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**Food Composition and Reproduction
of *Sorex araneus* Linnaeus, 1758
in the Light of Parasitological Research**

**Skład pokarmu oraz rozród *Sorex araneus* Linnaeus, 1758
w świetle badań parazytologicznych**

[With 11 Figs. and 4 Tables]

I. INTRODUCTION

Classical parasitological research carried out in the sphere of morphology, systematics and faunistics, aimed at obtaining an exact knowledge of the parasitofauna of a given area, or of a given species of host, was of cognitive value chiefly on account of the knowledge itself of the parasites. Investigations of the biology of parasites, however, the tracing of their individual and specific variations, discovery of the life cycles, the taking into consideration of phenological dynamics in close connection with the habitat of the first and second order, and finally the introduction into methods of parasitological research of biochemistry, ecology, cyto- and histology etc. — has gradually formed from the knowledge obtained about parasites a scientific discipline with many trends and many planes. In consequence this has led not only to an all-round knowledge of different groups of parasites, but will also affect access to other fields of natural science, facilitating an understanding of and documentation of a large number of general biological regularities.

An example, and simultaneously a proof of such possibilities, is the application of data from parasitology to drawing conclusions on the evolution of the animal world (Michajłow, 1960).

It would seem that research based on suitable methods in the sphere of parasitology may contribute to a better knowledge of the biology,

etology and ecology of animals playing, in relation to parasites, the role of intermediate and final hosts. This is possible when parasitological research grasps the phenomena and processes observed from the aspect of synecology, if it treats the parasite as one of the components of the given biocenosis.

On the basis of the literature available it may be concluded that parasitological research has not so far been utilised by theriologists, although — as we have endeavoured to show in this study — it can often both confirm facts already known or hypotheses as to the biology of defined groups of mammals (in our particular case — *Soricidae*), and also throw a new light on these problems.

In the present study an attempt has been made to interpret certain results of parasitological research (on *Cestoda* and *Trematoda* from *Sorex araneus*), from the aspect of their usefulness in theriology.

The chief problem which we intend to consider, on the basis of parasitological data, is the question of the food of the shrew, and certain questions from the reproduction biology of these mammals.

The material interpreted, both theriological and parasitological, was obtained from the Białowieża National Park (B.N.P.), from collections in the Mammals Research Institute of the Polish Academy of Sciences, situated in this area. Numerous investigations have been made in this Institute in the field of the occurrence and biology of small insectivorous mammals. Parasitological research was carried out in B.N.P. by: Sołtys, 1952; 1954; Kisielewska, 1958 a; b; 1959; 1960 a; b; 1961, and Pojmańska, 1959; 1961.

It must be emphasised that the fact of certain parallelisms (as regards place, and sometimes also time) of the parasitological and theriological investigations made undoubtedly contributes to increasing the probability and definiteness of the conclusions reached in the further part of this study.

II. FOOD OF *S. ARANEUS*

On the basis of the publications to which I had access on the subject of the food of the shrew and other representatives of *Soricidae*, it is possible to distinguish between two trends in research from the aspect of the methods used.

The first of these is the experimental trend. Conclusions as to the food of shrews were reached in this case on the basis of the feeding of these animals with different kinds of food under laboratory conditions (Tupikova, 1949; Borowski & Dehnel, 1952; Rozmus, 1961; Hawkins & Jewell, 1962). The authors gave the shrews various invertebrates (snails, insects, earthworms etc.) and vertebrates (small frogs, young rodents). The authors decided, from the degree of ability

displayed in attacking and overpowering these animals by the shrews, and from their eagerness or otherwise to eat them, which of them probably constituted the natural food of the shrew.

These data, although supplying much information, cannot reflect accurately what happens under field conditions. When interpreting results of this kind it is essential to take into consideration corrections as to the possibilities of escape, limited by the cage, of the animals attacked. In effect, an animal attacked and eaten by the shrew in a small cage may in the open be difficult to catch (e.g. the quickly running insects of the *Carabidae* group). Thus the data obtained from the experiments referred to supply evidence only of the multi- or even omnivorousness of the shrew, but do not give a cross-section of what this mammal eats at different periods of its life and at different times of the year, what, and when, is the predominating component of its food and what it feeds on in defined biotopes differing from each other as to the quality and quantity of the composition of invertebrate fauna.

The second trend in research on the food of shrews is represented by, *inter alia*, the studies by Pelikan (1955), Mezherin (1958) and Lapin (1961). These authors examined the stomach contents of the shrew and other representatives of *Soricidae* from areas in Czechoslovakia and the Soviet Union, caught in consecutive months of the year. This type of research gives a good chance of grasping the problem of the food of the shrew from the phenological aspect. Shrews, however, digest food very quickly, and as a result a certain percentage of the stomachs examined contained only a pulpy or granulous mass. In such cases identification of the food consumed proves difficult, especially if the specimens examined did not possess well formed skeletal elements (e.g. the larvae of insects, earthworms, shell-less snails).

A fairly important — as it seems — contribution to a knowledge of the composition of shrews' food and the seasonal variations occurring in it may be afforded by parasitological research on the development cycles of certain parasites. Data on biohelminths (*Cestoda*, *Trematoda*), that is, parasites which develop with the participation of an intermediate host, may be particularly instructive here. The larvae of biohelminths living in an intermediate host reach the definitive host by means of the food chain connecting both of the above groups of hosts. Therefore — in our particular case — the presence in shrews of defined species of biohelminths, where the ways taken by the cycle (that is the successive habitats of the egg — larvae — mature form), may serve as indirect evidence of the quality, and even of the quantity, of the composition of the food of these mammals.

1. Qualitative composition of the food of *S. araneus*

Research was carried out in the B.N.P. from 1953 to 1958 on the development cycles of tapeworms (Kisielewska, 1958 a; b; 1959; 1960 a; b) and trematodes (Pojmańska, 1959; 1961) of the Common Shrew, and on the dynamics of the occurrence of the different species of these parasites during the yearly cycles (Kisielewska, 1961; Pojmańska, 1961).

A complete list of the species of tapeworms and trematodes occurring in *S. araneus* in the B.N.P. and the species of intermediate hosts so far identified, are given in table 1.

As shown by the above table, the menu of the shrews living in B.N.P. contains representatives of at least three groups of invertebrates: *Insecta*, *Myriapoda*, *Gastropoda*. This indicates an already known fact, that is, the multivorousness of shrews.

On the basis of the materials in our possession (helminthological dissection of 2030 shrews during a period of 5 years), criteria were formed, which would serve to define in a more detailed way not only the quality of the shrews' food in general, but also the variations in the diet of these mammals at different periods of their lives, and at different times of the year.

These criteria are as follows:

1. The extensivity of infection of the shrews by different species of parasites,
2. Variations in the extensivity of infection of the shrews by different species of parasites depending on the age of the mammals and the season of the year. Mass occurrence (constant, or periodic) of a certain species of parasite in the shrews proves that its intermediate host — an invertebrate, forms a common and frequent food of these mammals. Contrarily — if the parasite occurs rarely (slight extensiveness) its intermediate host must form more sporadic food for the shrews. It is necessary here to take into consideration the abundance of occurrence of the given species of invertebrate in the area, and the degree of its infection by parasite larvae. These aspects will be borne in mind in discussing definite examples.
3. The degree of advancement in development of the parasites encountered during dissection. The presence of adult parasites is only evidence that invasion did in fact take place, but it is difficult to define the time of its existence with any degree of accuracy. If, however, dissection of the shrews reveals the presence of juvenile forms of *Cestoda* or *Trematoda*, this is evidence that at that very time, during that period,

Table 1.

Species of *Cestoda* (after Kisielewska, 1961) and *Trematoda* (after Pojmańska, 1961) occurring in the shrew in the B.N.P., and a list of their intermediate hosts.

