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**Trap Response and Estimation of Numbers of Shrews
in Removal Catches***

[With 8 Tables & 7 Figs.]

Trap response of shrews and the relative efficiency of three types of traps (pitfalls, live and snap traps) in catching small mammals were studied. Material was obtained from short and long-term trappings and from removal catches. Analysis of the index of trappability and percentage of shrews in total catch was made. The general preference for pitfalls shown by shrews, and for live and snap traps by rodents was observed during the summer season. During the period from late autumn to spring live and snap traps are a little more effective than pitfalls. Differences in trapping success and in percentage of shrews in catches were found in different habitats and in successive years. Each pitfall, as a multi-catch trap, catches on an average 1.27 individuals. Two or more (up to 11) individuals were caught in 20% of all successful pitfalls. This fact does not change seriously the picture of preference for pitfalls by shrews. Removal of shrews from the study area was not always possible. Total data for six censuses showed, however, a regular decrease in daily catch. Estimates of the number of shrews from linear regression equations and from truncated distributions differed only slightly. Estimates of population size of shrews based on data from pitfalls were more than three times higher than those from snap traps, during the summer, but they became similar during late autumn. Data obtained show that differential trap preference of small mammals influence trapping success and trappability related estimations.

1. INTRODUCTION

One of the most important problems in contemporary ecological research, in particular in the field concerned with estimating energy flow in the ecosystem, is the necessity for the most absolute estimation possible of the density of mammals. The methods used so far for ascertaining population numbers and density of mammals still fail to provide sufficiently satisfactory results, permitting only a relative assessment of these parameters. The problem has been better elaborated in relation

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to rodents than to insectivores. This is probably due to the greater interest taken in the first of these groups of mammals, in which there are more species and which are of some economic importance. The role of *Insectivora* in the energy flow in forest ecosystems is unknown, and there is thus an objective necessity for continuing and extending research on these mammals, particularly research aimed at estimating their density.

The main obstacle to elaborating an adequate technique (or techniques) for absolute estimation of the density of various species of small mammals is their trap response. By this is meant a whole complex of different and variable phenomena making a real assessment of population size, its structure and its role in an ecosystem impossible. It is not the purpose of this study to list all the known and presumed sources of error. They undoubtedly originate, however, with the animals themselves (individual variation in response to traps, different in different species and for different population size, role in a community, season, *etc.*) and also from the technique employed (kind of trap and bait, way in which the traps are set and serviced, capture technique, weather conditions *etc.* (cf. *e.g.* Sealander & James, 1958; Kucheruk *et al.*, 1963 and others). This leads to the conclusion that the results of captures made by different research workers cannot be compared with each other.

A good knowledge of these phenomena may facilitate the correct interpretation of the results already obtained from captures, and also in the future may lead to the discovery of more reliable methods for estimating the density of small mammals. For this reason studies of this kind should properly precede estimation of population density.

Many notes containing comparisons of different methods of trapping mammals are to be found in literature, particularly on types of traps, baits, ways of arranging traps, *etc.* The general conclusion reached, however, is that different results are obtained depending on the technique used (different estimation of population size, its structure, average length of life of individuals — to mention only a few of the best documented examples — Adamczewska, 1959; Kucherek *et al.*, 1963; Chełkowska, 1967; Pucek, Ryszkowski & Zejda, 1969).

The majority of the studies published are based on scarce numerical data, so that only a few studies give more realistic results of catches (Sealander & James, 1958; Kucheruk *et al.*, 1963; Chełkowska, 1967). For this reason the author has decided to present selected data from numerous series of trappings which could throw light on the problem of trap response and relative efficiency of different techniques of catching small mammals, especially shrews. A discussion

is also given of the possibility of using removal catches (the so-called Standard Minimum method — Grodziński, Pucek & Ryszkowski, 1966) for estimating the number of shrews.

2. MATERIALS AND TRAPPING METHODS

In the present studies analysis was made of different series of catches of small mammals carried out at different times and in different localities by the Mammals Research Institute, Polish Academy of Sciences, at Białowieża.

2.1. Trapping of *Micromammalia* was carried out from 1966—1968 in 18 localities in north-west Poland (Fig. 1). Each year mammals were caught in August, as far



Fig. 1. Map showing distribution of localities in which short-term catches of small mammals were carried out during the period from 1966—1968.

as possible in all habitats, using in almost all of them three types of trap: pitfalls, live traps and snap traps. Pitfalls are metal cones, especially made for trapping small mammals, from 13—15 cm in diameter and 45—50 cm deep, which are sunk in the ground flush with the surface as described previously (Pucek, 1964). The live traps used are wooden boxes with a glass "window" from the top, and a metal latch at the front (Olszewski, 1968). Snap traps are standard traps of the mouse type, but slightly larger (60 × 130 mm), which prevents excessive damage to skulls.

The traps, 20 of each type, were spread regularly in areas which are, as far as possible, homogeneous, arranged in three lines 20 m from each other. Each line contained a different type of trap. The lines were 20 m from each other. Where the habitat formed narrow belts (*Circaeo-Alnetum* in river valleys, *Phragmitetalia* round lakes or *Salici-Franguletum* round bogs), the traps were set in one irregular line, placing in turn 20 pitfalls, then 20 live traps and 20 snap traps. A different order was also used.

A choice was made from among the three-year catches (1966—1968) of those which had been made in comparable habitats in each year. A total number of 79 series of catches in different study areas were used. Each area was in operation for a different period of time, although this was most commonly 6—13 days (87% of cases), *i. e.* for about 9 days on an average. As a result of these catches 40,901 trap-nights and 6,064 small mammals were obtained for the analysis presented (Tables, 1, 2).

2.2. Use was made of certain data from a special experiment made in the Białowieża National Park from July 1955 to June 1956 in order to compare the effects of different methods of trapping mammals. Comparison was made at that time of the effectiveness of pitfalls, live and snap traps operating (1) continuously every second month, (2) every 10 days in a different place. In each case 50 traps were arranged in a 5×10 m grid over an area of 2500 m². A total of 76,100 trap-nights and 5,983 insectivores and rodents were obtained from these catches (Table 3).

2.3. Long-term catches were carried out on permanently operating plots in a *Quercus-Carpinetum* habitat in the Białowieża National Park (Sect. 371). During the first study period (1962—1964) one area was in operation, containing 50 cylindrical pitfalls spread in a 10×5 m grid over an area of 2500 m². During the next period (1965—1968) the cylinders were replaced by cones in this area. Two parallel trap lines, one containing 50 live traps as described above, and the other 50 mouse snap traps, were set up at 10 m intervals over a distance of 500 m on two sides of the area. During the second study period the area and the two lines operated in spring (from April 15th to May 30th) and autumn (from September 15th to October 30th).

