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Some Biological Aspects of the Sex-Ratio in the Common Shrew (*Sorex araneus araneus* L.)

Biologiczne aspekty stosunku płci u *Sorex araneus araneus* L.

I. Introduction 43
II. Material and methods 45
III. Sex-ratio in young shrews 47
IV. Sex-ratio in old adult shrews 51
V. Proportions of age groups 55
VI. Discussion of results 59
a) Remarks on trapping methods 59
b) The influence of activity and age on sex-ratio 61
c) Seasonal variations in the sex-ratio 64
d) Sex-ratio as the expression of regulation phenomena in the population 66
VII. Summary 67
References 69
Streszczenie 72

I. INTRODUCTION

The problem of the quantitative sex-ratio within the species has for many years interested large numbers of scientific workers, both biologists, breeders and zoo-technicians (P a r k e s, 1927). Two different trends, each of which aggregates an extensive amount of factual material, have become apparent in the development which

has so far taken place of opinions on this problem, opinions which endeavour to explain the various stages of the process of determination, regulation and heredity of sex. The first of these trends is based on the theoretical basis of formal genetics. It assumes that both types of heterogametes are produced in a ratio such as 1:1, and are equivalent in transmitting sex to progeny. On these grounds certain research workers have assumed that in accordance with mathematical probability, the real ratio of both sexes should be 1 : 1.

The second trend rejects the assumptions of the chromosome theory of heredity and limits itself to explaining the secondary sex-ratio by the influence on the parents of the conditions of their environment, in the widest sense of the word.

It would, however, appear impossible to approach these problems in so orthodox a manner. In formal genetics little is said of the sex-ratio of zygotes (primary sex-ratio), which however, like the process of fertilisation itself, must from the very start of its existence be subject to the influence of the external and internal environment of the parents.

In literature on this subject I found only a very small number of publications devoted entirely to the analysis of the sex-ratio in mammals, and there is no publication giving an exhaustive discussion of this problem in relation to the Common Shrew (*Sorex araneus* L.). On the other hand numerous authors, as a side line to the main work of a biological, ecological or morphological character, devote some attention to the sex-ratio in the species examined, while perhaps not always considering whether the material analysed is sufficiently representative.

The sex-ratio in *Sorex araneus* L. has been investigated by several authors (Adams, 1919; Middleton, 1931; Brambell, 1935; Stein, 1938; 1953; Snigirevskaja, 1947; Dehnel, 1949; Kubik, 1951; Borowski & Dehnel, 1952; Teplov, 1954; Becker, 1955; Dunajeva, 1955; Pelikan, 1955).

This problem has also been examined in related but perhaps less common species. In relation to *Sorex minutus minutus* L. — Brambell & Hall, 1936; Snigirevskaja, l. c., Dehnel, 1949 and Kubik, 1952; in relation to *Sorex caecutiens* Laxmann — Snigirevskaja, l. c.

We find some mention of this subject in relation to *Neomys fodiens fodiens* Schreb. in the work by Dehnel (1950), and in relation to *N. f. bicolor* Shaw. in the publications by Price (1953).

The aim of this present publication is to review the opinions held up to the present on the problem of the sex-ratio in *Sorex a. araneus* L. and to re-analyse it on the basis of sufficiently comprehensive material. It would seem essential, in view of the heterogeneity of the material obtained by trapping, to pay attention to certain of the methods employed, and especially to the problem of the value of the results obtained to the investigation of the sex-ratio and the proportion of age groups in the population.

The results obtained from investigations by Borowski and Dehnel, l. c. on the seasonal variations in sex-ratio, and by Dehnel, 1949; Kubik, 1951; Dunajeva, 1955 and others on the proportion of mature and sexually inactive individuals of *S. araneus* L. formed the starting point for the investigations described here.

II. MATERIAL AND METHODS

The material analysed below includes 9241 specimens of *Sorex araneus araneus* L., caught in the Białowieża National Park over the period from 1949—1958. Until 1952 collection was carried out by the Białowieża branch of the Forestry Research Institute, and from July 1952 this work was continued by the Mammals Research Institute.

The material comes from the permanent or movable trapping areas of the Münster type. (Münster trapping area — 50 cylinders on a rectangular area of 250 m².) Zimmer cylinders were chiefly used as traps, also snap and live traps. In the permanent trapping areas the traps were kept in action over a period of several years, or at least for many months of the year (e. g. throughout the summer-autumn) in the same places. In 1955 and 1956 part of these areas were movable, i. e. moved every ten days to another place, in connection with the experiments being carried out on trapping methods for small mammals.

Specimens were preserved in alcohol or formalin and kept at Białowieża.

The sex of the shrews was identified by means of autopsy made by technical workers, and this was checked in nearly all cases by the author or by other scientific workers.

A general comparison of the whole of the material discussed is given in Table 1.

Table 1.

Comparison of material of *Sorex a. araneus* L., after division into years and months [1]).

Months	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	Total	♂	♀	♂ : ♀
I – II	29	14	1	1	–	7	64	61	95	78	350	181	169	1.12
III	2	1	2	–	2	17	36	43	7	7	117	56	61	0.92
IV	54	14	5	6	19	88	31	45	9	30	301	196	105	1.87
V	25	10	1	1	41	25	10	2	20	4	139	97	42	2.31
VI	237	82	13	22	323	269	299	33	73	21	1372	843	529	1.59
VII	560	147	20	51	467	604	638	35	143	64	2729	1393	1336	1.04
VIII	607	124	27	83	325	451	334	90	99	84	2224	1084	1140	0.95
IX	172	69	22	94	173	205	357	76	66	46	1280	603	677	0.89
X	51	25	2	45	27	58	73	23	15	19	338	155	183	0.85
XI –XII	35	13	2	18	17	37	160	21	67	21	391	189	202	0.94
Total	1772	499	95	321	1394	1761	2002	429	594	374	9241	4797	4444	1.079
% ad.	20.20	23.85	24.21	16.51	19.36	27.03	20.68	36.83	18.18	17.20	22.11			

[1]) Data relating to sex-ratio over the period 1949—1952 was published in part in the work by Borowski & Dehnel (1952).

The material was divided into two age-groups:

1) Young adult s. Dehnel (1949) — young animals, sexually immature, caught during the period from June to March of the following calendar year.

