A C T A T H E R I O L O G I C A

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Energy values of body in small mammals[1])

[With 3 Tables and 5 Figs.]

Energy values of the body were examined in 5 species of small mammals prevailing in the forest and field ecosystems: *Sorex araneus* L., *Apodemus flavicollis* (Melch.), *Apodemus agrarius* (Pall.), *Clethrionomys glareolus* (Schreb.), and *Microtus arvalis* (Pall.). A total of 270 samples derived from 220 animals caught in 3 seasons (late winter and prevernal season, summer, and autumn) were burned in the bomb calorimeter. The caloric value per gram dry weight and the per cent water and ash were determined and the cal/g ash-free values and the values of biomass were calculated. In the examined rodents the cal/g dry weight value is the lowest at the end of winter (4508.44 cal/g). In the summer it goes up rapidly to reach 5261.05 cal/g and a similar value is maintained in the autumn (5204.08 cal/g). The caloric value of body for shrews does not show any seasonal changes, being low all the year round (4554.96 cal/g). The caloric value per gram ash-free weight exceeds by 10.2—13.7% the cal/g dry weight value, showing very similar specific and seasonal variations. The seasonal fluctuations and specific differences in these values depend mainly on the fatness and only slightly on the ash content. The energy value of biomass for all the species and seasons falls within a narrow range of 1301—1693 cal/g, with an average of 1501 cal/g. Consequently, either this mean value, 1.5 Kcal/g, will be used to calculate the productivity of populations of small mammals or the coefficient may be differentiated for seasons and species.

I. INTRODUCTION

There are numerous tables offering nutritive values of many plant and animal materials. The application of these tables for ecological studies is limited. They include only foods important to man and main fodders of domestic animals. Dieticians and specialists in feeding are interested chiefly in the nutritive values of

[1]) This study was carried out under the "International Biological Program" in Poland.

foodstuffs and not in their whole energy value. They base themselves rather on the analysis of the chemical composition of foodstuffs than on direct calorimetric measurements (Górecki, 1965).

The studies on ecological productivity require the expression of biomass in total caloric values. For this reason, many ecologists working at bioenergetics made determinations for different living materials in the bomb calorimeter. These data scattered in literature have been collected and tabulated by Golley (1959, 1961). His tables contain the caloric values of tissue of 64 plant species and 14 animal species. Out of these last determinations only 1 item concerns wild mammals.

The purpose of the present work is to determine the caloric values of body for 5 species of small mammals that predominate in the forests and fields of Central Europe. This work is to establish the first of the bioenergetics parameters studied under the "Rodents Project", embracing studies on the energy flow and net productivity of rodent populations in various ecosystems.

II. MATERIAL AND METHOD

Five species of small mammals, dominant in the forest and field ecosystems of Central Europe, were used for study. They are the common shrew *Sorex araneus* Linnaeus, 1758, yellow-necked field mouse *Apodemus agrarius* (Pallas, 1771), bank vole *Clethrionomys glareolus* (Schreber, 1780), and common vole *Microtus arvalis* (Pallas, 1771). It is well known that the bank vole, yellow-necked field mouse, and shrew are main inhabitants of both deciduous and coniferous forests. In cultivated fields and in some meadows the common vole and, to a smaller extent, the striped field mouse are dominant; this last occurs also in thickets and some forests.

Animals for determinations were caught mainly in beech forests (*Fagetum carpaticum*) in the Ojców National Park near Kraków (19°49′ E, 50°13′ N). Only a part of the striped field mice and voles were derived from Turew near Poznań, Dziekanów Leśny near Warsaw, Wrocław, and Białowieża [1]). The yellow-necked field mouse is the biggest of the species of rodents under examination (its average body weight calculated from the whole material is 24.26 g). The striped field mouse comes second (20.24 g), followed by the common vole and bank vole (18.47 g and 18.54 g respectively). Shrews are much smaller, their average body weight reaching 6.56 g in various seasons.

Animals used to determine caloric values were caught in 3 seasons in which small mammals generally differ in body fatness and reproduction: (1) late winter and prevernal season (February—April), (2) summer (July—August), and (3) late autumn (November—December). The whole material was collected in 1964. That year in Ojców was characterized by the late arrival of spring, which is disadvantageous to rodents, and by fairly good crops of beechmast in autumn. A total of 270 samples of 220 rodents and shrews were burned in the calorimeter. This number includes also 4 determinations made for new-born litters of a bank vole, yellow-necked field mouse, and common vole. These animals were born in the laboratory from females caught pregnant in box live traps.