2.4. Removal catches, carried out by the method described by Grodziński, Pucek & Ryszkowski (1966), and termed Standard Minimum (*SM*), were modified for catching shrews by adding one pitfall on each of 256 sites in addition to two snap traps, as described by Aulak (1967). These studies were made in the Białowieża National Park during the period from 1966—1968. In the *Circaeo-Alnetum* habitat a total of 6 *SM* catches were made, mainly in spring and autumn, and in *Pinetum typicum* and in *Quercus-Carpinetum* — one census each in July 1966.

Data which had been obtained by the same method in Augustów Forest for the purpose of defining the population density of *M. oeconomus* (Pallas, 1776) were also used here. The technique used for these investigations was described in detail in an earlier study (Buchalczyk & Pucek, 1968).

2.5. All the traps were inspected once daily, with the exception of removal catches (2.4), when inspections were made morning and evening, and the result totalled in order to obtain the daily catch.

Live and snap traps were baited with a standard bait, *i. e.* a piece of wick saturated with a mixture of flour fried in rape seed oil. During the special experiments (*cf.* paragraph 2.2) the standard bait consisted of pieces of bread fried in the same oil.

3. CHANGES IN INDEX OF TRAPPABILITY

In the present studies the total catch (N) expressed in percentages, in relation to all chances of capture, that is, to the number of trap-nights (t/n), was taken as the index of trappability:

$$T = \frac{N \times 100}{t/n} \%$$

In this way it is possible to avoid differences in the total number of mammals caught (total catch) caused by a different number of traps and different time for which they operated in different series of catches.

A general comparison of the index of trappability was made for all results of the three years of trapping mammals in north-west Poland, treated jointly (Table 1). The indices obtained are calculated for the sum total of trapped individuals in relation to the corresponding total number

Table 1.

Differences in index of trappability depending on the kind of trap used. Total material from three years of catches and different habitats (cf. Table 2) in North-West Poland is treated jointly for rough comparison.

Kind of trap	Pitfall	Live	Snap	Total
Number of trap-nights	13,994	14,139	12,768	40,901
Total catch:				
<i>Insectivora</i>	1,942	210	163	2,315
<i>Rodentia</i>	1,435	1,305	1,009	3,749
<i>Insectivora</i>				
Trappability index (%):				
<i>Rodentia</i>	13.9	1.5	1.3	—
<i>Rodentia</i>	10.2	9.2	7.9	—

of trap-nights, but are not average values from different series of catches. Theoretically speaking it may be assumed that as all three types of trap usually operated simultaneously in the same habitats and the same study areas (in several cases at least two types), then the chances of being caught, and thus also the index of trappability, should be the same in each type of trap. Table 1, however, reveals distinct differences, particularly in the case of *Insectivora*. The majority of this group of mammals was formed by representatives of the genera *Sorex* L. and *Neomys* K a u p. The fact that the index of trappability of *Insectivora* in pitfalls is about 10 times than in live or snap traps is evidence that shrews decidedly prefer this type of trap, at any rate during the

summer period (August). The highest trappability was also observed in pitfalls in the case of rodents, slightly lower in live traps and even lower in snap traps. When these tendencies are analysed it may be suggested

Table 2.

Changes in the index of trappability depending on the kind of trap used, habitat, and year.

P — pitfalls, *L* — live traps, *S* — snap traps.

Group	Habitats	Year	Number of trap-nights			Index of trappability (T)						
			<i>P</i>	<i>L</i>	<i>S</i>	<i>Insectivora</i>			<i>Rodentia</i>			
						<i>P</i>	<i>L</i>	<i>S</i>	<i>P</i>	<i>L</i>	<i>S</i>	
1	<i>Sphagnetum medii</i> <i>pinetosum</i>											
	<i>Carici elongatae-</i> <i>Alnetum</i>	1966	400	400	400	17.5	0.0	0.8	6.5	2.2	9.2	
	<i>Salici-Franguletum</i>	1967	450	370	2 ⁰	14.7	0.3	0.8	11.8	21.6	15.6	
	<i>Empetro nigri-Pinetum</i>	1968	1400	1547	1360	16.2	1.1	1.6	8.6	6.4	7.6	
	Subtotal, Avg.		2250	2317	2010	16.1	0.8	1.3	8.8	8.1	8.9	
2	<i>Quercu-Piceetum</i> <i>Betuletum pubescentis</i>											
	<i>Leucobryo-Pinetum</i>	1966	280	275	280	21.0	0.4	1.4	4.3	2.2	3.9	
	<i>Peucedano-Pinetum</i>	1967	2154	2038	2257	9.5	1.5	11.5	12.0	12.2	11.6	
	<i>Pino-Quercetum</i>	1968	2747	2718	2716	9.5	0.8	0.9	6.7	6.9	6.9	
	Subtotal, Avg.		5181	5031	5253	10.1	1.1	1.0	8.7	8.8	8.8	
3		1966	1746	1717	1518	16.9	0.6	1.7	8.2	3.6	4.9	
	<i>Circaeo-Alnetum</i>	1967	560	580	412	14.6	1.7	2.4	6.8	16.0	11.9	
	<i>Fraxino-Ulnetum</i>	1968	980	960	700	28.5	5.9	1.7	13.3	6.6	2.8	
	Subtotal, Avg.		3286	3257	2630	20.0	2.4	1.8	9.5	6.7	5.4	
4	<i>Fago-Quercetum</i> <i>Quercu-Betuletum</i>											
	<i>Quercu-Carpinetum</i>	1966	594	597	499	6.6	0.3	1.2	4.0	3.5	4.2	
	<i>Melico-Fagetum</i>	1967	917	1273	882	7.2	0.5	0.5	12.1	24.6	16.9	
	<i>Luzulo-Fagetum</i>	1968	280	280	280	11.0	0.7	0.4	15.7	12.1	12.5	
	Subtotal, Avg.		1791	2050	1661	7.6	0.5	0.7	10.0	18.0	12.3	
5	<i>Phragmitetalia</i> , <i>Caricetalia</i>	1967	914	779	619	13.4	4.1	1.1	19.5	8.7	7.9	
		1968	820	820	820	18.3	2.2	2.2	15.7	8.9	2.6	
	Subtotal, Avg.		1734	1599	1439	15.7	3.1	1.7	17.7	8.8	4.9	

that each of the types of trap referred to gives a different record of population size and density of small terrestrial mammals and the reciprocal proportions between their basic groups (*Insectivora*, *Rodentia*). Although some rodents (e.g. *Apodemus* sp.) can jump out of a pitfall

(Adamczewska, 1958; Olszewski, unpubl.) this type of trap is far more effective for catching other small mammals, particularly *Soricidae*.