2) Old adult s. Dehnel (1949) — animals which had lived through the winter, sexually mature, caught in traps between April and November/December inclusively [2]).

III. SEX-RATIO IN YOUNG SHREWS

I have assumed that if it is possible to assess the proportions of both sexes in the case of shrews, on the basis of material provided by capture, then the most objective results are those obtained by an analysis of the material formed by young individuals, in the mass sexually immature (Borowski & Dehnel, 1952).

Table 2 illustrates the course followed by seasonal variations, and the annual fluctuations in the ratio of males to females over a period consisting of 11 life cycles of *Sorex a. araneus* L. (1948/9—1958/9).

The genetic system used consists in allocating to the upper part of the table the young individuals born in the given calendar year, and the old adults, originating from the previous group, and at present in the second calendar year of their lives, to the bottom part of the table (Dehnel, 1949). This arrangement of the material ensures continuity and correct succession in time of the various generations. The course taken by certain phenomena, which begin in the young ones and continue in the old adults, can as a result be both traced and analysed.

The ratio of males to females in the case of young shrews in the various years undergoes important changes from 0.64 to 1.18, while the variations appear to be cyclic in character. During the period from 1949 to 1951 the preponderance of females over males increased, which is correspondingly expressed by the sex-ratio, from 0.95 to 0.64. It is, of course, true that 1951 is not represented by sufficiently numerous material, nevertheless the previous two years clearly revealed this tendency. In 1952 ratios are suddenly evened out (ratio ♂ : ♀ = 1.08) and in the next years we can observe a preponderance of the males over the females. The next

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[2]) In cases exceptional for the Białowieża conditions, and also later i. e. in the third calendar year of their lives.

Table 2.

Ratio of males to females of *S. a. araneus* L. in the life cycles 1948/9—1958/9.

Age	Months		1948/49	1949/50	1950/51	1951/52	1952/53	1953/54	1954/55	1955/56	1956/57	1957/58	1958/59	1949–1958	♂♂	♀♀
YOUNG ADULT	VI			1.62	1.10	0.71	2.60	1.21	1.00	0.96	0.42	1.29	1.29	1.16	533	461
	VII			1.03	0.52	0.45	1.44	1.12	0.93	0.87	1.30	1.28	1.31	0.97	1214	1252
	VIII			0.75	0.62	1.00	1.09	1.17	0.94	0.91	1.06	0.91	0.74	0.88	868	984
	IX			1.00	0.68	0.23	0.82	1.12	1.25	0.95	0.97	1.60	0.90	0.99	465	469
	X			0.74	0.37	–	1.29	1.33	1.13	0.81	1.00	0.60	1.37	0.97	113	116
	XI – XII			0.56	0.67	–	0.50	1.50	2.09	0.83	0.89	1.21	2.17	0.99	176	178
	I – II		0.61	1.80	–	–	–	–	0.91	1.35	1.32	1.00		1.08	180	167
	Total		–	0.95	0.64	0.64	1.08	1.15	0.99	0.91	1.01	1.18	1.05	0.98		
	N	♂♂	11	682	142	28	139	605	667	756	157	251	120		3558	
		♀♀	18	717	223	44	128	526	674	830	148	216	114			3638
OLD ADULT	III		1.00	–	–	–	1.00	1.12	0.89	0.54	1.33	6.00		0.92	56	61
	IV		1.70	1.00	0.67	1.00	5.33	1.84	2.44	1.25	0.80	6.50		1.87	196	105
	V		4.00	4.00	–	–	8.50	2.12	1.50	1.00	1.86	1.00		2.84	88	31
	VI		4.90	3.75	–	3.00	11.65	7.64	4.31	4.33	2.60	1.51		5.52	320	58
	VII		3.00	0.58	3.00	2.50	2.12	3.67	1.19	5.00	12.00	–		2.13	179	84
	VIII		1.42	1.12	4.00	2.50	1.32	2.57	0.65	3.00	2.00	1.00		1.38	216	156
	IX		0.55	0.47	0.20	0.50	0.54	1.19	0.38	2.25	0.75	5.00		0.66	138	208
	X		0.80	0.08	–	0.50	0.20	0.37	1.67	2.50	0.75	–		0.63	42	67
	XI – XII		0.17	–	–	–	1.00	2.00	0.33	3.00	1.50	1.00		0.54	13	24
	Total		1.69	0.86	1.27	1.12	2.03	2.09	1.11	1.43	1.70	3.27		1.57		
	N	♂♂	221	55	14	28	181	322	218	93	68	49			1249	
		♀♀	137	64	11	25	89	154	196	65	40	15				796

decrease in the numbers of males falls in 1955 (0.91), but is not so considerable as in 1951. In 1957 we can again observe a considerable preponderance of males over females (1.18).

The years directly following the period of preponderance of the males (1954), and also before the next such period (1956) have, practically speaking, a sex-ratio of 1:1. Statistically significant deviations from this ratio (χ^2) were observed in the case of young ones from the 1950/51 and 1953/54 cycles. In 1951/52 and 1955/56 the values χ^2 are very close to the limit χ^2 for P = 0.05.

Attention should be paid to the fact that in the years of decided predominance of one sex over the other, this phenomenon in general occurs in all the months of the given year (of course, when the material is sufficiently numerous, as for instance in 1953 and 1957). The divergences from this statement visible in 1957 are rather to be explained by the small number of specimens caught in certain months, e. g. in October of this year only 8 shrews were caught in traps, and their sex-ratio 0.60 cannot be taken into consideration at all.

The differences in sex-ratio between the various years during the investigation period are statistically significant [3]).

From the summarised comparison in Table 2 (right side) it will be seen that from June to February inclusive, in general for the whole material, the ratio of males to females is expressed by the figure 0.98. We have here, therefore, a small and insignificant predominance of ♀♀, not deviating from the theoretical ratio of 1:1 (χ^2 = 0.889, while χ^2 for P = 0.05 is 3.841).

In the various months we find only slight variations in the sex-ratio, deviating to a very small extent only from the average value for the whole material. Only in June is it possible to observe a predominance of males over females (sex-ratio 1.16), which appears to be connected with the preponderance of this sex in the embryos of the common shrew, expressed by the ratio 1.27 (Mystkowska, in print). It is therefore possible that the June specimens, forming the first spring generation of young shrews not mingled

[3]) The calculated χ^2 = 36.131, while the extreme χ^2 for a probability of 0.05, with 21 degrees of freedom, is 32.671. This leads to the conclusion that the differences in the total sex-ratio between the years are statistically significant. The significance of the difference is maintained even with a probability P = 0.02.

with older specimens as is the case in other months, still maintains the same state of predominance of the males as is present in the embryo stage. This June predominance of males is visible in the various years, especially where the material from this month is sufficiently numerous.