Group and species of parasite	Group and species of intermediate host
<i>Cestoda</i>	
<i>Staphylocystis furcata</i> (Stieda, 1862) Spassky, 1950	<i>Geotrupes stercorosus</i> (S.c.) <i>Insecta</i>
	<i>Pterostichus vulgaris</i> L. "
<i>Soricinia diaphana</i> (Cholodkovsky, 1906) Żarnowski, 1955	<i>Geotrupes stercorosus</i> (S.c.) "
<i>Neoskrjabinolepis singularis</i> (Cholodkovsky, 1912) Spassky, 1954	<i>Catops</i> sp. "
<i>Pseudodiorchis prolifer</i> (Villot, 1890) Kisielewska, 1960	<i>Glomeris connexa</i> Latz. <i>Myriapoda</i>
<i>Choanotaenia crassiscolex</i> (Linstow, 1890)	<i>Succinea putris</i> (L.) <i>Gastropoda</i>
	<i>Cochlicopa lubrica</i> (Mull.) "
	<i>Vitrina pellucida</i> (Mull.) "
	<i>Eulota fruticum</i> (Mull.) "
	<i>Zonitoides nitidus</i> (Mull.) "
	<i>Vitrea contracta</i> (West.) "
	<i>Goniodiscus rotundatus</i> (Mull.) "
	<i>Goniodiscus ruderatus</i> (Stud.) "
	<i>Clausilla ventricosa</i> (Drap.) "
	<i>Lacinaria plicata</i> (Drap.) "
	<i>Clausilidae</i> sp. sp. "
<i>Hymenolepis</i> (s.l.) <i>scutigera</i> (Dujardin, 1845)	host unknown
<i>Vigisolepis spinulosa</i> (Cholodkovsky, 1906)	host unknown
<i>Soricinia tripartita</i> Żarnowski, 1955	host unknown
<i>Trematoda</i>	
<i>Brachylaima fulvum</i> Dujardin, 1843	<i>Zonitoides nitidus</i> (Mull.) <i>Gastropoda</i>
<i>Pseudoleucochloridium soricis</i> (Sołtys, 1952) Pojmańska, 1959	<i>Goniodiscus rotundatus</i> (Mull.) "
	<i>Succinea putris</i> (L.) "
	<i>Perforatella bidens</i> (Chemn.) "
	<i>Zenobiella rubiginosa</i> (Schm.) "
<i>Opisthophleps</i> (O) <i>sobolevi</i> Schaldubin, 1953	host unknown
<i>Opisthophleps</i> (R) <i>exasperatum</i> (Rudolphi, 1819) Dollfus, 1949	host unknown
<i>Opisthophleps</i> (R) <i>opisthovitellinus</i> (Sołtys, 1954) Prokopič, 1959	host unknown

invasion is taking place, and therefore that the shrews are at that time feeding on the given invertebrate.

In analysing the qualitative composition of the food of *S. araneus* the data on tapeworms were taken as the chief basis. In the first place they are most numerously represented in the parasitofauna of shrews, and in

addition a greater variety from the systematic aspect occurs among their intermediate hosts. (The intermediate hosts of *Trematoda* are exclusively snails).

The variations in the quantitative and qualitative structure of the communities of tapeworms in the Common Shrew, at the same time

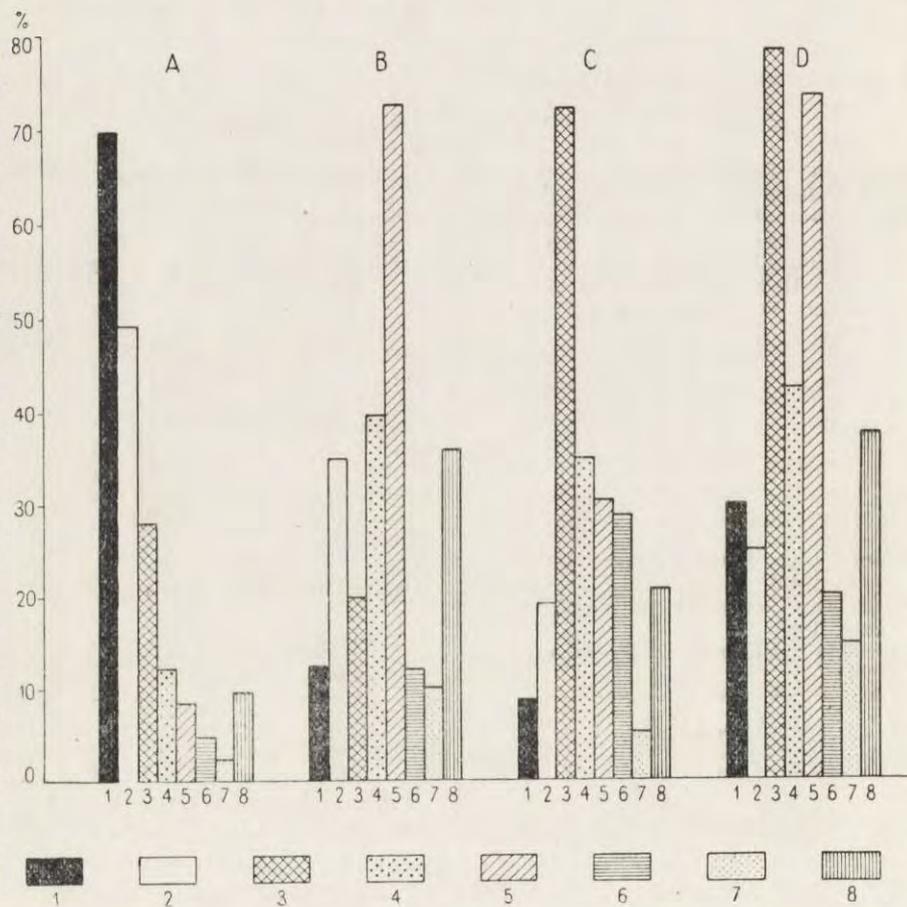


Fig. 1. Variations in the qualitative and quantitative structure of communities of tapeworms in the shrew depending on the age of the mammals and the season of the year.

A — young adults, June

B — young adults, summer (July—October)

C — young adults, winter (November—March)

D — old adults, summer (June—September)

1 — *Hymenolepis scutigera*, intermediate host — unknown, 2 — *Vigisolepis spinulosa*, intermediate host — unknown, 3 — *Neoskrjabinolepis singularis*, intermediate host — nest insect, 4 — *Soricinia diaphana*, intermediate host — coprophagous insect, 5 — *Choanotaenia crassiscolex*, intermediate host — snail, 6 — *Pseudodiorchis prolifer*, intermediate host — myriapod, 7 — *Staphylocystis furcata*, intermediate host — coprophagous insect, 8 — *Brachylaima fulvum*, intermediate host — snail.

indicating the basic components of the food of these animals in different periods, are shown in Fig. 1. Four periods have been distinguished in this diagram:

A. June — as the first period of independent feeding in the area of the young shrews from the first spring litter. This period has been distinguished as the only one in which we have available a population of young shrews of approximately uniform age and uniform time of feeding outside the nest.

B. July—October — as the first summer season for the young shrews. These animals form non-uniform material as regards age and time of feeding outside the nest, since they come from both the first and the following litters.

C. November to March — the winter season. March has been included in this period because, as stated by Borowski & Dehnel (1952): "from the macroclimatic aspect March and the beginning of April at Eia-łowicza differ very little from winter".

D. June—September — second summer season for the sexually mature shrews which have lived through one winter.

It is therefore possible to establish, on the basis of the above figure, the differences in the composition of the food of shrews depending on their age (very young, young adults and old adults) and on the season of the year (winter, summer).

The lack of knowledge of the development cycles of two species of tapeworm (*Hymenolepis s.l. scutigera* and *Vigisolepis spinulosa* — see table 1), occurring most numerous in young shrews in June, makes it impossible at present to determine which is their chief food during this period. It can only be assumed that as far as the invertebrate forming the intermediate host of *Vigisolepis spinulosa* is concerned, that it is very readily eaten by the shrews, particularly the young ones. The largest numbers of the juvenile forms of this tapeworm are encountered in the latter, and the infection by this parasite of shrews never attains elsewhere so high a level as it does in young shrews in June. As regards the tapeworm *Hymenolepis s.l. scutigera*, it may be considered that its host is either an ephemeral dominant in the biocenosis of B.N.P. in May and June, since it is during this period that both the young shrews and the old adults are numerous infected by the above parasite, or else it is a species far easier of access at this time as food than other species of invertebrates. The phenomenon of the periodical domination of this tapeworm is illustrated by Fig. 2.