A more detailed picture of variations in the trappability index of rodents and insectivores is given in Table 2. Data for each year were obtained by summing up the whole catch in floristically comparable habitats, but in different localities (from one or several study areas) within a given region examined in a given year (Fig. 1). Similarly, average values for different habitats are not arithmetical means but were recalculated for the total catch during the three-year study period and total number of trap-nights.

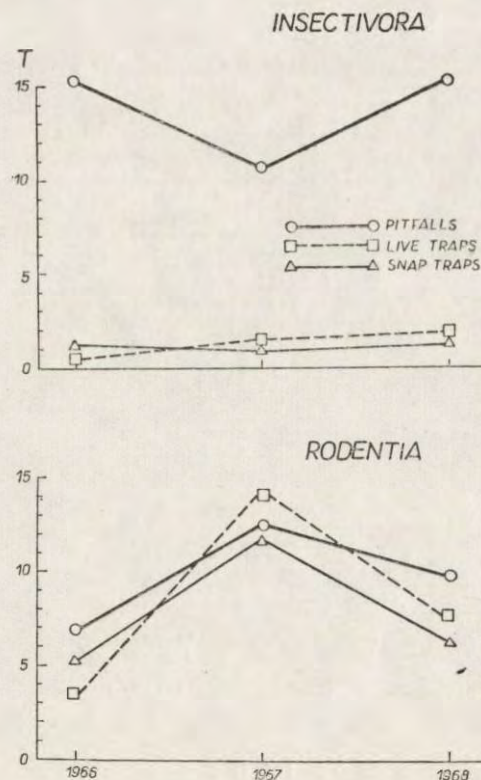


Fig. 2. Changes in average yearly index of trappability depending on the kind of trap used.

In addition to the relation discussed between the trappability of mammals and the type of trap, there are distinct biotopic differences. The highest trappability of *Insectivora* was noted in *Alnetum*, *Salicici-Franguletum* and *Vaccinio uliginosi-Pinetum*, and also *Phragmitetalia* and *Caricetalia*. Rodents, on the other hand were most frequently caught in a *Quercu-Carpinetum medioeuropaeum* habitat and different forms of the *Fagetum* habitat, and also sedges and rushes. The trappability of

insectivores and rodents is greatest in all types of traps in these biotopes, and in a few cases of *Rodentia* even higher in live and snap traps than in pitfalls (Table 2).

Table 2 also shows differences in the index of trappability in successive years, which are better expressed by averages calculated in a similar way to that described above for all the biotopes examined in a given year (Fig. 2). In 1967 trappability of *Insectivora* was lower and of *Rodentia* higher than in 1966 and 1968. This relation is observed in each of the types of traps to a greater or lesser degree, but it has the character of synchronous variations.

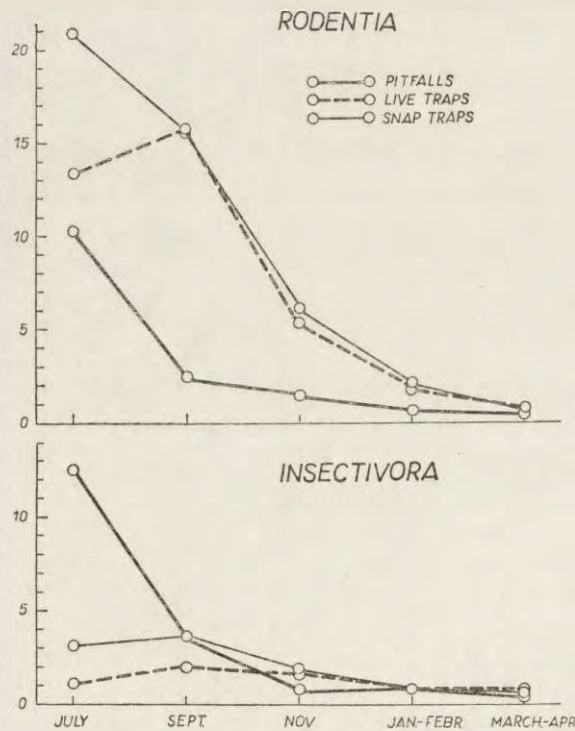


Fig. 3. Changes in index of trappability as affected by season of the year and kind of trap (Data of experiment described in section 2.2).

Catches made at different times of the year (cf. section 2.2) permit the analysis of variations in the index of trappability depending on the type of trap and season (Fig. 3). In this case the number of trap-nights was counted for traps distributed in a network, within a 10×5 m grid. The absolute values of the index are not therefore comparable with the above data for trap lines.

The general preference for pitfalls shown by shrews, and for live and snap traps by rodents, is very distinct (Fig. 3). Although trappability of both rodents and insectivores decreases abruptly in late autumn and winter, yet live traps and snap traps catch far more mammals than do pitfalls. During the period from late autumn (November) to spring (April) live traps and snap traps are thus more effective than pitfalls even for insectivores. The standard bait (bread fried in rape seed oil) may be more attractive to shrews during this period than in summer, or perhaps the chances of their being caught vary as the result of other causes.

4. PERCENTAGE OF INSECTIVORA IN CATCHES

The percentage of insectivores and rodents in catches in different types of traps is yet another measure of the preferences of these two groups of small mammals in relation to traps. The percentage of insectivores was calculated in relation to all mammals caught by the given type of trap in a given habitat. As in the case of the index of trappability, the material was combined in larger groups according to biotopes or years.

Table 3.

Changes in percentage of *Insectivora* as a fraction of total catch of small mammals (*N*) in a given type of trap. Short-term catches carried out in North-West Poland during August 1966—1968 (cf. Section 2.1).

Group of habitats ¹⁾	Pitfalls		Live		Snap	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
1	562	64.6	206	8.7	206	13.1
2	980	53.6	496	11.1	514	10.5
3	968	67.8	297	26.3	191	25.1
4	315	43.2	378	2.6	216	5.1
5	580	47.1	191	26.2	95	26.3
Total	3,405	57.4	1,568	13.4	1,222	13.5

¹⁾ The same forest habitats as shown in Table 2.