The fact of the rapid regulation of the sex-ratio in the following months is not clear. Beginning in July we find only very insignificant deviations from the average for this age class. Young shrews are also born and leave the nest (= fall into traps) in the following months, up to and including October. The occurrence of the predominance of males in this one month is on this account incomprehensible. Further deliberations, in view of the lack of convincing factual material, would be pure speculation. It is only possible to presume that in the following months (summer-autumn) the preponderance of ♂♂ among the young shrews leaving the nest is equilibrated by the specimens already occupying the given area, or that they are born in different proportions than in the early spring.

The second case, far more difficult to explain, is the quite considerable preponderance of females noted in August. The sex-ratio in this month for the whole of the 10-year collection is expressed by the figure 0.88. The material was analysed statistically. The test of significance of the difference χ^2 showed that it is impossible to establish that differences between the sex-ratios of the various months, were significant [4]).

It should be added that both in June and in August, the deviations from the theoretical ratio of 1:1 are statistically significant. (In June χ^2 = 5.215, whereas in August it is 7.266, with an extreme value χ^2 for P = 0.05, with 1 degree of freedom equal to 3.481).

Despite this the constancy of occurrence over the period of 10 years of the maximum ratio of males to females in June would appear to be a real phenomenon. The value of this ratio in August reveals, slightly greater fluctuations.

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[4]) Calculated χ^2 = 12.88, while the extreme value χ^2 with probability P = 0.05 and 7 degrees of freedom is 14.067, and is therefore greater than the previous one.

IV. SEX-RATIO IN OLD ADULT SHREWS

I have previously drawn attention to the fact that material obtained from captures of shrews which had survived the winter does not permit of an objective assessment of the real sex-ratio. There are too many factors influencing captures for their effect to be decisive in this case. The very fact of the literally enormous seasonal variations in the ratio of males: females of from 0.54 to 5.52 must give rise to serious doubts on the part of the scientific worker (Table 2). It is of course impossible that the real sex proportions of any species of mammal could vary within such vast limits from month to month! (In the period from October — December there is a preponderance of females of over 40%, whereas in June there are as much as five times as many males as females).

In certain years the predominance of males over females in June may be as great as over 11 times as many. (In June 1953— 70 ♂ were caught as compared with 6 ♀). Similar jumps in numbers may also take place in other months, but they are then caused by the small number of specimens (cf. Table 1).

The biology of *Sorex araneus* L. explains these results. As is well-known, the period from April to June is that of the greatest reproductive intensity. The mating period takes place in April. The young are born in May, and the nursing females are almost always pregnant for the second time (T a r k o w s k i, 1957).

During the mating period the activity of the females, and particularly of the males, increases considerably as a consequence of their search for partners of the opposite sex, or in connection with the fights between males for the females etc.

This is undoubtedly the cause of the almost double predominance of males during this period. In the final stage of pregnancy, and especially after birth, the females of necessity become less active, as they have to look after the nest, keep the young ones warm and of course feed the usually very numerous litter — B o r o w s k i & D e h n e l (l. c.), T a r k o w s k i (l. c.). The females' wanderings at this time must be limited to a very small range, and these individuals cannot be caught in the permanent trapping area. This all disproportionately increases the predominance of the males in the calculated sex-ratio. This does not, however, take place at the expense of an increase in their activity, but as I presume, as a result of the diminished activity of the females during this period.

caught (October — December). Several factors contribute to the small number of males in this period, including a decrease in their activity as a consequence of the termination of their sexual activity, which ends earlier than with the females, and of the occurrence of physiological senile mortality. The activity of the females simultaneously increases in connection with the ending of the reproductive period.

In a summarised comparison of all old adults, the preponderance of the males is also marked, and is expressed by the figure 1.57.

I presume that the average annual values of the sex-ratio obtained from captures has some permanent relation to actual proportions, and furthermore that their fluctuations in the various years are a true phenomenon. The maximum and minimum ratios of males to females amongst old adults occur in the years following the same values of this ratio in young individuals. Thus, for instance, in the case of the young ones, the greatest preponderance of males is noted in 1953 and 1957, and in old adults, in 1954 and 1958, i. e. in these same generations (genetic cycles). This gives the impression that these variations take place over the same intervals of time as in the case of the young ones (every 4—5 years, if it is possible to judge on the basis of a 10-year period of observations. This dependence is illustrated by Fig. 1.

There are many theories which endeavour to explain the causes of the occurrence of cyclic variations of a similar character. The observation period was too short to permit of closer examination of this problem, apart from the mere recording of the fact itself. These fluctuations undoubtedly arise in connection with the periodic variations in population density of this species (1949 and 1953 were periods of mass appearance of shrews in the Białowieża National Park).

The mechanism giving rise to mass appearance of small insectivorous animals is undoubtedly different from that in the case of rodents (D e h n e l, in litteris). Without making a detailed analysis of this problem, I would however like to add certain observations in connection with Table 2. In the years preceding mass appearance of shrews a fairly considerable preponderance of males over females can be observed in the case of young shrews, which increases to 60—80 % in the case of old adults. It is possible, therefore, that this increases the probability of mating, especially at the end of sum-

mer and autumn, when, on account of the decreasing number of males, not all of the females are pregnant or nursing.

The preponderance in process of taking place of males over females may lead in the autumn to a greater number of the females being mated than usual. Under favourable conditions they may produce more numerous offspring than usual. This in turn after the young have survived the winter and reached sexual maturity, may become one of the causes of the mass appearance of these animals.

In a year of mass appearance the sex-ratios in the case of the young are reversed, i. e. females predominate (Table 2, years 1950—1952 and 1954—1956), or as in the case of old adults become equal (1950 and 1955). In general fluctuations in sex-ratio are more clearly visible in the case of animals which have lived through the winter, decreases are more violent, followed by periods of gradual increase in the preponderance of males until the next maximum.