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The preparation of animal material for determinations was based, to a great extent, on the results of American ecologists working at bioenergetics (Odum, 1960; Connell et al. 1960; Golley, 1960, 1961). The procedure for burning a mouse or shrew in the calorimeter consists, firstly, in drying its tissue and, secondly, in crumbling it. The detailed technique was presented in the previous paper (Górecki, 1965) and, therefore, only the most important operations will be mentioned here.

Mammals caught in snap-traps were dried in the vacuum oven. Fast drying is important on account of the progressing breakdown of fats, which as a result change their energy value. Drying in the vaccum oven may be carried out at lower temperatures (about 70°C). Animals were dried "to a constant weight", which was checked several times. Next they were ground in an electrical mill with rotating blades. After grinding, the material was additionally mixed in a china mortar and divided into a few samples weighing 1.2—1.5 g. Such samples were not usually formed into pellets but placed in a crucible for burning and redried in the dessiccator. Samples were burned in the Polish Berthelot KL-3 calorimeter. The ash left after burning was weighed and the amount of acids produced in the bomb calorimeter determined by titrating them in 0.1 N NaOH.

The cal/g dry weight and the percentage water and ash were established by measuring. In addition, the cal/g ash-free weight and the caloric value of biomass were calculated.

Apart from this, the ash content of the body of whole animals was determined using an eletrical muffle furnace. Fifteen rodents and shrews were examined in this manner, and the ash content obtained was very like the value from the samples in the calorimeter.

The statistical analysis of results includes the calculation of the mean, standard deviation, percentage coefficient of variation, and standard error of the mean. Student's test t was applied in comparisons of the caloric values for various species and for successive seasons.

III. RESULTS

1. Caloric Value per Gram Dry Weight

There are differences between rodents and shrews in the seasonal changes of the caloric value per gram dry weight. In the four species of small rodents examined the lowest values occurred at the end of winter; then they increased rapidly in the summer, and in the autumn were kept at a similar, high level (Fig. 1, Table 1). The caloric value per gram dry weight of body for shrews changes very slightly in the annual cycle. In the winter it lies within the range of the values for rodents, but in the summer and autumn rodents exceeded shrews in this respect remarkably.

During the winter the vole and the yellow-necked field mouse have the lowest caloric values (4363.61 and 4369.19 cal/g respectively), whereas this value was evidently the highest in the yellow-necked field mouse (4829.30 cal/g). Striped field mice collected in this season, however, showed a relatively great fatness of body. Highly significant statistical differ-

Table 1.
Energy values per gram dry weight of body of small mammals.

Season	Number Samples	Dry wt. of body in g Mean ± S.D.	Value cal/g dry weight		
			Mean ± S.D.	Coefficient of variation (%)	S. E. of Mean
Sorex araneus					
WINTER *)	10	2.15 ± 0.45	4532.91 ± 188.05	4.1	59.46
SUMMER	12	2.35 ± 0.61	4449.17 ± 717.20	16.1	156.60
AUTUMN	5	1.98 ± 0.22	4682.73 ± 207.45	6.3	148.36
Apodemus flavicollis					
WINTER	21	8.80 ± 1.57	4369.19 ± 277.62	5.5	87.73
SUMMER	20	6.66 ± 2.65	5361.35 ± 429.10	8.0	95.90
AUTUMN	21	6.47 ± 2.36	5274.72 ± 266.21	4.0	58.09
Apodemus agrarius					
WINTER	18	5.97 ± 0.87	4829.30 ± 542.60	11.2	171.30
SUMMER	16	7.39 ± 1.70	5396.08 ± 265.70	4.9	66.44
AUTUMN	20	5.51 ± 1.23	5310.70 ± 261.61	4.9	58.50
Clethrionomys glareolus					
WINTER	20	5.27 ± 0.99	4471.70 ± 220.80	4.9	69.82
SUMMER	20	5.68 ± 1.44	5170.65 ± 517.50	10.0	115.71
AUTUMN	20	5.35 ± 0.81	5160.76 ± 339.73	6.5	75.96
Microtus arvalis					
WINTER	23	6.70 ± 1.32	4363.61 ± 325.52	7.4	90.28
SUMMER	12	5.91 ± 1.17	5116.15 ± 513.60	10.0	148.20
AUTUMN	14	4.08 ± 0.93	5090.15 ± 226.52	4.4	60.54

*) Winter + prevernal season

ences occurred between the extreme species, that is, between the striped field mouse and the vole, and statistically significant ones between the two mice, the yellow-necked field mouse and the striped field mouse.