Table 3 illustrates differences in the percentage of insectivores in catches in different types of traps and in different study habitats. As can be seen, in biotopes rich in insectivores they are caught 2—5 times, more often and in habitats less favourable to these mammals even as much as 5—15 times more often in pitfalls than in live and snap traps. In general the percentage of insectivores in live and in snap traps is similar, and is about 4 times smaller than in pitfalls.

Data totalled for all the habitats examined in successive years are illustrated by Fig. 4. In addition to the decided preference shown by

insectivores for pitfalls, a lesser abundance of these mammals is revealed in all types of traps in 1967 in comparison with 1966 and 1968.

Data contained in Table 4 for long-term catches of mammals on permanent study areas, and also for removal catches carried out by the SM method (Table 5) show that seasonal differences can be seen both in the index of trappability and in the percentage of insectivores. The highest percentage of shrews is caught in pitfalls during summer, and a smaller percentage in autumn and winter. This points to seasonal variations in these mammals' preferences for pitfalls. Variations of a similar character are evident in the case of snap traps also (Table 5). This is undoubtedly the explanation of the far higher percentage of shrews in pitfalls in

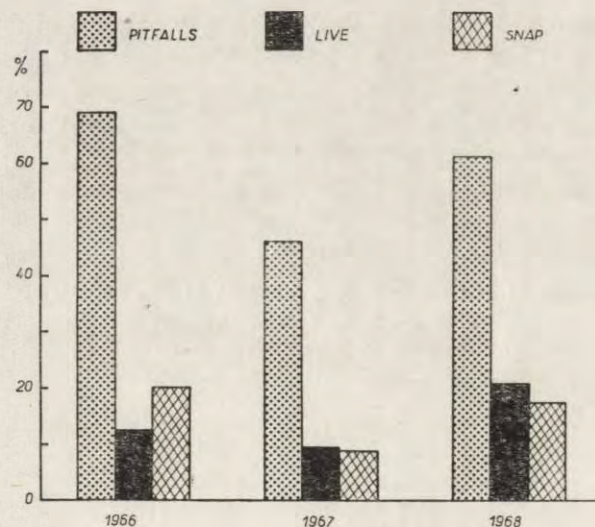


Fig. 4. Changes in average yearly percentage of *Insectivora* caught in different kinds of trap.

catches from whole years, in comparison with the spring and autumn periods (Table 4). This table also shows that in the case of the two species dominating in the group of rodent species (*Clethrionomys glareolus* and *Apodemus flavicollis*) there are also differences in trappability depending on the type of trap. More than twice as many *C. glareolus*, and conversely — over 3 times less *A. flavicollis* — were caught by live traps than by snap traps. These differences are highly significant when tested by the χ^2 test ($P < 0.001$).

The situation is similar in the case of different species of *Insectivora*. By computing totalled data for six censuses (SM method) made in a *Circaeo-Alnetum* habitat (Table 5) it was found that 81.0% of *Sorex ara-*

Table 4.

Proportion of *Insectivora* and *Rodentia* depending on the method of capture. Cumulated long-term catches carried out in Białowieża National Park on permanently working plots (for details see section 2.3).

C.g. — *Clethrionomys glareolus* (Schreber, 1780), *A.f.* — *Apodemus flavicollis* (Melchior, 1834).

Method of capture, period of time	Rodents				Shrews	Total
	<i>C.g.</i>	<i>A.f.</i>	Other	Subtotal		
Pitfalls working whole years round, n	666	204	259	1129	803	1932
1962—1964	34.5	10.5	13.4	58.4	41.6	100
Pitfalls, spring and autumn, n	399	205	77	681	166	847
1965—1968	47.1	24.2	9.1	80.4	19.6	100
Live traps line, Spring and autumn n	300	83	8	391	15	406
1965—1968	73.9	20.4	2.0	96.3	3.7	100
Snap traps line, Spring and autumn n	466	846	37	1349	23	1372
1965—1968	34.0	61.6	2.7	98.3	1.7	100

Table 5.

Percentage of *Insectivora* as a fraction of total number of mammals caught in removal catches (SM method, — cf. Section 2.4).

(Data for 1966 according to experiments published by Aulak, 1967).

Habitat and census date	Pitfalls		Snap traps		Total	
	N	%	N	%	N	%
<i>Circaeo-Alnetum</i>						
29.VII—4.VIII.66	523	77.6	287	24.7	810	58.9
26.V—1.VI.67	175	44.0	241	1.2	416	19.2
26.VII—1.VIII.67	365	71.2	283	21.6	648	49.5
12.X—16.X.67	120	36.6	260	16.2	380	22.6
20.VI—25.VI.68	500	68.6	272	3.7	772	45.7
17.X—21.X.68	177	46.3	258	11.2	435	25.5
<i>Pinetum typicum</i>						
26.VII—1.VIII.66	153	77.8	34	0	187	63.6
<i>Quercu-Carpinetum</i>						
14.VII—20.VII.66	166	51.2	356	4.2	522	19.2
Total, Avg.	2,179	59.2	1,991	10.4	4,170	38.0

neus and 94.0% of *Sorex minutus* were caught in pitfalls, if only these two dominating species of insectivores are taken into consideration (N.B. the remaining species formed only about 8% of all *Insectivora* caught). Although these differences proved to be highly statistically significant (χ^2 test, $P < 0.001$), it would seem that the chances of catching such

small mammals as *S. minutus* in standard snap traps are quite simply smaller than of catching *S. araneus*. Individuals of the first species are probably not heavy enough to start the trigger mechanism.

5. PITFALLS AS MULTI-CATCH TRAPS

In all the materials analysed here comparison has been made simply of the results of catches in pitfalls and in live or snap traps. Everyday practice, however, justifies the expectation that both live and snap traps can catch two individuals only in exceptional circumstances. The pitfall, on the other hand, is in principle a multi-catch trap. On the basis of material from *SM* censuses carried out in the Białowieża National Park (cf. section 2.4) a check was made of the degree to which these traps can be considered as multi-catch. As shown in Table 6 almost 20% of

Table 6.

Distribution of number of mammals caught per pitfall at Standard-Minimum removal catches (five census carried out during 1967—1968). Groups 1 and 2 include separate mammal species as well as two or even three different species caught in one pitfall. Group 3 include these cases when representatives of two main group (*Rodentia*, *Insectivora*) were caught in one pitfall. O.R. — observed ranges of averages for different censuses.

