during three days. The maximum three--day catch size was 109 individuals (Fig. 9).

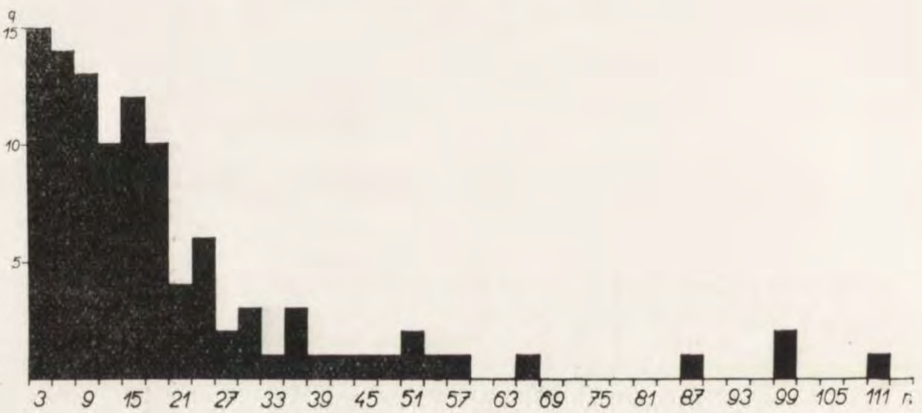

Fig. 9. Frequency of three-day catch sizes of all species (n) on quadrates (q).

The three-day catch sizes varied mainly in relation to the seasons of the year and to the type of habitat investigated. Thus, in early spring, the catches were relatively small in connection with the low numbers (0—24 individuas, avg. 8); in autumn, the catches were 4 to 5 times higher (2—98 individuals, avg. 22).

Also, the catches of individual species varied from one another. The highest average and maximum values were attained by our most frequent forest mammal, *C. g.* (avg. 10.3, maximum 57 individuals in a three-day catch, i.e., about 57 individuals per hectare). The three-day catches of *A. f.* were slightly lower (avg. 7.4, maximum 50 individuals, i.e., about 40 individuals per hectare). The catches were substantially lower in the remaining species which are no more typical forest mammals: *A. s.* avg. 2.4, max. 24 individuals (about 19 individuals per hectare); *M. a.* avg. 4.9, max. 14 individuals (about 14 individuals per hectare); *S. a.* avg. 2.5, max. 9 individuals (for the estimation of hectare number there is insufficient evidence). Of the remaining species, only single individuals were trapped in the quadrates (they are not given in Tab. 6).

Having studied the application of the quadrate method solely in forest habitats, we obtained, at the same time, fundamental knowledge on the numbers of small mammals in certain types of forest plant communities. Through the investigations in southern Moravia and Silesia, we gained a relatively good idea of the numbers of small mammals in several types of deciduous forest communities. The highest average and maximum three-day catches were obtained in alder stands with admixed poplars, limetrees and ashes on humus, moist enclaves in dry oak woods (avg. 31 individuals). Beyond doubt, the rather high spring numbers and the very high autumn numbers are due to the concentration of small mammals in these habitats, surrounded with dry, grassy oak woods. Somewhat lower

Table 7.

Catch sizes in quadrates in various habitats.

Habitat	No. of quadrates	Three-days' catch	
		$\bar{x}$	max.
Lowland deciduous forest	11	25.3	57
Oak woods	34	18.5	99
Alder woods	15	31.0	109
Other deciduous forests	17	12.9	28
Spruce forests	24	8.3	30
Pine forests	10	4.8	16

average catches were obtained in lowland forests, flooded with ground water to only a smaller extent (avg. 25.3 individuals). The lowland forests with their heterogeneous deciduous trees, well developed shrub stratum and herbaceous vegetation provide very satisfactory habitats for forest small mammals, so that the autumn catches frequently attained their maximum values and the species *A. f.* and *C. g.* their peak densities.

The oak woods were the most systematically investigated forest communities. By their average three-day catch size (18.5 individuals) they appear to be less satisfactory habitats. This is due both to their being drier and more grassy and to the considerable variability of their carrying capacity. Even in these oak woods, considerable numbers of *C. g.* and *A. f.* (maximum numbers of 40 to 100 individuals of both species within three days!) were ascertained in the autumns of the years following a good harvest of acorns. In the years with bad harvests of acorns, their numbers were permanently low, even in autumn (less than 10 individuals).

The remaining types of deciduous forests (linden monocultures, oak--hornbeam forests, beech forests) as well as the mixed deciduous and coniferous forests have not been systematically investigated so far; thence, with respect to the considerable changing of the carrying capacity, our knowledge of this group of habitats is still incomplete.