The occurrence in young shrews in June of other species of tapeworms also — although in the minority — is proof that they also eat *Myriapoda* of the genus *Glomeris*, nest insects of the genus *Catops*, various species

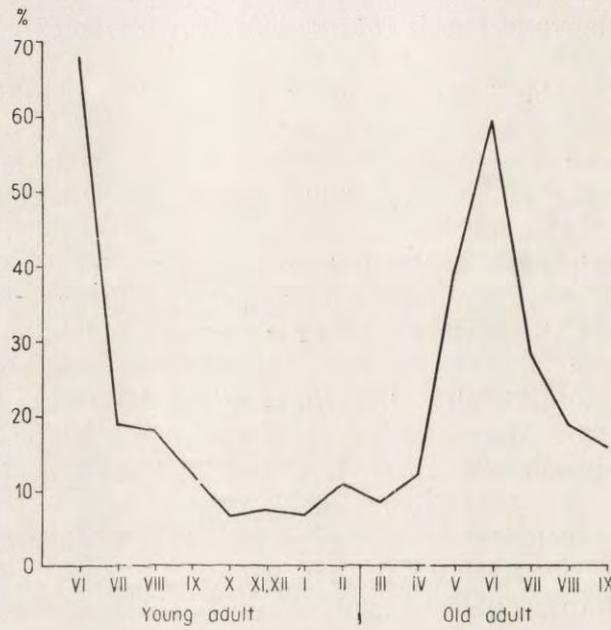


Fig. 2. Extensiveness of infestation of young adult shrews and old adults by *Hymenolepis (s.l.) scutigera* (after Kisielewska, 1961).

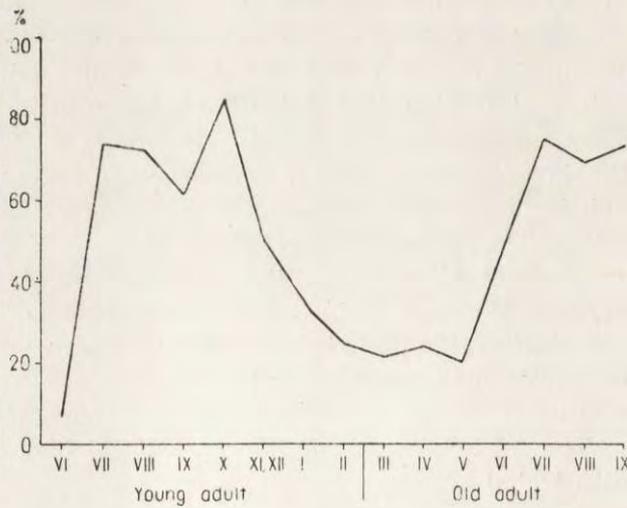


Fig. 3. Extensiveness of infestation of young adult shrews and old adults by *Choanotaenia crassicolex* (after Kisielewska, 1961).

of land snails and even relatively large coprophagous insects — *Geotrupes stercorosus*.

Thus the young shrews in the first period of feeding in the open introduce into their menu the elements on which the older shrews and old adults feed.

It is interesting to find that as early as in the young shrews from the first spring captures, both the juvenile forms of parasites and also adult specimens are encountered, e.g. tapeworms with uterine segments. In 1953 the first young shrew was caught on May 27th. It was infected by several specimens of the tapeworm *Hymenolepis s.l. scutigera*. Three young shrews were caught on May 28th of the same year of which two were infected by: 1. one tapeworm of the species *Hymenolepis s.l. scutigera*, 2. three tapeworms of the species *Neoskrjabinolepis singularis*. In all the cases the presence of uterine segments was noted. In 1954 the first two young shrews were caught on June 2nd. One of them had the following *Cestoda* fauna: *Neoskrjabinolepis singularis* (numerous) and *Hymenolepis s.l. scutigera* (numerous) — also with uterine segments. Many such examples could be given.

Even under optimum conditions for development, the tapeworm does not mature sexually and does not begin egg production earlier than a few days (or more depending on the species of parasite) after the moment it reaches the intestines of the final host. The presence of mature forms of tapeworms in such young shrews therefore leads to the conclusion that the shrews begin to feed on animal food far earlier, before they leave the nest completely. It is possible that they themselves feed in the nest, or near the nest, or else on food brought by the mother shrew. It is true that Dehnel (1952) did not observe the progeny being fed by the females, nor the independent feeding of the young shrews, but perhaps the laboratory conditions exerted an influence here, e.g. the absence of nest fauna.

Only suitable theriological research can confirm the correctness of the above hypothesis, or indicate a different explanation of the fact discussed. The parasitological data only contributed to putting the problem forward.

During the months from July to October the predominating component of the young shrews' food would appear to be numerous species of land snails (Fig. 1, B). The following data bear this out: 1. During this period numerous juvenile forms of the tapeworm *Choanotaenia crassiscolex* (intermediate host — snails — see tab. 1) are encountered in the alimentary tract of shrews. This is evidence, as already mentioned, of the constantly recurring primary and secondary invasions, and thus of the constant feeding of the shrews on snails. 2. during the period from July to October the percentage of shrews infected by the tapeworm

Choanotaenia crassiscolex (Fig. 3) constantly increases. 3. this tapeworm, during the above period, is the indisputed dominant in the communities of tapeworm parasites of *S. araneus*. 4. corresponding data for the trematodes *Brachylaima fulvum* and *Pseudoleucochloridium soricis* (intermediate host — also snails — see tab. 1) — in fact generally rarer than tapeworms — confirm the results obtained by an analysis of tapeworm communities (P o j m a ń s k a, 1961). For purposes of comparison the data on the occurrence of the trematode *Brachylaima fulvum* have been given (Fig. 1). 5. The extensiveness of infection of snails by larvae of the tapeworm *Choanotaenia crassiscolex* is relatively low (Table 2). This also applies to infection by the metacercaria of *Trematoda* (P o j m a ń s k a, 1961). The low percentage of invasion of snails by the larval forms of *Cestoda* and *Trematoda* is even stronger evidence that snails form a commonly used food.

Table 2.

Extensiveness of infestation of certain species of snails in the B.N.P. by the larvae of *Choanotaenia crassiscolex* during the summer and early autumn season (The table does not include species for which there are no data from the corresponding months, although larvae were found in them in May, June, or November).

Species of snail	% of infestation by larvae			
	VII	VIII	IX	X
<i>Succinea putris</i>	0.9	—	2.0	2.0
<i>Cochlicopa lubrica</i>	—	15.3	—	5.3
<i>Eulota fruticum</i>	—	1.2	0.6	0
<i>Zonitoides nitidus</i>	1.7	2.5	1.9	1.2
<i>Clausilidae sp. sp.</i>	1.0	—	0.8	0.6

In comparing what has been stated above with the fact that all the remaining species of tapeworms occur far more rarely in shrews, it must be admitted that snails form the predominant component of young shrews in the B.N.P. during the summer and early autumn months, at least among those invertebrates which are known to be intermediate hosts.

The case with the species of tapeworm *Staphylocystis furcata*, the chief intermediate host of which is *Geotrupes stercorosus*, (*Scarabeidae*) is different. The larvae of this tapeworm were also found in a representative of the *Carabidae* family — *Pterostichus vulgaris* (see table 1), but only once.

Geotrupes stercorosus, on account of its way of life (coprophagous) and owing to the fact that it occurs in very great numbers in the B.N.P. (B o r o w s k i, 1960) and as it crawls over the litter forms an easily accessible

prey for the shrews, is highly predisposed to the role of intermediate host of parasites. It would, however, seem that it does not fulfil this role within the limits of its ecological possibilities. The reasons for this should be sought for in the fact that the insects of this species are not a food favoured by shrews. This is indicated by the small percentage of shrews infected by *Staphylocystis furcata*, with a simultaneous high degree of invasion of the insects themselves by the larvae of the parasite (Table 3).