Group	Number of individuals/pitfall									n	O.R.	Avg.
	1	2	3	4	5	...	10	11				
1. <i>Insectivora</i>	495	83	14	2	2	—	1	—	597	1.00—1.46	1.22	
2. <i>Rodentia</i>	338	40	6	—	1	—	—	—	385	1.06—1.28	1.14	
3. <i>Insectivora</i> + <i>Rodentia</i>	—	39	9	5	1	—	—	1	55	2.00—3.16	2.56	
Total	n	833	162	29	7	4	—	1	1	1,037	1.12—1.31	1.27
	%	80.3	15.6	2.8	0.7	0.4	—	0.2		100	—	—

the pitfalls take more than one mammal, *i.e.* from 2—5, and only sporadically (0.2% of cases) as many as 10 and 11. It is noteworthy that most frequently two or more individuals of the same species are caught, and less often individuals of two different species of *Insectivora* (0—5.8% of the cases in different censuses) or of two different species of *Rodentia* (0 to 0.8% of the cases).

Representatives of two different groups of mammals — *Insectivora* and *Rodentia* were caught together in the same pitfall in 3.0 — 6.8% ($\bar{x} = 3.4\%$) of all successful pitfalls with $N = 1037$ (Table 6).

Since *Insectivora* prefer pitfalls there was more chance of double, triple *etc.* captures. This is shown by the higher arithmetical mean of

catches per pitfall (Table 6). In general it may be said that each pitfall catches on an average 1.27 individuals, and this figure can be used for correcting data in any comparisons made of the trappability of small mammals in different types of trap. The value of this coefficient is limited to removal catches and cannot as yet be generally applied.

In this series of removal catches there were two snap traps and one pitfall at each station. Only 16.8% of all insectivores removed ($N = 718$) were caught in snap traps. It is an interesting fact that out of 121 successful trap stations it never happened that two insectivores were caught at a station (per 2 snap traps), although in the case of rodents an average of 1.15 individuals is caught per two traps at a station.

6. ESTIMATION OF NUMBER OF SHREWS IN REMOVAL CATCHES

6.1. Removal of Shrews From the Study Area

Removal catches were first adopted by Aulak (1967) for estimating the number of shrews. He found that a distinct decrease in daily catch is not always obtained on consecutive days of removal, which makes it impossible to estimate correctly the density of these mammals from an equation of linear regression (Hayne, 1939; Grodziński *et al.*, 1966). In view of the fact that a considerable number of Standard Minimum censuses are now available (cf. paragraph 2.4 and Table 5) it was possible to make a more detailed analysis of these materials.

Earlier studies have shown that the number of rodents decreases on successive days during the period of intensive removal catches (Hayne, 1949; Buckner, 1957; Calhoun, 1963; Grodziński *et al.*, 1966; Aulak, 1967). When pitfalls were used for removal catches a decrease in the daily catch was generally found in the case of shrews also. Although a decrease in the number of insectivores caught and removed was not always observed in different censuses, the mean values for six SM censuses in the Białowieża National Park (Fig. 5) clearly illustrate this tendency. It will also be observed that in the case of snap traps deviations from the regression line calculated for the first 4 days are smaller than in the case of pitfalls (calculated for 5 days). The tendency to increase in the daily catch appears in the final phase of removal catches, *i.e.* on the 5th — 7th day.

It must be emphasised that the removal rate of insectivores expressed by the coefficient of regression a is in general higher in the case of pitfalls than snap traps. In addition, removal rate for insectivores measured in this way is as a rule lower than for rodents, as will be seen from the comparison of the present data with those contained in earlier publications (Grodziński *et al.*, 1966; Aulak, 1967). This is also ob-

vious from the fact that the percentage of insectivores increases on successive days of removal catches (Figs. 6 and 7). Increase in the percentage of insectivores in successive daily catches takes place in snap traps up to the third or even to the fifth day inclusive, whereas with pitfalls

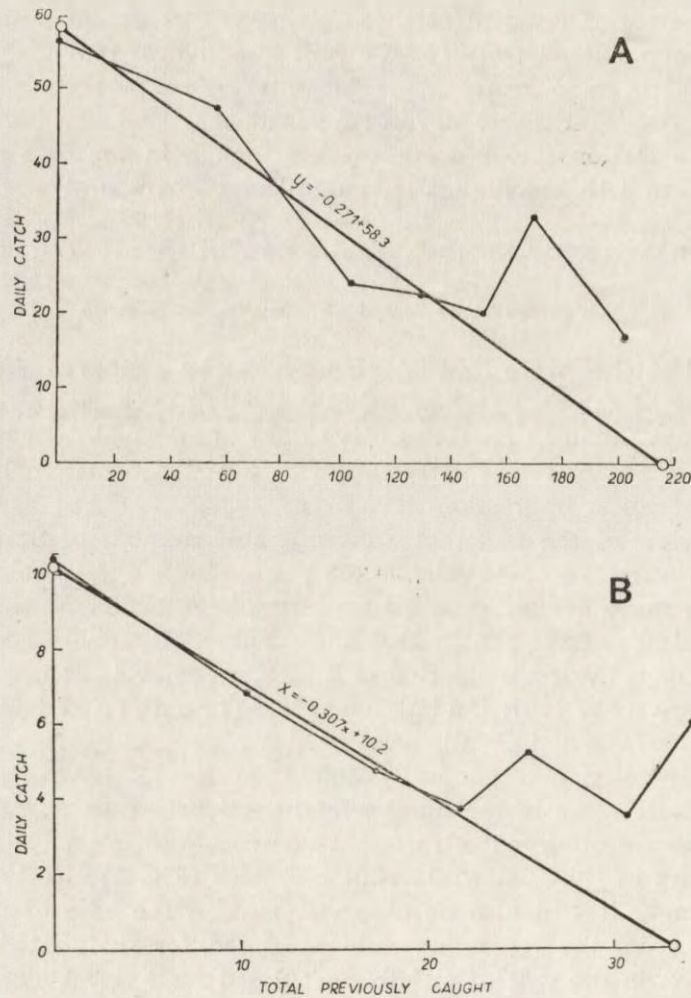


Fig. 5. Dependence of daily catch on numbers of *Insectivora* previously removed by pitfalls (A) and by snap traps (B). Average data for 6 SM censuses are compared with regression lines calculated for 5 (A) and 4 (B) days.

a distinct difference can be observed between the first and following days. In the final phase of removal catches a tendency appears for further increase (pitfalls) or decrease (snap traps) in the percentage of insectivores in the daily catch.