Following up the above reasoning, it is possible to make certain predictions, i. e. in the summer of 1959 a considerable increase should be expected to take place in the population of *Sorex araneus* L. inhabiting the Białowieża National Park area, and indeed in this geographical region as a whole [5]). In 1960 a successive peak of mass appearance of *Sorex araneus* L. will probable be reached.

If we make a comparison of the material as a whole, without division into young animals, and old adults (Table 1), the conclusion can be reached that the ratio of males to females of *Sorex araneus* L. is expressed by the figures 1.08, i. e. that males form 52.4% of the total number. This result differs in a statistically significant manner from the theoretical sex-ratio 1:1 ($\chi^2 = 13.484$, while the extreme value $\chi^2 = 3.841$, for $P = 0.05$, with 1 degree of freedom).

The above data approximate most closely to the figures given by Brambell (1935), and probably by chance, are almost identical with Adam's results (1910). The considerable preponderance of males among the old adults exerts a basic influence on the total sex-ratio for the whole of the collection, and distorts the actual values.

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[5]) The recent disastrous years were also noted in Germany and England, which gives grounds for the assumption that these phenomena have a wide geographical range and are caused by factors which act uniformly over extensive areas.

V. PROPORTIONS OF AGE GROUPS

In the *Sorex araneus* L. population during the period from June to December, we encounter a considerable predominance of young individuals. The majority of the authors cited had previously confirmed this fact. Dehnel (1949) notes that in Białowieża the ratio of young animals to old adults is 3:1, Kubik (1951) at Puławy — 5:1, Borowski & Dehnel (l. c.) — 3.8 : 1. The results which I obtained are set out in Table 3.

At the end of March, and in April and May, 100% of the shrew population is formed by old adults (sexually mature). The first young ones do not begin to fall into the traps until the very end of May, or more usually, in the first ten days of June (Borowski & Dehnel, l. c.). From this time on the percentage of old adults, in relation to the whole population, and the group of young ones, varies depending on the month and the year of collection. The final column of Table 3 shows the percentage of old adults in the whole material obtained during the period June—February. In June these animals form about one-third of the numbers of *Sorex araneus* L. captured (27.55%). The percentage falls violently in July (9.64%), after which it rises in the following months to attain a second maximum in October (32.25%), and in November and December again decreases to the July level (9.46%).

While the reality of the value in percentage of old adults in the whole population for the various months and given year may well provide grounds for essential objections (too small a number of specimens), the summarised data for the 10-year period seem closer to reality.

Omitting the years in which a small number only was collected (1951—1952, 1958) and the autumn months, it should be stated that the percentage of old adults in the material obtained from collections made in the various months may vary from 5.00 to 48.48.

In the whole material from the period June—December distinguished on the whole by a sufficiently large number of shrews (8334 specimens), the animals which have lived through the winter (old adults) form 18.06%, that is, approximately $\frac{1}{6}$ of the total number collected.

If however we calculate the percentage of old adults in relation to the whole population, taking into account the spring months, we

Table 3.

Seasonal variation in percentage of old adults *Sorex a. araneus* L. in captures made over the years 1949—1958.

MONTHS	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1949-1958
June	24.90	23.17	7.69	18.18	23.53	35.32	24.43	48.48	24.66	23.81	27.55
July	10.00	12.92	20.00	13.73	5.35	10.93	8.93	34.29	9.09	6.25	9.64
August	12.36	13.71	18.52	16.87	20.00	16.63	25.75	17.78	15.15	4.76	16.73
September	36.05	31.89	27.27	12.77	31.21	39.51	21.29	17.11	21.21	13.04	27.03
October	35.29	56.00	50.00	13.04	22.21	44.83	32.88	30.43	46.67	-	32.25
November December	20.00	23.08	-	16.67	11.76	8.11	5.00	19.05	7.46	9.52	9.46
Total /VI - XII/	16.67	20.43	19.77	14.70	17.12	21.30	18.05	24.46	15.55	8.23	18.06
n ad.	277	94	17	46	228	346	336	68	72	21	1505
n iuv.	1385	366	69	267	1104	1278	1525	210	391	234	6829

obtain higher results. Table 1 and fig. 2 illustrate these data. It will be seen from these that the fluctuations over a period of several years not only take place on a different level, but reveal a slightly greater amplitude. The percentage of old adults in the whole collec-

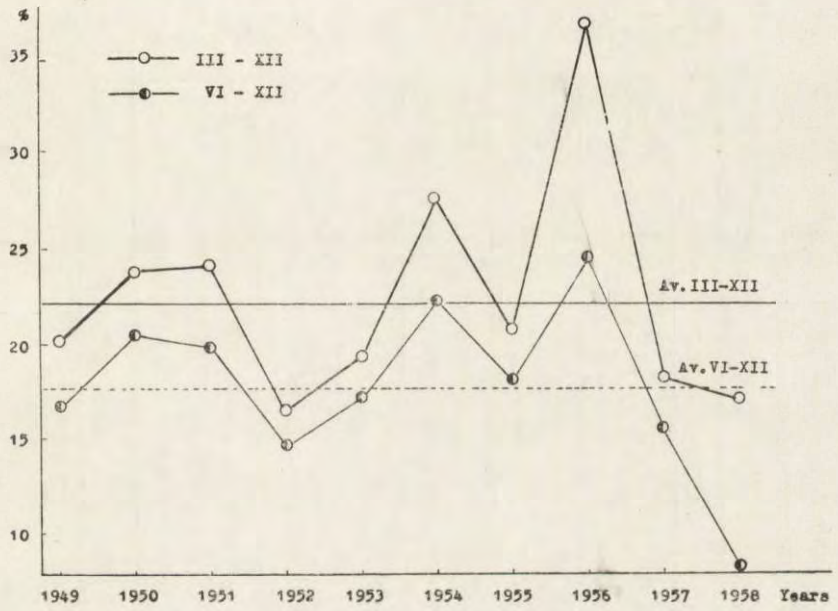

Fig. 2. Variability in percentage of old adult shrews in captures.

tion is 22.11, which corresponds to the ratio of young to old adults as 3.5:1.

These results are on the whole in agreement with those obtained by Borowski & Dehnel (l. c.) but differ from the figures obtained by Kubik (1951).