The case with necrophagous insects [*Silpha obscura* L., *Necrophorus vespilloides* (Herbst) and *Silpha* (T) *sinuata* Fabr.] is similar, Kisielska & Prokopič (1963) finding in these insects at Šumava (Czechoslovakia) infection by the larvae of *Staphylocystis furcata* of up to 50%. At the same time the occurrence of the adult forms of this parasite in *S. araneus* was even lower than in the B.N.P.

It must be added that in *Geotrupes stercorosus* in the B.N.P. the larvae of a second species of tapeworm — *Soricinia diaphana* (see Table 1) also

Table 3.

Extensiveness of infestation of *Geotrupes stercorosus* by the larvae of *Staphylocystis furcata* during the summer and early autumn season.

Year	% of insects infested by larvae					
	V	VI	VII	VIII	IX	X
1957	—	—	4.7	13.5	4.5	3.9
1958	16.7	5.5	16.0	17.2	19.5	—
1959	11.1	6.0	—	26.5	—	—

occur — the shrews being invaded to a greater degree by this species than by *Staphylocystis furcata*. This fact has not, however, been taken into account in the above considerations, since *Soricinia diaphana* probably has yet another intermediate host, to which the greater abundance of occurrence in shrews is due (Kisielska, 1961).

During the winter period the structure of communities of tapeworms in *S. araneus* undergoes distinct transformations, which must to a great extent be caused by the fundamental change in the shrews' diet.

In the first place the role of dominant is taken over by *Neoskrjabinolepis singularis*. Numerical data bearing this out are supported by the results of dissection: throughout the winter numerous juvenile forms of this tapeworm are encountered (in the scolex stage or early phase of strobilation). As has been mentioned several times — this proves constantly recurring invasion. The intermediate host of *Neoskrjabinolepis singularis* are insects of the genus *Catops* sp. (Kisielska, 1958b)

and 1961), which live in the nests of small mammals. The hitherto unpublished data obtained by Wysocka (USSR, Leningrad) indicate that certain species of *Catopidae* are constant inhabitants of the nests of small mammals, including those of *Soricidae*. The domination of *Neoskrjabinolepis singularis* shown by Fig. 1, C would indicate that *Catopidae* also form one of the basic components of the animal food of shrews living through the winter.

The tapeworm *Pseudodiorchis prolifer* (intermediate host — *Myriapoda*, *Glomeris connexa* — see table 1), is also worthy of note. It is true that it is not a dominant in the winter communities of tapeworms, but it is the second species in addition to *Neoskrjabinolepis singularis*, the frequency of occurrence of which in shrews increases in the winter months. It must therefore be considered that *Myriapoda* of the genus *Glomeris* form a commoner food of shrews in the winter than during the spring-summer season (Fig. 4).

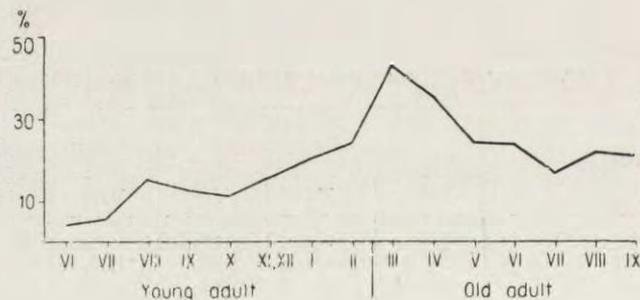


Fig. 4. Extensiveness of infestation of young adult shrews and old adults by *Pseudodiorchis prolifer* (after Kisielewska, 1961).

Invasion of shrews by all the other species of *Cestoda* decreases distinctly in relation to the summer season (this also applies to *Trematoda* (Pojmańska, 1961). This is caused by the majority of the hibernating invertebrates (especially those which dig themselves into the soil, such as *Geotrupes stercorosus*), becoming more difficult of access, or completely inaccessible, to the shrews.

Species of tapeworms, by which the shrews are not infected in the winter, are preserved from the summer and autumn invasions, but their number decreases as a result of spontaneous disinfestation (Kisielewska, 1961).

Among the tapeworms which decrease in numbers in the winter, *Soricinia diaphana* and *Choanotaenia crassiscolex* are species the juvenile forms of which are encountered in dissected shrews in the winter as well (Kisielewska, 1961). Pojmańska (1961) also finds a few juvenile

forms of *Brachylaima fulvum* during this period. Thus the shrews at least certain species of snails to their wintering place and eat them during this period.

Seeds and remains of plants probably play a large part in the food of shrews during the winter. This is apparent from dissection of the stomachs of shrews (Pelikan, 1955; Lapin, 1961), but parasitological data in this field are not of any practical use.

During the summer season as many as two dominants occur in shrews: 1. *Choanotaenia crassiscolex* (in the same way as in young shrews), the frequency of occurrence of which increases sharply with the mass appearance of snails in the spring (Fig. 3), and 2. *Neoskrjabinolepis singularis*, which maintains its domination from the winter (Fig. 5). This

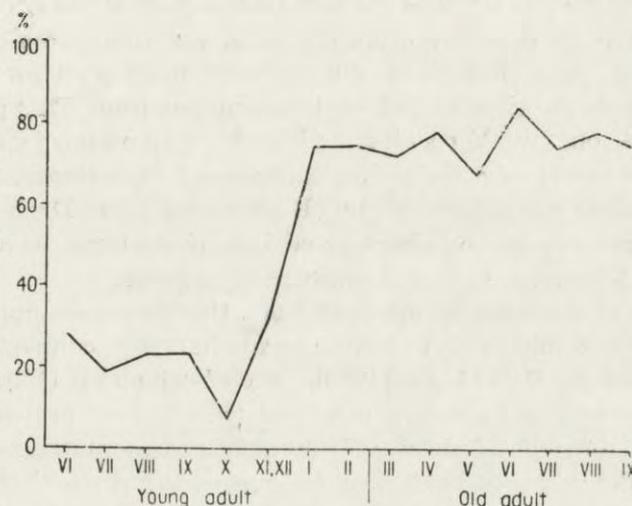


Fig. 5. Extensiveness of infestation of young adult shrews and old adults by *Neoskrjabinolepis singularis* (after Kisielewska, 1961).

last species is perhaps connected with the breeding season of the shrews which at that time (particularly the females) are strongly bound up with the nest and have more frequent contact with nest invertebrate fauna. Thus the dominating component of the food of old adult shrews are land snails and insects of the family *Catopidae*.

In addition invasions by the remaining species of tapeworms increases — probably in connection with the spring appearance in the area of their intermediate hosts. On the other hand invasion by *Pseudodiorchis prolifer* decreases, which is proof that *Glomeris connexa* (the intermediate host of this parasite) takes a secondary place as food in view of the abundance of other more accessible invertebrates.

The discussion given above shows that:

1. One of the basic components of the food of shrews in the B.N.P. in the summer is formed by different species of land snails.

In this connection it is worth paying attention to a certain hypothesis put forward by Borowski & Dehnel (1952). These authors observed increased activity of *S. araneus* in the area (more numerous captures) during rain. They explained this phenomenon by the energetic search made by the shrews for insects which the rain renders inactive, and as a result difficult of access as food. In the light of the arguments which we have so far put forward this interpretation cannot be maintained, since — as shown — snails can satisfy the main food needs of the shrews, and snails emerge from their hiding places on to the surface of the ground during rain — they are therefore more accessible to the shrews during rain than when it is dry. Therefore the otherwise indisputable fact of the considerable activity of shrews during rain must wait for a different explanation than the shortage of food during this time. This problem has been touched on by Mystkowska & Sidorowicz (1961) in discussing the effect of weather on captures of *Insectivora*. They found that the connection described by Borowski & Dehnel (1952) between the activity of the shrews and insects does not have a decisive effect on the formation of the abundance of captures.