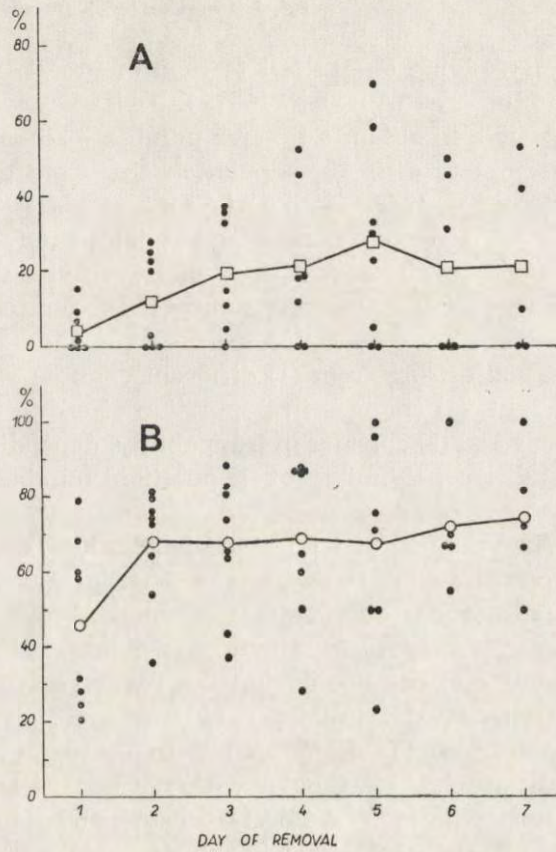


Fig. 6. Percentage of *Insectivora* on successive days of removal (SM census) as compared for snap traps (A) and pitfalls (B). Total catch for the given day was taken as 100% in these calculations. The same SM censuses are used as those listed in Table 5.

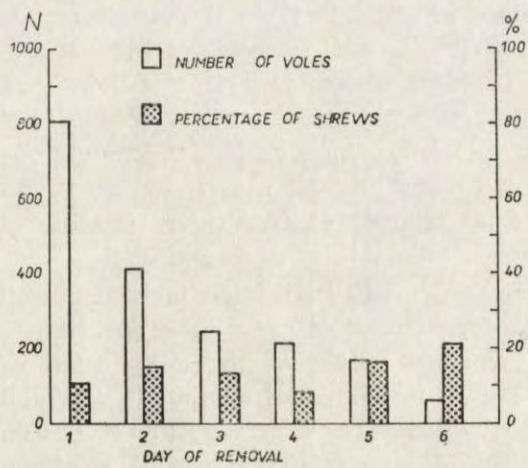


Fig. 7. Percentage of *Sorex araneus* as compared with the numbers of *Microtus oeconomus* on successive days of removal catches. The diagram is based on totaled numbers obtained from pitfalls (five SM censuses made in Augustów Forest).

6.2. Estimation of Number of Shrews

By adding one pitfall to each of the 256 stations of the Standard Minimum area (Aulak, 1967; Buchalczyk & Pucek, 1968) it proved possible to obtain a greater number of insectivores removed, and also to attempt to estimate population size from the linear regression equation (Hayne, 1949; Grodziński *et al.*, 1966). Materials obtained from 13 SM censuses were analysed jointly (cf. paragraph 2.4, and Tables 7 and 8). In all cases calculations were made for a number of days which were as far as possible uniform, *i.e.* for the first 3—4 days of removal catches. The reason for this was the endeavour to reduce errors in estimation arising from (1) different chances of particular individuals being caught, (2) changes in population size due to birth, mortality or migrations and (3) changes in trappability, depending on such factors as weather conditions, thinning of population numbers during the final phase of removal catches, *etc.*

The method of truncated distributions, described by Janion, Ryskowski & Wierzbowska (1968) was used for comparison of number estimates obtained by the method of linear regression. This method made it possible to estimate the number of mammals with variable probability of capture during the various days of the removal period. Calculations were usually made for the first three days of the removal period also (Table 7, 8), but in the case of considerable variations in daily catch the estimates were not correct and it was necessary to accept a longer period (1—4 or 1—5 days), and also to estimate density on later days (2—4 or 3—5), when a decrease was observed in the number of *Insectivora* removed on successive days.

The results given in tables 7 and 8 show that it was not always possible to estimate from the linear regression equation the population size of the two main species of *Insectivora*, *i.e.* *S. araneus* and *S. minutus*, or of all *Insectivora* treated jointly. Relatively more often it was possible to estimate the number of *Insectivora* caught in pitfalls than in snap traps, which probably depends on the absolutely greater number of these mammals caught by the first type of trap. (Cases in which the total number of *Insectivora* caught was less than 10 were not included in calculations).

The truncated distribution method permits an estimate to be made in a greater number of cases than does the regression method, since cases with varying values of the daily catch can be included. There were, however, situations even when it was employed, in which mean probability of captures were very low ($P < 0.05$).

It can also be seen that estimates of number obtained by the two

Table 7.

Comparison of *S. araneus*, *S. minutus* and all shrews numbers per plot (5.76 hectare) as estimated from liner regression equation ($N_{\text{Regr.}}$) and from truncated distributions (N_{Td}).

All calculations made for first three days of removal period if not other indicated. Data for removal catches carried out in Białowieża National Park, in 1966—1968, and those for 1966 published in part by Aulak (1967). Arithmetical means were calculated only for comparable pairs of estimates.

N — total numbers of animals actually removed during the whole period of catches,
 ? — calculation impossible or unreliable.