The results obtained by Dunajeva (l. c.) for a fairly numerous collection more or less agree with the calculated total percentage of old adults in the captures made at Białowieża in the June—December period, since she obtained 16.9% of these animals. This result is undoubtedly caused by making the collection over the period from May to September. As is well-kown, captures of shrews in May yield very scanty results, and the collection made during the months June—September are decisively important here.

The results discussed above bear witness only to the percentage of old adults among the animals captured, and not to their actual

Table 4.

Percentage of old adults (males and females) in captures of *Sorex araneus araneus* L.

MONTHS	SEX	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1949–1958
VI	♂♂	20.68	18.29	7.69	13.64	21.76	31.23	23.08	39.39	17.81	14.29	23.32
	♀♀	4.22	4.88	–	4.55	1.86	4.09	5.35	9.09	6.85	9.52	4.23
VII	♂♂	7.50	4.76	15.00	9.80	3.64	7.95	4.86	28.57	8.39	6.26	6.56
	♀♀	2.50	8.16	5.00	3.92	1.71	2.98	4.08	5.71	0.70	–	3.08
VIII	♂♂	7.50	7.26	14.81	12.05	11.38	11.79	10.18	13.33	10.10	2.38	9.71
	♀♀	5.11	6.45	3.70	4.82	8.62	4.66	15.57	4.44	5.05	2.38	7.01
IX	♂♂	12.79	10.14	4.54	4.26	10.98	21.46	5.88	11.88	9.09	10.87	10.78
	♀♀	23.26	21.74	22.73	8.51	20.23	18.05	15.41	5.26	12.12	2.17	16.25
X	♂♂	15.69	4.00	–	4.44	3.70	12.07	20.55	21.74	20.00	–	12.43
	♀♀	19.60	52.00	–	8.89	18.51	32.76	12.33	8.70	26.67	–	19.82
XI–XII	♂♂	2.86	–	–	–	5.88	5.40	1.25	14.29	4.88	4.76	3.32
	♀♀	17.14	23.08	–	16.67	5.88	2.70	3.75	4.76	2.99	4.76	6.14
n ad.		277	94	17	46	228	346	336	68	72	21	1505

numbers in the area. Such great fluctuations occurring from month to month are impossible. It is true that some disaster may take place which diminishes this percentage by 3 times as much, but no reverse phenomenon can take place which would cause the number of old adults to increase by 3—4 times over the course of one month!

The causes of the above phenomenon should probably be sought for in the differences between the activity of young shrews and old adults, and also in the variations of activity of old adults, depending on their sexual activity. The data given in Table 4 throw some light on this problem, since the percentages of male and female old adults are shown here separately, divided according to month and year. From the summarised comparison it is possible to ascertain how the influence of males and females on the high percentage of old adults in the captures. Thus in June male shrews form 23% of the 27% of old adults, while in October a greater percentage of females is caught (almost 20 out of 32%).

The percentage of old adults for the June—December period over a period of 10 years reveals fluctuations of from 8.23 to 24.46%, and in relation to the whole population — from 16.51 to 36.83% (Tables 1 and 3).

From the enclosed diagram (fig. 2) it will be seen that there is a high correlation, in a two-fold manner, between the values of the calculated percentage of old adults and that curves of their variation follow almost parallel courses.

While taking into account the relativity of figures, the variations in the percentage of old adults in the various years should, however, be considered as really existent, and undoubtedly connected with the population dynamics of *Sorex araneus* L.

VI. DISCUSSION OF RESULTS

a. Remarks on trapping methods

I have more than once emphasised above that my reasonings refer only to the ratio of both sexes and proportions of age groups in the material obtained by trapping [6]).

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[6]) As a footnote I would add that not only are the data obtained by the most varied trapping methods incapable of reflecting the actual state of the animals, but also the material obtained from the pellets of owls, and from analysis of the stomach contents of larger mammals (**Nasimovič** et al., 1948).

Many authors [5]) are aware of the possibilities of modification of actual ratios in an area where unsuitable capture methods are used, and have clearly emphasised this in their publications (Kučeruk & Dunajeva, 1948; Nasimovič et al., l. c.; Wasilewski, 1952, 1956; Beer et al., 1958; Sealander & James, 1958). Others, however, give no opinion on this subject at all, although they record a certain sex-ratio in the species examined.

Their data are often uncritically cited by authors of compilatory works (e. g. Teplov, 1948) who, on this basis, may draw often far-reaching conclusions of very doubtful value.

It seems to me that on the basis of the trapping methods in general use (Zimmer cylinder, snap and live traps of all kinds, etc.) it will be very difficult to give a correct reply as to the numerical sex-ratios or proportions of age groups in a population. For such purposes the method consisting in catching a whole colony of small mammals inhabiting a defined and sufficiently large area, would appear to be more useful and correct. Results closer to the truth are also obtainable from excavation of the nest as was done by Maksimov (1948). It would not seem, however, contrary to the statement made by the above author, that the results so obtained gave 100% guarantee of truth, although they come very close to this. Depending on the mating season, the time of year, bioclimatic conditions prevailing, wanderings of part of the population, the real number of occupants of the nests (families, colonies) may vary, which then is clearly apparent in the results obtained by this method.

The case is completely different as regards animals bred in captivity (Žegalov, 1950). If we assume that artificial breeding conditions are the same, or closely approach, conditions in a natural environment (I personally consider this as problematical for the majority of mammals except domestic ones), we may consider the numerical results on sex-ratio in the animals investigated with a cer-

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[5]) It appears from the enclosed list of references that authors have several times tried to solve the problem of sex-ratio in species which they have investigated, and have given their works widely differing titles. It is therefore quite impossible to trace all notes on this subject. For this reason, apart from literature on the subject to which I had access, I have only cited a few works as examples in which there is a greater or smaller amount of material devoted to the problem of sex-ratio in mammals of other species.

tain degree of confidence. On the other hand it is known that the influence of domestication, on the fertility and heredity of sex may be very considerable. (Jointly with the action on metabolism and bio-physiological and biochemical properties of the organisms examined from the point of view of feeding, climatic and other conditions, — Schröder, 1956).