In the light of research by other authors, the mass consumption by the shrews of snails would seem to have a local character, connected with the type of biocenosis. Pelikan (1955), Mezherin (1958) and Lapin (1961) did not find a large amount of these invertebrates when they dissected the stomachs of shrews. They gave representatives of different groups of *Arthropoda*, in particular *Insecta* as the shrews' chief food. It would seem that this divergence may be explained by the specific conditions of the biocenosis of the B.N.P. The Białowieża Primaeval Forest is a lowland forest, wet and with an abundance of snails. On the other hand it is a known fact that shrews are not distinguished by any special selectivity in regard to their food. Hence considerable differences can be observed in their diet depending on the area from which they come, or even on the climatic conditions in the same area. Thus Mezherin (1958) gave a list of the food eaten by *S. araneus* from two different districts, and from the same area but in two successive years (one wet and one dry year). In both these lists there are considerable differences in the percentages of composition of the food.

2. Shrews do not readily eat coprophagous and necrophagous insects of the genus *Geotrupes*, *Necrophorus* and *Silpha*.

This is further borne out by the results given by Lapin (1961), who succeeded in identifying the contents of the stomachs of shrews, often

with accuracy as to the genera. The author states that he encountered representatives of the genus *Geotrupes* sp. and *Aphodius* sp. in small numbers (1.3% of the stomachs examined) in the autumn only, *Silpha* sp. (1.3%) only in the summer, and some *Scarabeidae* sp. not more exactly defined in the spring (4.8%).

3. In the winter the shrews in the B.N.P. feed on the fauna hibernating in nests (*Catopidae*) and in decayed tree stumps (*Myriapoda*).

The data given by Mezhzherin (1958) confirm the above observations. This author, of the four seasons studied, most often encountered shrews, in the stomachs of which there were the remains of *Myriapoda* in the winter (spring — 1.9%, summer — 1.6%, winter — 5.6%). Also in the winter he found in 58.8% of the stomachs the remains of various *Coleoptera*, to which *Catopidae* also belong (unfortunately not more exactly identified by the author).

2. The feeding grounds of *S. araneus* and certain other *Soricidae*.

In the summer the shrews feed chiefly on the surfaces of the forest litter, or in its shallow strata. Ferreting about among the fallen leaves, under pieces of bark separated from the trunk, in the damp depressions in the ground, they most often encounter the small land snails nesting there. The old adults, which are then in the breeding season, and thus strongly tied to their nests, also consume in the summer the fauna living in, or visiting, their nests. When feeding on the surface of the litter or in the nests the shrews also encounter several other forms of invertebrates, which presumably fall prey to them, and about which nothing can be said from the parasitological aspect. Mezhzherin (1958) and Lapin (1961) found in the shrews' stomachs representatives of such groups of invertebrates as *Lumbricidae*, *Araneidae*, *Diptera*, *Lepidoptera*, *Formicidae*, *Staphylinidae*, *Chrysomelidae* and many others, among which — up to the present — no intermediate hosts of parasites have been found.

The specific feeding conditions in the winter, when these invertebrates hide in the deeper layers of the litter, under the bark on tree trunks, and even dig themselves into the soil, force the shrews to greater effort to obtain the food essential to them. They look for it in nests, where constant or periodical fauna specific to these habitats live, in decayed stumps and in the deeper layers of the litter, where snails, and in particular, *Myriapoda*, hibernate. This is shown by Mezhzherin's data (1958), from which it will be seen that the shrews during the winter period eat more than at other seasons, representatives of *Araneida* (47.6%), *Myriapoda* (5.6%), *Carabidae* (42.0%), *Hymenoptera* (16.8%), *Diptera* (16.8%). The representatives of these groups of invertebrates hibernate in three stumps

under the bark of trees and in the nests of small mammals. The consumption of representatives of the *Carabidae* group is particularly characteristic. These insects are not very favoured as food by the shrews, particularly when there is enough of other invertebrates, since they have a hard chitinous armature and are armed with a stinging fluid, ejected for defence purposes from the abdomen. Consumption of representatives of this group of insects is expressed in the following figures (acc. to Mezhzherin, 1958); spring — 24.7%, summer — 13.6%, autumn — 14.4%, and in the winter — 42.0%. The distinct increase in the consumption of *Carabidae* in the winter is probably caused by the fact that they hibernate in places to which the shrews have comparatively easy access (underneath the bark of trees, in decayed treestumps).

The list of the parasites of the Common Shrew, and their intermediate hosts, indicates that these mammals feed solely on the land. The same may be said of the species living in B.N.P. *Sorex minutus* Linnaeus, 1766 and *Sorex caecutiens karpinskii* Dehnel, 1949. On the other hand *Neomys fodiens* (Pennant, 1771) and *Neomys anomalus milleri*, Mottaz, 1907 feed mainly in a water habitat. This is proved by tapeworms which parasitize their alimentary tract, the intermediate hosts of which are representatives of *Gammaridae* (Prokopič & Groschafft, 1961; Kisielewska & Prokopič, 1963). The studies referred to above are concerned with mountain areas in Czechoslovakia. In the B.N.P. the development cycle of the above tapeworms has not been worked out in detail, but it must be expected that here also the intermediate hosts would prove to be water invertebrates. In the case of *Neomys fodiens* tapeworms are sporadically encountered which have land intermediate hosts (*Staphylocystis furcata*) (Sołtys, 1954). This would confirm the hypothesis put forward by Borowski & Dehnel (1952) that *N. fodiens* extends its area of occurrence (and feeding) in the wetter summer months, to areas at greater distances from water.

3. Intensiveness of feeding in the *S. araneus*.

The fact that shrews, in connection with their high metabolism, feed very intensively, is well known among theriologists (Tupikova, 1949; Hawkins & Jewell, 1962). Tupikova even states that the daily portion of food often exceeds the body weight of these mammals.

Evidence of the intensive feeding of shrews is provided indirectly by parasitological data, namely the rate of invasion of these mammals by tapeworms under natural conditions; a. very intensive parasitisation of the shrews, varying in individuals scarcely two- to three months old within limits of 90—100% (Kisielewska, 1961), b. the occurrence of

multi-species communities of tapeworm (5—6 species in one individual),
c. permanent re-invasion.

The process of increasing infestation is easier to trace in young individuals at the initial period of their independent life. Shrews from the first spring litter in the given breeding season have been taken into consideration here, as the most uniform material from the aspect of age and time of feeding in the area.

Young shrews in the B.N.P. are most often caught at the beginning of June. In the years taken into consideration in the present study (1953—1958), it was only in 1953 that the first young individuals were caught as early as May 27th. The intensiveness of infestation of the shrews by tapeworms (by all species jointly) in the first period of their independent, active life in the open, is illustrated by Fig. 6.

It will be seen from this that: 1. From the very beginning of the captures (the last ten days of May or the first ten days of June) a large percentage of the shrews were already invaded by tapeworms. In 1957 the figure was 66.7%, and in the other years studied it varied in limits of 40%. 2. In the second ten days of June (or correspondingly for 1953 — in the first ten days) as many as 80% of the young shrews were infested by tapeworms (1953, 1954, 1956), while in 1957 and 1958 100% infestation was found in the material obtained by capture.

The data contained in Fig. 6, expressing the rapidly progressing process of infestation of the young shrews, cannot by themselves visualise the intensiveness with which the shrews feed. This information can only be supplied by an analysis of the extensiveness of invasion of intermediate hosts — invertebrates — by the larvae of parasites. In May and June this invasion was as follows:

for *Geotrupes stercorosus* — an average of 11.5% (for both species of tapeworm)

for *Glomeris connexa* — 7.8%

for different species of snail from 0.5% to 6.6% (average 2.8%) (data after K i s i e l e w s k a, 1961).

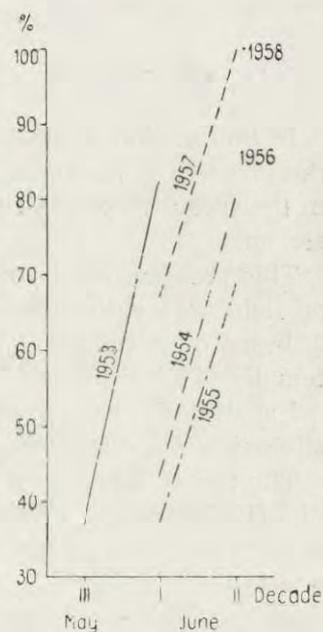


Fig. 6. Increase in extensiveness of infestation of young adult shrews by tapeworms in the first decades of their active life in the open.