The coniferous forests are less densely populated by small mammals (Tab. 7). In pure stands of coniferous trees, either spruce (the environs of Opava, or Bohemia-Moravia Highland) or pine ones (southern Moravia), small mammals were especially scarce. This is evident from the average (4.8) and maximum (16) catch size in pine monocultures. In spruce forests, both the average (8.3) and maximum (30) value is twice as high. However, this is not due to a greater suitability of these habitats for small mammals. In spruce forests, most of the greater catches were obtained in clearings which, owing to the development of the shrub stratum, bear a rather mixed character. These places, very much limited in space, are again the places in which the small mammals (especially *C. g.)* concentrate.

VIII. CONCLUSIONS

It is our principal belief that by applying the snap traps laid in a quadrate it will be possible to obtain altogether reliable data on the absolute population densities. Of course, the degree of reliability depends on further development of this method, above all, on obtaining further information on the vagrancy of the individual species. Further evidence on the size of home ranges and vagrancy of the individual species and sexes in different habitats, with different trophic conditions, in different seasons of a years and under different population densities are essential for further increasing of the reliability of this quadrate method.

Apart from these factors, the satisfactory knowledge of which is a question of additional investigations, the results can be influenced by factors intrinsic to the method itself, that is, by the size of the quadrate, as already stated by B o l e (1939), and by the number of traps applied to the selected area.

In our opinion, the area of 50×50 m is satisfactory for the study of populations of *C. g.*, *M. a.* and other microtines with much the same vagrancy. On the other hand, this area is still too small to obtain suitable population samples of such more vagrant species with greater home ranges as, e.g., the members of the genus *Apodemus*. This question will require further studies as well.

In our opinion, a sufficient number of traps applied to the selected area is of equal importance as it enables to obtain a possibly unbiased population sample from an area in a shortest possible period of time. The steeper the catch curve on the first days of trapping, the less influenced the sample by individuals migrating from greater distances from the quadrate. In this respect, the 5 × 5 m grid of traps applied in our investigations is quite satisfactory or, at least, equally effective as the biological method using still more traps to the same area, as applied by Bole (1939, cf. the comparison of results in the chapter on total catch curve).

Provided that the area of the quadrate be sufficiently large and sufficiently covered with traps (as in case of the quadrate of our type), a three-day catch already can provide a reliable basis for estimating the absolute population density, the interpretation of the data thus obtained being of primary importance. Moreover, this three-day catch (1) corresponds more or less to the character of a population in a habitat with respect to the appartenance of individuals to the study area, the vagrant component being trapped proportionally; (2) the sex ratio in the catch corresponds to the actual state in the study area; and (3) the percentages of adult and subadult individuals are the least biased.

If a quadrate of such type is exposed for a longer period of time the catch curve, starting from the fourth day of trapping, can be a suitable index of expansibility of the individuals in the population with respect to population density; sex and maturity of individuals.

Thus, obtaining a population sample by means of a suitable type of quadrate of snap traps may serve us both to estimate the population density and to obtain further, relatively little biased, information on the structure of the population studied. We arrive at the same opinion as Buckner (1957), that this method is satisfactory wherever a short-term estimation of population density is desired, as, e.g., in controlling injurious species, checking their numbers in various habitats, etc. This method is less satisfactory in long-term ecological studies, as it invariably removes a part of the population, which, beyond doubt, can affect the population dynamics in the habitat under investigation.

IX SUMMARY

1. In various forest habitats, a total of 123 quadrates 50 × 50 m in size were plotted off, each covered with 121 snap-traps in a 5 × 5 m grid. Most of the quadrates were exposed for five days, the catch removed daily, and the traps rebaited if neccessary.

2. In these quadrates, the total catch curve declines from 100% on the first day to 53.9, 35.4, 25.2 and 22.2% on the subsequent days, resp. These results are in agreement with those obtained by Bole (1939) who used quadrates of the same size but with a higher number of traps applied in a biological way.

3. In the forest species, *A. f.* and *C. g.*, the catch curve shows a normal course; in the vagrant *S. a.* as well as in *M. a.* which, under our conditions, is a field species

but likewise rather vagrant in forest habitats, the catch curve is much less steep, the vagrant component of the population distinctly prevailing.

4. With high population densities, the catch curve shows a moderate decline till the third day, becoming balanced thereafter. With low population densities, the catch curve declines abruptly; from the second day on, the catches are very low, slightly increasing on the last days of trapping.

5. The sex ratio was analyzed in the catches of the two most frequent species. In *C. g.*, the sex ratio is balanced during winter; during summer, that is, in the reproduction period, males distinctly predominate (57.3%), obviously owing to their greater vagrancy compared to the females. Considering only the sexually active individuals in the catch, the predominance of males increases conspicuously in the subsequent days of trapping. The sex ratio of sexually inactive individuals is still balanced.