Habitat and census date	Pitfalls			Snap traps			Calculated for:
	N	$N_{\text{Regr.}}$	N_{Td}	N	$N_{\text{Regr.}}$	N_{Td}	
<i>S. araneus</i>							
<i>Circaeo-Alnetum</i>							
29.VII—4.VIII.1966 (1)	261	249.1	242.3	58	37.2	37.4	*1—4 ds.
26.VII—1.VIII.1967 (3)	179	131.5	138.5	51	28.9	26.2	
12.X—16.X.1967 (4)	32	33.1*	32.3	34	?	53.3	
20.VI—25.VI.1968 (5)	185	84.9	110.0	8	?	?	
17.X—21.X.1968 (6)	49	?	64.2*	24	?	?	
<i>Pinetum typicum</i>							
26.VII—1.VIII.1966	72	49.9	35.9	0			
<i>Quercu-Carpinetum</i>							
26.VII—1.VIII.1966	51	?	64.0*	15	?	24.4*	*3—5 ds.
Total, Avg.	829	109.6	111.8	190	33.0	35.3	
<i>S. minutus</i>							
<i>Circaeo-Alnetum</i>							
29.VII—4.VIII.1966 (1)	124	81.7	123.2	11	8.0	8.0	*1—4 ds.
26.VII—1.VIII.1967 (3)	54	?	51.8	3	?	?	
12.X—16.X.1967 (4)	11	12.6*	12.2	2	?	?	
20.VI—25.VI.1968 (5)	120	96.7	93.8	0	?	?	
17.X—21.X.1968 (6)	24	?	38.4*	1	?	?	
<i>Pinetum typicum</i>							
26.VII—1.VIII.1966	47	35.2	33.0	0			
Total, Avg.	380	56.6	65.6	17			
<i>Insectivora</i>							
<i>Circaeo-Alnetum</i>							
29.VII—4.VIII.1966 (1)	406	393.2	367.2	71	48.3	47.3	*1—5 ds., 1+2 ds. cumulated **1—4 ds.
26.V—1.VI.1967 (2)	77	64.5*	61.7**	3	?	?	
26.VII—1.VIII.1967 (3)	260	198.6	204.1	61	53.5	53.3	
12.X—16.X.1967 (4)	44	51.0	49.7	42	55.1	53.6	
20.VI—25.VI.1968 (5)	345	230.0	225.4	10	?	3.8	
17.X—21.X.1968 (6)	80	?	?	29	?	46.4*	
<i>Pinetum typicum</i>							*2—4 ds.
26.VII—1.VIII.1966	119	83.6	80.3	0			
<i>Quercu-Carpinetum</i>							
26.VII—1.VIII.1966	85	?	139.2*	15	?	24.4*	*3—5 ds.
Total, Avg.	1,416	170.2	164.7	231	52.3	51.4	

methods differ slightly in certain cases. This is particularly clearly visible when the average values for 5—6 censuses are compared (Table 7, 8). It would seem that estimations for *S. araneus* and *S. minutus* from truncated distributions tend to be higher than those from linear regression (Table 7 and 8). Total estimates for all *Insectivora* (Table 7) exhibit the reverse tendency. It is therefore difficult to say whether these differences are real ones.

The slight differences between estimates, the possibility of making use of a larger number of cases and of taking into consideration cases in which probability of capture varies on different days, and also the less laborious calculation involved would appear to justify recommending the method of truncated distributions instead of linear regression.

Table 8.

Comparison of *S. araneus* numbers per plot (5.76 ha) estimated using linear regression equation and truncated distributions methods.

Data for removal catches in Augustów Forest peat-bog study area (cf. Section 2.4).

Method of calculation	Census number and kind of trap ¹⁾							Avg. 3—7 p
	3 p	4 p	5 p	6 sn	6 p	6 sn+p	7 p	
Removal period (days)	10	8	5	6	6	6	7	—
Actually removed (Total <i>N</i>)	16	17	35	77	54	131	41	32.6
Estimated <i>N</i> (regression for 4 days)	∇ 14.1	∇ 16.3	∇ 29.4	∧ 79.3	∇ 46.2	∇ 112.6	—	∇ 26.5
Estimated <i>N</i> (truncated distributions, 1—3 or 1—4 days —*)	∧ 16.0	∧ 18.0	∧ 45.0	∇ 76.0*	∧ 48.4*	∧ 133.9	34.8	∧ 32.4

¹⁾ p — pitfalls, sn — snap traps.

Two types of traps (pitfalls and snap traps) were in operation simultaneously on the same areas. This made it possible to compare estimations of the number of insectivores obtained from removal catches from either pitfalls only, or snap traps only (Table 7, 8). As can be seen the average estimates from pitfalls are more than three times higher than those from snap traps, and numbers of shrews actually removed differ even more. These averages reflect seasonal preference of shrews for pitfalls (cf. Fig. 3). Estimates of number of shrews from snap traps become similar with those from pitfalls, and even exceed them, during late autumn (cf. e.g. census no. 4, Table 7, or census no. 6, Table 8 both carried out in October). This is the evidence that estimation of popula-

tion size and density depends on the type of trap, and that the given trap may register the number of mammals differently, depending on the season of the year.

7. DISCUSSION

It is quite clear from the data presented that *Insectivora* exhibit a decided preference for pitfalls. This preference is maintained even when correction is made for the multi-catch character of pitfalls (Table 6). In relation to rodents this type of trap has proved to be, if not the best, at least equally as effective as live or snap traps. These results agree to a greater or lesser degree with the data given by other authors who compared pitfalls and other types of trap (e.g. Buckner, 1957; Sealander & James, 1958; Kucheruk *et al.*, 1963; MacLeod & Lethieq, 1963; Brown, 1967). They all, and other authors as well, show that *Insectivora* are easier to catch in pitfalls of different construction, and furthermore, that this type gives a better idea of the species composition of the mammal community as a whole (e.g. Borodin, 1966). The diametrically opposed views of certain other authors (cf. views quoted in the study by Kucheruk, 1963) cannot withstand criticism in the light of the data presented.

It becomes clear in connection with the foregoing that the reactions of individuals belonging to different species of mammals are selective in relation to the type of trap and capture technique. This in effect gives a picture, which is distorted to an unknown degree, of parameters based on the capture of mammals. For instance, Wiegert & Mayenschein (1965) showed that estimates of population density may depend on the differential response of individuals to the traps. Chęłkowska (1967) demonstrated not only species differences in the trappability of *Apodemus agrarius* and *Clethrionomys glareolus* in live traps and in pitfalls, but also the differences in this respect between different categories of individuals of the same species (young, ephemeral). Similar data were obtained by Buchalczyk & Pucek (1968) for *Microtus oeconomus* (Pallas, 1776), which led to a different estimate of population size depending on the type of trap. Pucek, Ryszkowski & Zejda (1969) proved that estimates of the average length of life of *Clethrionomys glareolus* (Schreber, 1780) differ for comparable materials obtained from pitfalls and from live or snap traps. This is due to different registration of the age structure of the population by each of the different types of traps referred to above. The consequences of this type of differentiation in an estimate of population size turnover and

other parameters of importance in productivity studies of mammal populations are obvious.