It should also be emphasised that, in general, in investigation of sex-ratio it is essential to base the work on comprehensive series of material, if possible obtained from all the months and seasons over a period of several years, and also from the full life cycles of the animals examined. It seems to me to be of great significance on account of the variability of sex-ratio and age groups depending on the season and year, which is demonstrated in this publication. This has been described by other authors in respect of several other species. Żegalov's (1950) statement that the sex-ratio is not subject to the law of great numbers would appear to be unfounded. There are, of course, individuals (examples among domestic animals) with special hereditary tendency to transmit offspring of one sex (among others, McWhirter, 1956). This may even be repeated regularly in a series of successive litters. This fact does not, however, solve the problem completely, and single litters are not sufficiently decisive here to make it possible to form an opinion on the actual sex-ratio in a given species.

b. The influence of activity and age on sex-ratio

With the majority of mammals, as is well-known, we encounter a preponderance of males over females. This applied at least to the population of young individuals, populations in nests or embryos (the so-called secondary and tertiary sex-ratio). The primary sex-ratio, over the course of the whole life cycle, undergoes far-reaching changes depending on a great number of factors (Parkes, 1927; Crew, 1952, and many others).

Different sex-ratios, depending on the age class of *Sorex araneus* L. were confirmed by many authors (Brambell, 1935; Snigirevskaja, 1947; Dehnel, 1949; Kubik, 1951; Borowski & Dehnel, 1952; Stein, 1953; Teplov, 1954; Dunajeva, 1955; Pelikán, 1955).

Snigirevskaja finds 29% ♂♂ among young shrews, and 67% ♂♂ (n = 1583) in the case of adults. Teplov also records somewhat strange ratios in his rather scanty collection, i. e. 61% ♂♂ among young shrews and 54% ♂♂ among adults. These figures do not agree with the ones reported above. If, however, these authors' data for adult specimens (or as I call them, old adults) can be explained in the light of the biology of shrews, this great preponderence of one sex over the other among the young (i. e. sexually immature, Z. P.) animals would seem to be highly problematical. Snigirevskaja's work has been strongly criticised by Dunajeva (1955), who asserts that Snigirevskaja made many errors in her methods. These could also be the cause of these strange sex-ratios. Not knowing the original work by Snigirevskaja and her methods of differentiating between „young" and „adult", it would be difficult to judge whether the results obtained are correct.

Dehnel (1949) treats not only the data given by Brambell (1935); Stein (1938) and others very critically, but even his own data on the preponderance of males over female shrews.

Stein (1953) also takes a very critical view of methodical problems.

My data on the sex-ratio of young shrews correspond very closely to the results obtained by Dunajeva (1955) in numerous material (n = 2458) from the Moscow district. This ratio is therefore close to unity, and does not differ statistically from this value. From her tables differences are, however, revealed between the various months, which come within the limits of from 47.6 to 56.2 per cent of males. The authoress in addition finds seasonal differences in the sex-ratios of old adults which had, in fact, been observed earlier by other authors (Dehnel, 1949; Peliká n, 1955).

From several works on the related species — *Sorex minutus* L. — it appears that we are concerned here with an even greater preponderance of males in th whole collection than in the case of *Sorex araneus* L. (Brambell & Hall, 1936; Dehnel, 1949; Kubik, 1951).

With *Sorex caecutiens* Laxmann, as is stated by Snigirevskaja (1947) we have 83 per cent. of males among the young animals, and correspondingly for the adult animals 46 per cent.

The problem of differences in sex-ratios depending on the age group of other species of mammals has engaged the attention of many authors (Parkes, 1927). It is course impossible to give them all here, but I have given a few only of the publications of recent years as examples, e. g. for *Microtus arvalis* Pallas we have Maksimov's (1948), Stein's (1953) and

Pecker's (1958) data; for *Rattus norvegicus* Berk. — Schein (1950), Leslie et al. (1952); for *Castor* sp. — Osborn (1953) and many other authors; for the Muskrat — Reeves & Wiliams (1956). Shorten (1954) dealt with this problem in connection with *Sciurus carolinensis;* and Kubik (1952) with *Sicista betulina* Pallas. We have Wasilewski's data for certain *Microtinae* (1952, 1956). Stein (1953) gives the sex-ratio in the various age groups of many Central European species of *Microtinae*, genus *Apodemus* Melch., *Sorex* L. and *Talpa* L., and Beer et al. (1958) for the American species of small rodents (*Microtinae* and *Zapus* Coues.

An analysis of the sex-ratio within the various age groups is essential in view of the far-reaching differences in the activity of both sexes amongst sexually mature and immature individuals. Sexual activity of shrews (as in the case of other small mammals) has a decisive influence on the quantitative result of captures. Depending on the physiological state of sexually mature individuals (mating period, care and feeding of the young) their activity will be subject to variations, and therefore the probability of their falling into traps will also differ. According to the above, drawing conclusions as to the sex-ratios of the majority of species of small sexually active mammals, on the basis of material obtained by capture, in fact never affords complete certainty that it agrees with the actual ratios in the given area. In the case of certain species, data closer to the actual facts may be obtained from an analysis of the population during the period of the winter cessation of activity of the gonads.

Generally speaking, we find that the young individuals of *Sorex araneus* L. do not reach sexual maturity in the first calendar year of their life. It may therefore be assumed (Borowski & Dehnel, 1952) that during the period from June to March the population is ± homogeneous from the standpoint of sexual activity. It follows that the material captured by the cylinder or trap methods (the standard bait, if it acts at all on shrews, acts uniformly on both sexes) should be sufficiently representative to permit of drawing conclusions as to the real sex-ratios in a given area. My reasonings have been based on this assumption.

The quantitative composition of the various age groups is subject to seasonal variations (Table 3). This involves the necessity for making collections over a lengthy period, over several successive seasons and years. In material captured on a small scale and in selected periods (usually spring-summer) wide deviations from significant sex-ratios can be found. For instance, in the spring when 100% of the population forms one age group of sexually active

shrews, captures reveal an almost double preponderance of males over females, which does not, of course, agree with the actual sex-ratios of this species.

c. Seasonal variations in the sex-ratio

Seasonal variations in the sex-ratio of *Sorex araneus* L. were demonstrated by Brambell (1935) and of *Sorex minutus* L. — Brambell & Hall (1936). These authors found a considerable increase in the preponderance of males over females in April and May. It is now known that this is caused by the increasing activities of the animals (especially males) during this period, on account of the mating season. For this reason sex-ratios in material from captures made during this period may vary greatly (cf. Table 2).