Therefore, in order that the shrew might be invaded by one of the species of tapeworm peculiar to it, it must theoretically eat over 30 snails, about 12 *Myriapoda*, or about 10 insects of the *Geotrupes stercorosus*. It may of course happen that the invertebrate first encountered and eaten by the shrew will be a carrier of tapeworm larvae and thus cause invasion. It is, however, difficult to accept this as a rule with so numerously occurring invasions and with so high a percentage of infestation of young shrews.

It must also be added that the food of shrews is not formed exclusively by the intermediate hosts of tapeworms, but also by other invertebrates not playing any part in the development cycles of biohelminths, and thus not included in the control of parasitological research.

It may therefore be taken as an indisputable fact that the very large food requirements of shrews in the first period of their life outside the nest must be satisfied by abundant and varied food.

III. THE PROBLEM OF THE REPRODUCTION OF *SOREX ARANEUS*

In this section we shall consider, on the basis of parasitological data, the problem of the reproduction of the shrew, and therefore of variations in the intensity of the sexual activity of females during the breeding season.

This problem has been worked on in the B.N.P. in two ways: 1. based on field observations from 1947—1950 (Borowski & Dehnel, 1952), 2. based on histological examination of sexual apparatus and nipples in females (Tarkowski, 1957) during the breeding season of 1954.

I shall dwell longer on this latter study, as I have at my disposal parasitological material from that year.

The course taken by breeding in the season investigated by Tarkowski (1957) was as follows: First oestrus in the last ten days of April. Birth of the first litters between May 10th and 20th (pregnancy lasts 20 days acc. to Dehnel, 1952). Appearance in captures of young shrews as from June 2nd. Taking the period in the nest as 22 days (Dehnel, 1952), the appearance in the captures would coincide in time with the departure from the nests of the young shrews. The second pregnancy, occurring in the majority of the females immediately after the birth of the first litter (nursing females already pregnant for the second time were caught on May 12st). Birth of the second litter between June 4th and 14th.

According to Tarkowski (1957) the first two litters were wave-like in character. This is the result of the first oestrus occurring in old adult females suddenly and simultaneously (it is not spaced out in time). As a result the birth of the first litters, and later the date on which the

young shrews leave the nest, also occurs in narrow divisions of time (approximately two weeks). The same applies to pregnancy and birth, since the oestral cycle in the majority of females takes place during this period in such a way that ovulation and mating take place immediately after the first birth.

Parasitological data confirmed the results obtained by Tarkowski (1957) with a remarkable degree of accuracy.

Fig. 7 illustrates the invasion of young shrews by tapeworms in 1954 during the whole breeding season. The young shrews from the first litter, after appearing in the area (beginning with June 2nd) very quickly acquire tapeworm fauna (as shown in the section on food), and as a result the percentage of infested individuals rises sharply. At the end of June

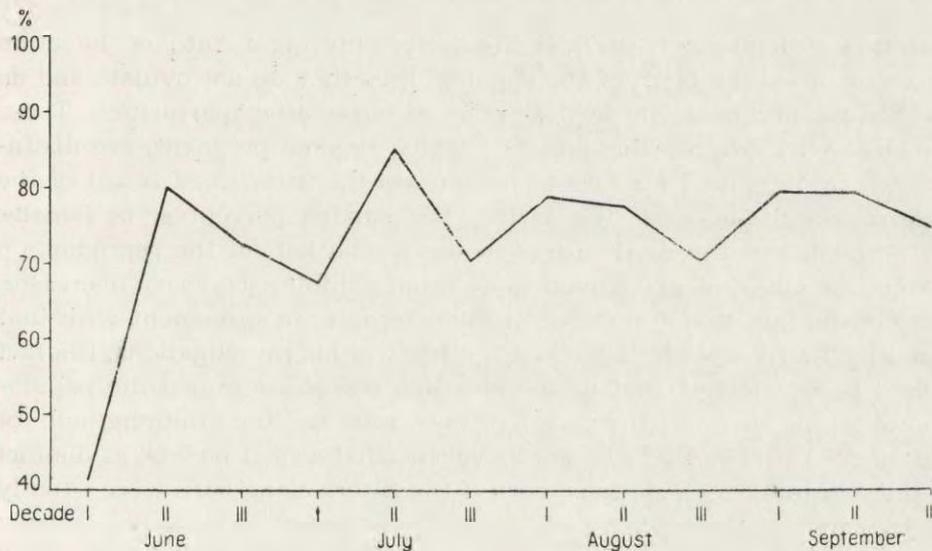


Fig. 7. Extensiveness of infestation of a population of young adult shrews in the summer months of 1954.

and beginning of July, however, there is a distinct decrease in the number of infested animals. Tarkowski (1957) states that the births of the second litter took place about 4th—14th of June. Therefore, counting the 22 days of nest life of the young shrews, the second litter moves out into the area approximately between June 26th and July 6th, that is, the very time when a distinct decrease in invasion is shown on Fig. 7. This may be explained by the fact that the shrews which have just left the nest are not as yet subject to such mass invasion as those which have been feeding since the beginning of June and thus „thin out” the intensively infested population of young shrews from the first litter. Finally, after a short

time (as early as between July 10th—20th) the extent of infestation of the dual-age population of young shrews evens out (Fig. 7).

The second decrease in infestation can be observed in the last ten days of July. In order to explain this it is necessary to refer again to the data on the reproduction biology of the shrew. After the second birth a certain part of the females ovulate again and enter into their third pregnancy (Tarkowski, 1957). Knowing the period of pregnancy and nesting the cycle may be described as follows: births of the second litter June 4th—14th — immediate pregnancy — births of the third litter June 25th — July 5th — departure into the open of the third litter July 18th—26th, that is, the last ten days of July (cf. decrease in infestation during this time shown on Fig. 7).

The activity of females decreases during the second half of the breeding season (Tarkowski, 1957), the majority entering a state of lactation anoestrus after the birth of their young, thus they do not ovulate and do not become pregnant, or at least not at once after parturition. Those females — in fact not numerous — which become pregnant, are distinguished by the small number of progeny in the litter. As a result of the lack of simultaneity in the births, the smaller percentage of females giving birth and the small litters in the second half of the reproduction season, the curve of extensiveness does not exhibit such sharp decreases. Despite the fact that the curve in this section is in agreement with that given by Tarkowski (1957) on the basis of his investigations, the fact cannot be overlooked that as the breeding season continued the population of young shrews is increasingly numerous and the „thinning out” of the infested shrews by those not as yet invaded cannot now be as distinct in the percentage calculations, even if the litters being born were equally as numerous as those at the beginning of the season. This is particularly important in those breeding seasons in which, similarly to 1954, the main intensity of litters occurred at the beginning of the season. The observations made by Borowski & Dehnel (1952) show that the situation may be different, as do also parasitological data.

The curve of infestation in 1954 (Fig. 7) provides complete confirmation of the course taken by reproduction of shrews as described by Tarkowski (1957), and at the same time indicates that it is possible to reach conclusions on the basis of analogical curves as to the reproduction dynamics in other years also.

Thus, for instance, Fig. 8 illustrates the degree of invasion — and one is tempted to risk affirming that it also illustrates the course taken by reproduction of the shrews in 1953.

The first oestrus of the old adults must have occurred slightly earlier that year, since the first young shrews appeared in captures as early as

May 27th. Therefore, according to theoretical calculations, reproduction took the course illustrated by table 4. Taking May 27th as a starting point, as the date of the first capture of young shrews, other dates interesting us were calculated, of course only for purposes of orientation. It is perfectly clear that in reality the phenomena given in table 4 (birth, pregnancy, exodus of the young shrews into the open) include at least 10—14 day divisions of time.