6. In the catch of *A. f.*, males predominate both during summer and winter. However, the predominance of males in the sexually active component decreases in the successive days, contrary to the previous species; the differences in sex ratios among the sexually active and inactive part of the population are insignificant.

7. In the summer catch, the ratio of sexually active/inactive individuals changes in successive days of trapping. The sexually active component of the population is strongly removed during the first three days of trapping; the in active individuals are trapped more frequently. The ratio of both these components becomes balanced on the fourth and fifth day of trapping.

8. The relative catch size, i.e., the index "catch per cent of trap-nights" is the greatest on the first day of trapping, decreasing gradually thereafter but with an exposition of the quadrate for five days, these differences are statistically insignificant.

9. On the marginal squares of traps, the catch is absolutely and relatively greater than on the squares inside the quadrate.

10. The following were the three-day catches of all the species trapped: 8 quadrates (7.0%) did not yield any catch; 74 (65.0%) yielded a catch of 1 to 18 individuals, 20 (17.5%) a catch of 19 to 39 individuals; 7 (6.1%) a catch of 40 to 60 individuals; and only 5 (4.4%) a catch greater than 60 individuals. The maximum three-day catch was 109 individuals. 9 quadrates were not evaluated.

11. In the five most frequent species, the following maximum three-day catches were obtained: *C. g.* 57 (about 57 per hectare); *A. f.* 50 (about 40 per hectare); *A. s.* 24 (about 19 per hectare); *S. a.* 9 (?); and *M. a.* (about 14 per hectare). These maximum densities are substantially lower than certain exaggerated data in literature and they are considered to be very real.

REFERENCES

1. Andrzejewski, R. & Głogowska, J., 1962: The influence of the lay-out of traps and length of time for which they remain set on the distribution of capture of small rodents. Ekol. pol., A, *10*, 10: 285—293.
2. Andrzejewski, R. & Wrocławek, H., 1962: Settling by small rodents a terrain in which catching out had been performed. Acta theriol., *6*, 9: 257—274.
3. Bole, B. P., 1939: The quadrat method of studying small mammal populations. Sci. Publ. Clev. Mus. Nat. Hist., *5*, 4: 15—77.

4. B r a n t, D .H., 1962: Measures of the movements and population densities of small rodents. Univ. Cal. Publ. Zool., *62*, 2: 105—184.
5. B u c k n e r, C. H., 1957: Population studies on small mammals of Southeastern Manitoba. J. Mamm., *38*, 1: 87—97.
6. D i c e, L. R., 1931: Methods of indicating the abundance of mammals. J. Mamm., *12*: 376—381.
7. D i c e, L. R., 1938: Some census methods for mammals. J. Wildl. Mgt., *2*, 3: 119—130.
8. F o w l e, C. D. & E d w a r d s, R. Y., 1954: The utility of break-back traps in population studies of small mammals. J. Wildl. Mgt., *18*: 503—508.
9. O b r a z t s o v, B. V. & Š t i l m a r k, F. R., 1957. Lesochozjajstvennoe značenie myševidnych gryzunov v dubravach evropějskoi časti SSSR. Trudy Inst. Lesa, *35*: 5—121.
10. P e l i k á n, J. & Z e j d a, J., 1962: Comparison of two methods of estimating small mammal populations. Zool. Listy, *11*, 3: 227—242.
11. S t i c k e l, L. F., 1946a: Experimental analysis of methods for measuring small mammal populations. J. Wildl. Mgt., *10*, 2: 150—159.
12. S t i c k e l, L. F., 1946b: The source of animals moving into a depopulated area. J. Mamm., *27*, 4: 301—307.
13. T u r č e k, F. J., 1949: Populations of some small mammals in a hardwood forest near Banská Štiavnica. Věst. Čsl. Spol. Zool., *13*: 348—363.
14. T u r č e k, F. J., 1953: Ecological analysis of a population of the red-backed vole on Polana-Mt. in Slovakia. Práce Výzk. Úst. Les., *3*: 325—374.
15. T u r č e k, F. J., 1954: Methodologische Fangversuche einer Kleinnagerbekämpfung im Walde. Podohosp., *1*, 3: 336—346.
16. T u r č e k, F. J., 1957: Über die Zuverlässigkeit des Indexes „Ausbeute in 100 Fallennächten" bei quantitativen Untersuchungen der Populationen von Kleinsäugetieren. Biológia, *12*: 362—373.
17. T u r č e k, F. J., 1958: Zönologische Arbeitsmethoden für Wirbeltiere. [In B a l o g h, J.: Lebensgemeinschaften der Landtiere: 415—450].
18. T a n a k a, R., 1960: Evidence against reliability of the trap-night index as a relative measure of population. Japan. J. Ecol., *10*, 3: 102—106.
19. W i l l, R., 1962: Comparative methods of trapping small mammals in an Illinois woods. Trans. Ill. State Acad. Sci., *55*, 1: 21—34.