Only the use of pitfalls in the present study made it possible to estimate the density of *Insectivora* from extensive removal catches. Since these mammals do not prefer snap traps, at any rate not during the summer season (cf., e.g. Buckner, 1957 and Tables 2, 4 and Fig. 3 of this paper), it becomes easy to understand the difficulties encountered by Gentry, Golley & Smith (1968) in estimating the populations of *Insectivora* using this type of trap only.

Although pitfalls were used it was shown that removal of *Insectivora* proceeds more slowly than that of *Rodentia* (cf. also Aulak, 1967) and in addition complete removal was never attained, despite the fact that this happened quite often in the case of *Rodentia*, at least in cases of low population numbers (Grodziński *et al.*, 1966; Buchalczyk & Pucek, 1968). It is thus likely that the whole complex of population and habitat factors and the trapping mechanism affecting the trappability of *Insectivora* act in a different way in this group of mammals than in the case of *Rodentia*. It is thus difficult to say whether estimates obtained by the same method for *Insectivora* and *Rodentia* are absolutely comparable.

On the other hand the range of differences shown in estimates obtained from pitfalls and from snap traps jointly are the reflection of the shrews' preference for pitfalls during different seasons (cf. Table 7 and Fig. 3). Thus the seasonal changes in trap preference of the given group (or species) of mammals influence their trappability, and trappability related estimations.

Another source of error may also be exploitation of the population, if removal catches are carried out in the same study plot several times within one year. A situation of this kind occurred in our investigations in both the Białowieża National Park and in Augustów Forest. Although the gap thus caused in the population can be relatively quickly replaced in the quantitative sense, it is not certain whether the composition of the mammal community and also the population structure of the different species is re-formed, to the same extent as was the case before removal. Data given by Novik & Gamalejev (1966) indicate that such situations are really possible. These authors found differences, in the species and age composition of *Soricidae* caught in trapping trenches kept either in constant, or periodic operation, during the warm period of the year.

Estimation of population density of *Insectivora* in our case was usually possible with greater abundance of mammals, when a decrease in daily

catch on successive days of the removal period was observed. Intensity of removal of *Insectivora* by pitfalls is greater than by snap traps, at least during summer, and as a result it proved possible to obtain a decrease in the number of mammals caught and removed. The results obtained therefore differ from the data cited by Calhoun (1963) for snap traps. This latter author found that dominant species in a mammal community are thought to have a larger home range, to contact more traps and are therefore removed at a greater rate than the subordinates. When the dominants are removed the subordinate species may expand their home ranges and increase their chances of being caught. In Calhoun's studies rodents dominate in all cases, and the trappability of shrews increases in further days of the removal period. The pitfall, as a multi-catch trap, and preferred by *Insectivora*, undoubtedly creates greater chances of capture for this group of mammals, and as a result a decrease is recorded in the daily catch, at least during the first successive days.

In the light of data, particularly on the different response of *Insectivora* to the different types of traps, of the existing variations in trappability at different times of the year (depending on the current population density) and also on different successive days of the removal period, the question arises as to which of the number estimates is correct — that obtained from pitfalls or that from snap traps. Although the phenomena discovered make a critical evaluation of the results obtained necessary, it would seem that estimates obtained by means of pitfalls are more reliable. This would appear sound in view also of the fact that usually it is only this method which permits the calculation of shrews number from the linear regression equation or also (more often) from truncated distributions. This conclusion must, however, be checked in further comparative studies of the effectiveness and action of different methods of trapping mammals on the results obtained. Studies of this kind will permit not only a critical judgment of the results obtained earlier, but will also make it possible to use in the future more economical methods of relative estimation of population size and conversion of the data obtained into absolute estimates.

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REAKCJA NA PUŁAPKĘ A OCENA ZAGĘSZCZENIA RYJÓWEK
METODĄ WYŁOWU

Streszczenie

Ocena roli owadożernych w ekosystemie wymaga znajomości ich zagęszczenia. Przeszkodą do uzyskania możliwie absolutnych ocen zagęszczenia ssaków jest ich zmienna reakcja na pułapkę, przynętę czy procedurę połowu. W celu lepszego poznania tych zjawisk badano współczynnik łowności owadożernych (niemal wyłącznie *Soricidae*), w zależności od typu pułapki (stożek, żywołówka, zatrzask) i pory roku.

Do badań użyto różnych serii materiału z połowów na pułapko-liniach, kwadratowych działkach o powierzchni 0,25 ha, a także z wyłowu metodą Standard Minimum (SM) z powierzchni 5,76 ha. Wyniki opierają na ca 240 000 pułapko-dni, i 13 cenzusach SM, które w sumie dały ponad 20 000 drobnych ssaków.

Zarówno współczynnik odłowu jak i procent owadożernych w materiale wskazują na ogólną preferencję stożków przez ryjówek a pułapek żywołownych i zatrzasków przez gryzonię — przynajmniej w porze letniej (Tabele 1, 3, 4, 5, Ryc. 2, 4). Wykazano ponadto zróżnicowanie tych wskaźników w zależności od typu środowiska (Tabela 2) i w kolejnych latach badań (Ryc. 2, 3). Łowność gryzoni i owadożernych gwałtownie spada późną jesienią i zimą a żywołówki i zatrzaski łowią więcej ssaków (w tym również i *Soricidae*) niż stożki (Ryc. 3).

Stożek jako pułapka wielołówna łowi przeciętnie 1,27 ssaka. Tylko 20% wszystkich efektywnych stożków łowiło 2 i więcej (do 11) ssaków (Tabela 6). Uwzględnienie tej poprawki nie wyrównuje jednak zdecydowanego preferowania stożków przez ryjówek w porze letniej.

Zastosowanie stożków obok zatrzasków w metodzie SM umożliwiło uzyskanie wyłowu ryjówek w większości przypadków (Tabela 7, Ryc. 5). Pozwala to na oszacowanie populacji tych zwierząt z równania prostej regresji i z rozkładów uciętych, przynajmniej dla pierwszych dni wyłowu. W dalszych dniach wyłowu (5—7) obserwowano bowiem wzrost procentu owadożernych (Ryc. 6, 7).

Stwierdzono, że oceny liczebności ryjówek uzyskane dwoma sposobami kalkulacji różnią się między sobą nieznacznie (Tabele 7 i 8). Można zatem zalecić mniej pracochłonną metodę rozkładów uciętych, umożliwiającą poza tym ocenę i w tych