Table 4 in comparison with Fig. 8 is evidence that the reproduction season in 1953 was unusually dynamic. All, or almost all of the females gave birth in turn to three litters. These litters must have been large ones, as is shown by the deep incision at the start of the curve in Fig. 8. (Inten-

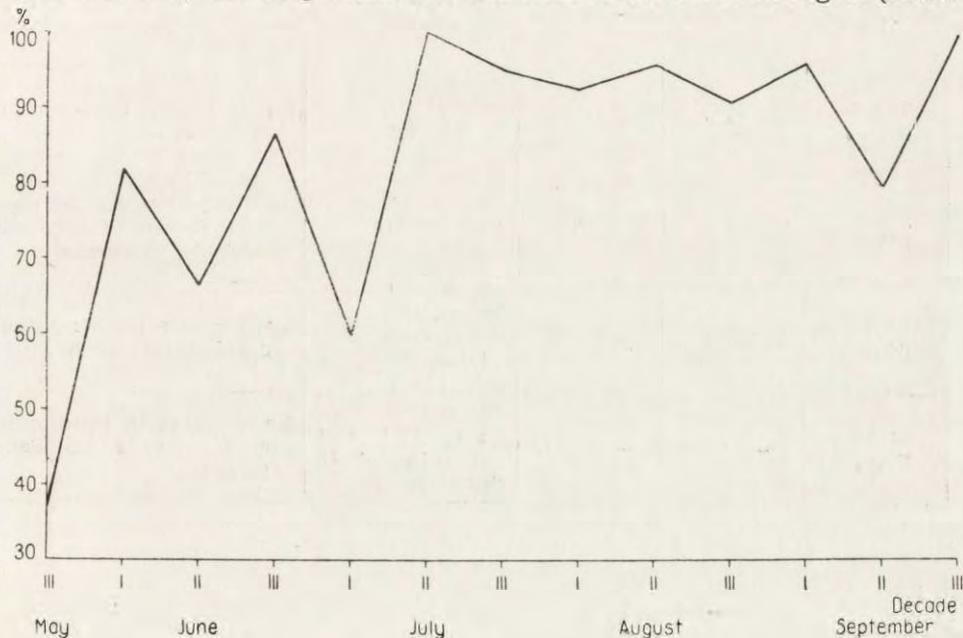


Fig. 8. Extensiveness of infestation of a population of young adult shrews in the summer months of 1953.

sive „thinning” of the population of young shrews living in the area). The fourth and fifth litters were slightly smaller (or more weakly expressed in the comparisons of percentages), but more distinctly marked than in 1954. The sixth litter, from which the young shrews emerged into the open after September 10th, is interesting. A fairly sharp decrease in infestation of the population of young shrews during this period suggests a sort of return of the reproduction potential of the females. This would provide confirmation of the observations made by B o r o w s k i & D e h n e l (1952), who stated that in different years the greatest reproductive activity of the females occurs either in the spring, or summer, or at the

Table 4.

Theoretical course taken by the reproduction of the Common Shrew in the B.N.P. in 1953.

Order of litter	Beginning of pregnancy	Birth date	Departure into the open of the young shrews	Remarks on fig. 8
First litter	15.IV.	5.V.	27.V.	
Second litter	6—7.V.	26—27.V.	17—18.VI. (II decade)	See decrease in infestation on figure
Third litter	27—28.V.	16—17.VI.	8—9.VII. (I decade)	See decrease in infestation on figure
Fourth litter	18—19.VI.	7—8.VII.	29—30.VII. (end of III decade)	See tendencies to decrease in III decade of July and I decade of August
Fifth litter	8—9.VII.	28—29.VII.	19—20.VIII. (end of II decade)	See decrease in infestation in III decade of August
Sixth litter	29—30.VII.	18—19.VIII.	10—11.IX. (end of I and beginning of II decade)	See decrease in infestation in II decade of September

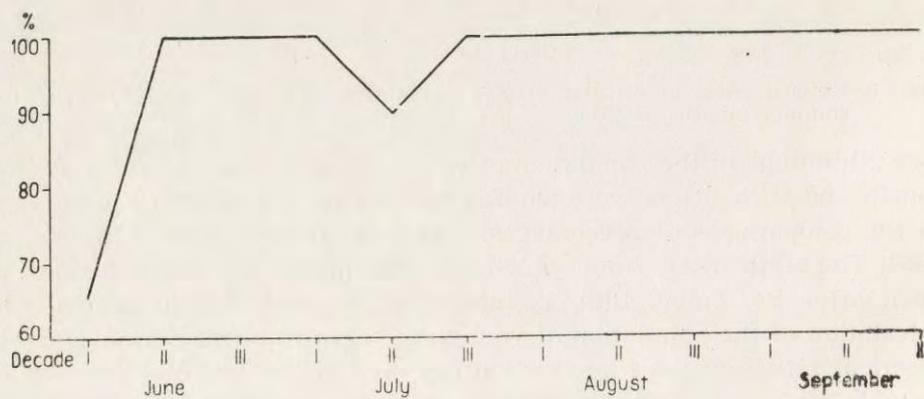


Fig. 10. Extensiveness of infestation of a population of young adult shrews in the summer months of 1957.

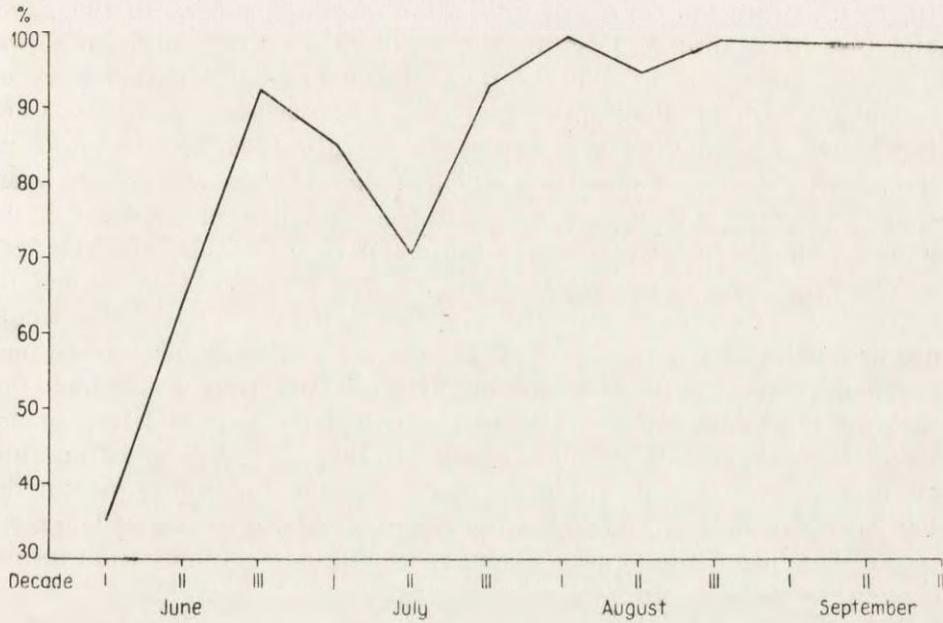


Fig. 9. Extensiveness of infestation of a population of young adult shrews in the summer months of 1955.

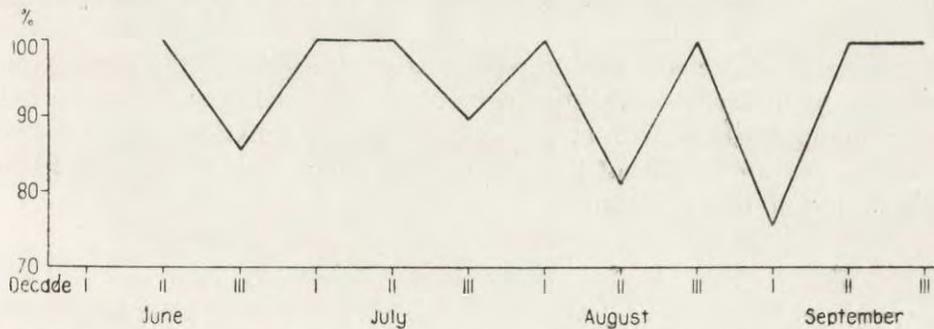


Fig. 11. Extensiveness of infestation of a population of young adult shrews in the summer months of 1958.

beginning of autumn. It may be that the period in which reproduction is most intense is one of the factors determining the size of the shrew population in the following year. It must be emphasised that by the sixth litter is meant the sixth successive appearance of young shrews in the area, but it is not to be taken to mean that it is the sixth litter of a certain group of females.