Borowski & Dehnel (l. c.) have now, however, established the problem of seasonal variations in sex-ratio on a proper footing. These authors, despite the fact that the material at their disposal was insufficiently comprehensive, demonstrated the existence of variations in sex-ratio in the various months. Stein (1953) and Pelikán (1959) also approach this problem from the point of view of seasonal variations, especially when analysing the sex-ratio of *M. arvalis* Pallas. Stein's data on *Sorex araneus* L. (Table 2 in his work) reveal certain differences in sex-ratios in the various seasons, and in successive years. A general feature of the whole collection of this author is the unexplained and considerable preponderance of males over females in the case of young animals (males form 55.50%; n = 582). Stein's data for old adults for the period from April to September are in close agreement with my corresponding results. The sex-ratio for old adults from Germany is 1.99. At Białowieża from April to August inclusively, the average ratio is expressed by the value 2.07. September is a month of considerable preponderance of females, and if included in these calculations, causes a decrease in the sex-ratio to 1.62.

Similar seasonal variations of sex-ratio of the common shrews are also shown in the data given by Becker (1955), Dunajeva (1955) and Pelikán (1955).

A summarised comparison of all young shrews for each particular month (Table 2) reveals the interesting fact that there is a considerable predominance of males in June and females in August.

Although the August preponderance of females, greater than in other months, is not statistically significant, it would seem that it has same connection with the strange turning point in many physiological processes which is apparent in July, to which Borowski & Dehnel (1952) drew attention, and which is so far unexplained. During this period a transitory deterioration in the condition of the shrews can be observed. The involution processes of the thymus (Bazan, 1952) are intensively apparent. From July onwards it is possible to observe the phenomenon of the resorption of the bones of the brain-case, leading to a flattening of the skull for the winter period (Pucek, 1955; 1957). The capacity of the brain-case begins sharply to decrease, and in particular the weight and volume of the brain (Cabon, 1957; Bielak, in manuscript).

No special changes have so far been observed in the life environment of shrews which could evoke or explain these far-reaching changes.

Exceptionally in August, a preponderance of females over males (Mystkowska, in press) was found in a sufficiently extensive series of embryos of shrews, which agrees with the same ratios in young animals obtained from the area. It is therefore possible that the unexplained causes discussed above act on the developing embryos in July and August, and also on the shrews still in the nest, which exactly in August begin to fall into the traps. This of course is only a supposition which requires working out in detail and checking by means of actual material, and in particular, a full analysis of the environmental conditions of shrews in July.

Seasonal variations in sex-ratio in other species have several times been emphasised by many authors. Many of earlier works are cited by Parkes (1927). Price (1953) draws attention to this in the case of *N. fodiens bicolor* Shaw. The results obtained by Maksimov (1948) on the seasonal and cyclic variations in the sex-ratio of *Microtus arvalis* Pallas, which are repeated in the various years, are very interesting. We have a certain amount of data on this subject in the works by Crew (1952), Reichstein (1956), Frank (1957), Beer et al. (1958).

To sum up, it should be stated that seasonal variations in sex-ratio amongst captured mammals are to a great extent caused by the different acivity of each particular age group in both sexes. This activity is dependent in the first place on reproduction processes. Certain variations can also be caused by factors which alter from season to season and from year to year, the population dynamics of the given species. The conclusion must therefore be reached that

the results closest to reality as regards the sex-ratio can be obtained by capturing sexually immature animals (Borowski & Dehnel, 1952), of from animals during the period of winter suspension of gonad activity.

d. Sex-ratio as the expression of regulation phenomena in the population

Variations in sex-ratio may be treated as the expression of specific regulating phenomena of biological importance to the species. It would seem appropriate that under conditions specially unfavourable to the species it saves itself by increasing the preponderance of females over males. On the other hand reverse ratios are observed during periods of mass increase and overcrowding of the population (Maksimov, 1948; Stein, 1953; Reichstein, 1956).

Regulation of the ratics of both sexes reaches as far as the moment of fertilisation, expresing itself in a non-uniform power of transmitting sex to offspring by means of the sex elements produced by both parents (Żegalov, 1950). Further, a regulating influence may be exercised by the different mortality in both sexes during the pre- and post-implantation period (Lindahl & Sundell, 1958; Crew, 1952) in young and adult individuals, brought about by both physiological and pathological causes (Kučeruk & Dunajeva, 1948; Maksimov, 1948; Żarkov, 1957; Mertc, 1957; Stein, 1957).

Sex-ratio is also dependent on the size of the litter (Żegalov, l. c.).

All the above is not without significance to the population dynamics of the species.

The influence of pathological mortality (infections) on both sexes can be manifested in different ways in the various age groups, which may be caused by their varying activity [8]).

I therefore consider that the methods used to obtain material (captures, collection of dead animals etc.) (Kučeruk & Dunajeva, l. c.) do not give true results of the sex-ratio in animals infected by epizooty. It is not therefore advisable to draw conclusions from this material as to the greater or lesser mortality of one of the sexes.

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[8]) It is somewhat difficult to establish the mortality rate not occurring during a period of mass appearance, since the diseased animals usually hide in their holes and die there.

As in the case of shrews, we encounter in many other species a wide divergence in sex proportion in embryos and foeti, and also in young shrews in their nests after birth (W r a n g e l, 1939; P e r r y, 1945; S t e i n, 1957 etc.). As the animals age, these proportions either more or less quickly undergo very significant changes, establishing themselves in the various age groups of the given species on a definite level, varying in accordance with the successive life cycles through which they pass.

The fluctuations in sex-ratio shown above in each separate year are undoubtedly an expression of the variations in the population dynamics of *Sorex araneus* L. in the area investigated. A certain light is thrown on this problem by the curve of the number of shrews caught on the parmarent collection surface (Fig. 1). Independently of the objections raised above, this must be in some way related to the number of animals in the area. Unfortunately my data are not complete, and it was impossible to make an analysis of the whole period from this point of view. The matter is also complicated by the complete absence of any data on the genesis of the mass appearance of shrews, and on the turning point in their numbers. This hiatus seriously hinders a thorough examination of the problem of the quantitative ratio of both sexes.

VII. SUMMARY

Examination was made of 9241 specimens of *Sorex araneus araneus* L. obtained from captures made in the M ü n s t e r type permanent trapping areas in the Białowieża National Park during the years 1949—1958 (Table 1). The total sex-ratio for the whole material is 1.079 (= 51.90 % ♂ ♂ and differs statistically significant from the theoretical ratio 1:1 (χ^2).