Czechoslovak Academy of Sciences,
Institute of Vertebrate Zoology.
Brno, Drobného 28.

STRESZCZENIE

W różnych biotopach leśnych założono 123 kwadraty odłowne (Ryc. 1) o powierzchni 50 × 50 m. Na każdym z nich ustawiono 121 pułapek w więźbie 5 × 5 m. Większość powierzchni była eksponowana przez 5 dni. Pułapki obsługiwano codziennie, zabierano złowione zwierzęta i jeżeli zachodziła potrzeba — uzupełniano przynętę.

Na powierzchniach odłownych stwierdzono, że krzywa odłowu spada ze 100% w pierwszym dniu, odpowiednio do 53,9; 35,4; 25,2 i 22,2% w dniach następnych

(Ryc. 2). Wyniki te są zgodne z danymi otrzymanymi przez Bole (1939), który używał kwadratów tego samego wymiaru, lecz o większej liczbie pułapek

Dla gatunków leśnych, jak *Apodemus flavicollis* (Melchior, 1834) i *Clethrionomys glareolus* (Schreber, 1780) krzywa odłowu wykazuje przebieg normalny u gatunków migrujących, *Sorex araneus* Linnaeus, 1758, jak też *Microtus arvalis* (Pallas, 1779), który w naszych warunkach jest gatunkiem polnym, ale również raczej migrującym do biotopów leśnych, krzywa odłowu jest bardziej stroma. Migrująca część populacji wyraźnie przeważa (Ryc. 3).

Przy wysokim stanie liczebnościowym populacji, krzywa odłowu wykazuje umiarkowany spadek do trzeciego dnia, po czym wyrównuje się. Przy niskim stanie populacji krzywa odłowu spada nieprzerwanie (Ryc. 4). Od drugiego dnia odłowy są bardzo małe, lecz lekko wzrastają w ostatnich dniach.

Stosunek płci analizowano u dwu najbardziej liczebnych gatunków. U *C. glareolus* stosunek płci podczas zimy jest wyrównany, w lecie zaś, tj. w okresie rozrodu, wyraźnie przeważały samce (57,3%), dzięki ich większej migracyjności w porównaniu z samicami. Biorąc pod uwagę tylko osobniki płciowo aktywne, przewaga samców w odłowach wzrasta w poszczególnych dniach w sposób widoczny. Stosunek płci u osobników płciowo niedojrzałych jest raczej wyrównany. W odłowach *A. flavicollis*, zarówno w zimie jak i w lecie, przeważały samce. Jednakże przewaga samców w grupie osobników płciowo dojrzałych, w przeciwieństwie do poprzedniego gatunku, spadała w następujących po sobie dniach odłowu. Różnice między stosunkami płci w płciowo aktywnej i płciowo nieaktywnej części populacji były nieistotne.

Stosunek osobników płciowo aktywnych do nieaktywnych zmienia się w kolejnych dniach odłowów. Część populacji składająca się z osobników płciowo nieaktywnych jest „spychana" w ciągu pierwszych trzech dni odłowów i osobniki aktywne płciowo łowią się częściej. Stosunek tych obu komponentów populacji wyrównuje się czwartego — piątego dnia odłowów.

Względna wielkość odłowu, tj. wskaźnik „odłów w procentach pułapko-dni" jest największy pierwszego dnia odłowów, po czym spada powoli, lecz przy uruchamianiu powierzchni na pięć dni, różnice te nie są statystycznie istotne (Ryc. 6).

Odłowy na zewnętrznym kwadracie (por. Ryc. 7) są absolutnie i względnie większe niż na kwadratach wewnętrznych.

Trzydniowe odłowy dały następujące wyniki w stosunku do wszystkich złowionych okazów: na 8 powierzchniach (7,0%) nic nie złowiono, na 74 (65,0%) złowiono 1—18 osobników, na 20 (17,5%) — 19—39 osobników, na 7 (6,1%) — 40—60 osobników i tylko na 5 (4,4%) powierzchniach złowiono więcej niż 60 osobników. Maksymalny odłów w przeciągu trzech dni wynosił 109 okazów (nie uwzględniano tu powierzchni 9). Dla pięciu najczęstszych gatunków otrzymano następujący maksymalny odłów za okres trzech dni: *C. glareolus* 57 (około 57/ha), *A. flavicollis* — 50 (około 40/ha), *A. sylvaticus* — 24 (około 19/ha), *S. araneus* — 9 (?) i *M. arvalis* — 14 (około 14/ha) (Ryc. 9). Te maksymalne gęstości są istotnie niższe niż pewne wyolbrzymione dane z literatury i są uważane za bardzo realne.