In general it may be said that from the aspect of reproduction dynamics, it is possible to distinguish optimum, average and pessimum years with shrews. B o r o w s k i & D e h n e l (1952) also found this to occur. Figs. 9,

10, 11 illustrate the curves of infestation of young shrews in 1955, 1957 and 1958 (the captures of young shrews in 1956 were scanty, and it was therefore impossible to split the numbers up into decades and draw up statistically reliable diagrams). The years previously discussed, 1953 and 1954, must be accounted as optimum years, while 1955, 1957 — and from the scanty captures it must be concluded that 1956 as well — are years characterised by a distinct decrease in the reproduction potential of the females. Finally in 1958 a new intensification of the number of litters can be observed. The curves of infestation in 1955 and 1957 (Figs. 9 and 10) even suggest that the second litter appears in the open later. This would mean that the females, or at least the majority of them, did not become pregnant immediately after giving birth to the first litter, but after suckling the young shrews. This can be calculated theoretically, e.g. for 1955: the first captures of young shrews in this year were noted on June 4th. Taking this date as an approximate index of the appearance of the first litter in the area, the following calculations can be made. The birth of the first litter took place about May 15th — lactation period lasting about three weeks, ending about June 2nd—3rd — ovulation and second mating June 3rd—4th, — birth of the second litter about June 23rd—24th — departure from the nests of the second litter about July 15th—16th, that is, in the second decade of July (cf. with the fall in the curve on Fig. 9). The above provides yet one more confirmation of the fact that all phenomena connected with the reproduction dynamics of the shrew (rate, number of litters, size of litter, percentage of females ovulating directly after giving birth, or with an interval during the lactation period) are not constant features either of the species, or even of a given population, but are subject to distinct variations.

IV. CONCLUSIONS

Certain questions connected with the biology of *Sorex araneus*, interpreted on the basis of parasitological, or more strictly speaking — helminthological research, are discussed in this study. I should like to conclude the arguments contained in the two preceding sections with a few general remarks.

1. Parasitological data may form in certain cases a contribution to our knowledge of host species, may confirm already existing hypotheses, or refute them, and may assist in bringing to light new problems not as yet described. They should not, however, be treated as a key to the final solution of these problems.

For example: on the basis of the development cycles of biohelminths it is possible to draw conclusions as to the food of the final hosts of these parasites. Everything which the host species eat, and which does not participate in the ontogenesis of parasites, automatically evades the parasitologist's control.

2. Not all groups of parasites are uniformly useful in interpreting these problems.

For example: geohelminths, that is, parasites with a simple form of development — without the participation of an intermediate host — cannot provide evidence.

even partly of the quality and quantity of food, although this does not mean to say that in other fields of the biology of their hosts, that they might throw some light on this problem.

3. Not every type of parasitological investigation is suitable for use in other branches of knowledge beyond the science of parasitology. Abundance and continuity in collecting material, and uniformity of time and place of collection are of particular importance. For example: it is not possible to draw conclusions as to the biology of the shrew in general, but only as to the population living in this particular area, on the basis of parasitological investigations.

4. Despite the above limitations and despite the fact that — perhaps — further theriological research will question some of the statements contained in the present study, it seems to me that what is most worthy of note here are the new methodological values and the fact that parasitology is indicated as a supplementary discipline in the solution of problems of the biology of host species.

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STRESZCZENIE

W pracy niniejszej podjęto próbę wykorzystania wieloletnich badań nad tasiecmami (*Cestoda*) i przywrami (*Trematoda*) przy interpretacji zagadnień związanych z biologią ich żywicieli ostatecznych — *Sorex araneus* Linnaeus, 1758 w Białowieskim Parku Narodowym.

W oparciu o dane parazytologiczne rozpatrzono dwa główne problemy: pożywienie ryjówki aksamitnej oraz dynamikę rozrodu tych ssaków (wyłącznie w odniesieniu do badanego terenu).

a. Pożywienie *Sorex araneus*.

Skład pokarmu ryjówek oraz jego zmienność w zależności od pór roku i wieku ssaków opracowano na podstawie znanych cykli rozwojowych przywr i tasiemców (Tabela 1).

Za podstawowe kryterium przyjęto ekstensywność zarażenia ryjówek poszczególnymi gatunkami pasożytów oraz występowanie (bądź nie występowanie) młodocianych postaci pasożytów w jelicie ssaków. Duże zarażenie ryjówek jakimś gatunkiem pasożyta w danym okresie, w zestawieniu z raczej niską ekstensywnością zarażenia żywicieli pośrednich (Tabele 2, 3) świadczy, że odpowiedni żywiciel pośredni jest masowo spożywanym pokarmem ssaków. Potwierdzają to również często spotykane przy sekcjach młodociane postaci pasożyta świadczące o aktualnie powtarzających się wtórnych inwazjach (a więc także o stałym spożywaniu przez ryjóweki danych żywicieli pośrednich).

Skład jakościowy oraz ilościową zmienność diety pokarmowej ryjóweki aksamitnej ilustrują ryc. 1, 2, 3, 4, 5. Można z nich wnioskować co następuje: 1) masowo wykorzystywanym pokarmem przez ryjóweki w okresie lata na terenie BPN są ślimaki (ryc. 1 B, D, 3) 2) w zimie przy trudnościach w zdobyciu zwierzęcego pokarmu ryjóweki penetrują gniazda i pniaki, odżywiając się bytującymi tam owadami i wijami (ryc. 1 C, 4, 5) 3) fauną gniazdową odżywiają się także i w lecie ryjóweki dorosłe — związane z gniazdami w okresie rozrodu (ryc. 1 D, 5) 4) w maju—czerwcu ryjóweki z BPN odżywiają się okresowo jakimś nie zidentyfikowanym jeszcze gatunkiem bezkręgowca, pojawiającym się prawdopodobnie masowo, ale na krótko i łatwo dostępnym (ryc. 1 A, 2) 5) ryjóweki bardzo młode nie wykorzystują ślimaków jako pokarmu w tak dużym stopniu jak nieco starsze i dorosłe (ryc. 1 A, 3) 6) ogólnie biorąc w skład pokarmu wchodzi przedstawiciele przynajmniej trzech grup bezkręgowców: wijów, owadów i ślimaków (o pożywieniu roślinnym oraz innych bezkręgowcach nie biorących udziału w cyklach rozwojowych tasiemców czy przywr — z punktu widzenia parazytologii nie można się wypowiadać).

W dalszym toku pracy omówiono zagadnienie intensywności odżywiania się ryjówek (ryc. 6) oraz zróżnicowania nisz ekologicznych, w których żerują: ryjóweka aksamitna i niektórzy inni przedstawiciele *Soricidae*.

b. Dynamika rozrodu ryjóweki aksamitnej w BPN.

Przeanalizowano ekstensywność zarażenia tasiemcami populacji młodych ryjówek w okresie od maja do września (sezon rozrodczy) w latach 1955—1958 (ryc. 7, 8, 9, 10, 11). Na podstawie konfrontacji przebiegu tych krzywych z badaniami teriologów prowadzonymi na tymże terenie i częściowo w tym samym czasie (Tabela 4) wysunięto przypuszczenie, że krzywe ekstensywności przedstawione na wyżej wspomnianych wykresach obrazują jednocześnie w przybliżeniu przebieg rozrodu *Sorex araneus* w kolejnych sezonach rozrodczych. Mianowicie — obniżenia krzywych odpowiadają pojawom w terenie kolejnych miotów ryjówek. Młode ryjóweki opuszczające gniazda rodzicielskie jako niezarażone pasożytami jelitowymi, albo zarażone w niewielkim stopniu, „rozrzedzają” populację młodych już jakiś czas żerujących w terenie, a zatem zarażonych silnie. Stąd spadki ekstensywności zarażenia w populacji młodych wskazują na liczbę miotów w danym sezonie rozrodczym, oraz na tempo rozrodu *Sorex araneus*.

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