The most accurate possible sex-ratios obtained from captures of young sexually immature animals, in which activity of males and females is ± uniform (Table 2 — 0.98). χ^2 does not permit of establishing the reality of the deviations from the ratio 1:1.

In the total material obtained over a period of 10 years the highest sex-ratio for young animals is to be observed in June, directly after they leave the nest (1.16). In August exceptionally, a considerable preponderance of females is found (0.88). There are statistically significant differences between these values and the theoretical ra-

tio. In the remaining months the deviations from the average sex-ratios for all the young animals are slight and not significant.

The differences in the sex-ratio in the various months (young animals from June to February) are not statistically significant (χ^2), nevertheless the preponderance of males in June and females in August would appear to be a regular phenomenon.

The sex-ratio of old adults is subject to wide seasonal fluctuations as a result of the variable acitvity of both sexes, especially in connection with the mating season, nursing and care of the young. We find the extreme values of this ratio in June — 5.52 and in November — 0.54.

The ratio of males to females reveals variations over the period of successive years (in the case of young animals from 0.64 to 1.18). Years in which one sex predominates over the other are repeated in a cycle (Fig. 1). Extreme values do not deviate in all of the years to a statistically significant extent from the theoretical ratio of 1:1.

Analogical variations in sex-ratio in young animals and old adults are undoubtedly connected wih the population dynamics of *Sorex araneus* L. Sex-ratio may be regarded as the expression of regulating pheromena which are of biological importance to the species.

Old adults form 22.11% of the total material, which corresponds to a ratio of young to old equal to 3.5:1 (Table 1). During the period from June to February inclusively the old adults form 18.06% of the collection. The percentage of old adults (which decide the reproduction of *Sorex araneus* L.) is subject to seasonal fluctuations in captures depending on the activity of both sexes (of from 9% in July and in November to 32% in October). The high percentage of old adults in captures made in the spring and summer is chiefly caused by the males, and in the autumn the majority of this age group are females.

The percentage of old adults in captures is subject to variations in different years (from 16.51% in 1952 to 36.83 in 1956). These fluctuatiors have an undoubted connection with the actual ratios in the area, and are probably connected with the population dynamics of *Sorex araneus* L.

Attention is drawn to the influence of capture methods, of the activity of the animals caused by age, and state of sexual maturity, mating, nursing and care of the young etc. and of other factors on

the sex-ratio and proportions of age groups in the material obtained from captures made on the permanent trapping areas.

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STRESZCZENIE

Przebadano 9241 okazów *Sorex araneus araneus* L. pochodzących z odłowów na stałych powierzchniach typu Münstera, na terenie Białowieskiego Parku Narodowego w latach 1949—1958 (Tabela 1). Ogólny stosunek płci dla całego materiału wynosi 1.079 (=51.90% ♂♂) i statystycznie istotnie różni się od teoretycznego stosunku 1:1 (χ^2).

Możliwie najbardziej objektywne proporcje płci uzyskuje się w odłowach okazów młodych, płciowo niedojrzałych, u których aktywność samców i samic jest ± jednakowa (Tabela 2 — 0.98). χ^2 nie pozwala na stwierdzenie istotności odchyleń od stosunku 1:1.

W całości materiału z 10 lat, najwyższy stosunek płci u młodych obserwuje się w czerwcu, zaraz po wyjściu z gniazda (1.16). W sierpniu wyjątkowo stwierdza się znaczną przewagę samic (0.88). Wartości te statystycznie istotnie różnią się od stosunku teoretycznego. W pozostałych miesiącach odchylenia od przeciętnego stosunku płci dla wszystkich młodych są niewielkie i nieistotne.

Różnice stosunku płci w poszczególnych miesiącach (młode od czerwca do lutego) nie są istotne (χ^2), tym niemniej przewaga samców w czerwcu a samic w sierpniu wydają się zjawiskiem prawidłowym (Tabela 2).

Stosunek płci przezimków ulega dużym sezonowym wahaniom uwarunkowanym zmienną aktywnością obu płci, przede wszystkim w związku z rują, karmieniem i wychowywaniem młodych. Skrajne wartości tego stosunku znajdujemy w czerwcu — 5.52 i w listopadzie — 0.54.

Stosunek samców do samic wykazuje zmiany w ciągu następujących po sobie lat (u młodych od 0.64 do 1.18), przy czym lata przewagi jednej płci nad drugą powtarzają się cyklicznie (Ryc. 1). Skrajne wartości nie we wszystkich latach statystycznie istotnie odchylają się od teoretycznego stosunku 1:1.

Stwierdza się analogiczne zmiany stosunku płci u przezimków (roczne wahania od 0.86 do 3.37).

Wahania stosunku płci u młodych i przezimków mają niewątpliwie związek z dynamiką populacji *Sorex araneus* L. Stosunek płci można rozpatrywać jako wyraz zjawisk regulacyjnych, biologicznie ważnych dla gatunku.

W całym materiale przezimki stanowią 22.11% co odpowiada stosunkowi młodych do przezimków równemu 3.5:1 (Tabela 1). W okresie zaś od czerwca do lutego włącznie przezimki stanowią 18.06% zbioru. Procentowy udział przezimków (decydujących o rozmnażaniu się *Sorex araneus* L.) ulega sezonowym wahaniom w odłowach w zależności od stopnia aktywności obu płci (od 9% w lipcu i w listopadzie do 32% w październiku). Wysoki procent prze-

zimków w odłowach wiosną i latem powodują głównie samce, jesienią zaś większość tej grupy wiekowej stanowią samice (Tabele 3 i 4).

Udział procentowy przezimków w odłowach ulega zmianom w poszczególnych latach (od 16.51% w roku 1952 do 36.83% w roku 1956) — (Tabela 1. Wahania te niewątpliwie pozostają w jakimś odniesieniu do rzeczywistych proporcji w terenie i prawdopodobnie są związane z dynamiką populacji *Sorex araneus* L.

Zwraca się uwagę na wpływ metodyki odłowu, aktywności zwierząt powodowanej wiekiem, stanem dojrzałości płciowej, rują, karmieniem i wychowywaniem młodych itp. czynników na stosunek płci i proporcje grup wiekowych w materiale, uzyskiwanym z odłowów na stałych powierzchniach pułapkowych.

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