In the middle of the summer all the rodents have the maximum caloric values per gram dry weight, and it exceeds by about 580—990 cal/g the values for the late winter and prevernal season. The values for the mice come near each other (5361.35 and 5396.08 cal/g) and are visibly higher than those for both the voles (5090.15 and 5160.76 cal/g). However, these differences between the mice and voles are not statistically significant. In shrews the caloric value per gram dry weight not only does not rise but even drops slightly (by 84 cal/g). Owing to this fact the caloric values of body for shrews in this period are lower by as much as 812 cal/g than the values for rodents. In consequence, there are statistical differences between the shrews and all the other species in this season, and these differences are strongly significant. In the summer the material is characterized by the greatest variability in nearly all species. The coefficient of variation is generally twice as high as in the other seasons (Table 1). It reflects a great age differentiation in the summer.

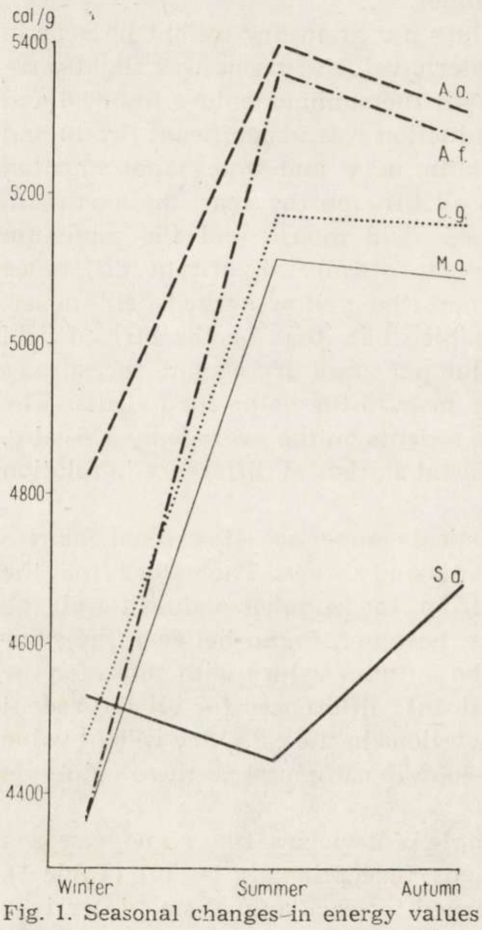
Late in the autumn the caloric values per gram dry weight lie near to those for the summer (Fig. 1). The caloric value of tissue was slightly reduced in both mice in comparison with the summer values (by 86.6 and 85.3 cal/g), whereas in shrews this reduction was insignificant (by 10 and 26 cal/g). As a result, the means for both mice and voles approximated somewhat. In this season, as well as all through the year, the maximum value for the rodents fell to the striped field mouse and the minimum value to the common vole, but the statistically significant difference occurred between the common vole and the yellow-necked field mouse, the material of which was less variable than that of the striped field mouse. In the autumn the energy value per gram dry weight for shrews increased to 4682.73 cal/g and came near to the value for rodents. The autumn shrews, however, differ from rodents on the average by 526 cal/g, which is expressed by a highly significant statistical difference in relation to all the species of rodents.

It is instructive to carry out a statistical comparison of seasonal changes in the caloric values of tissue for rodents and shrews. The values from the winter differ highly significantly from the summer values for all the rodents. No statistical difference was, however, found between the summer and autumn. A comparison of the autumn values with those for the preceding winter reveals very significant differences for all the rodent species again. In shrews, seasonal fluctations in the cal/g dry weight value do not go beyond limits of 4449.17—4682.73 cal/g, and so these values do not differ significantly.

It should be emphasized that a sample of a species for a given season consisted generally of 15—20 specimens (exceptionally 5—10) (Table 1). A sample of the body was usually burned for each animal (in winter 1—2 samples). The coefficient of variation for the value examined is comparatively small, ranging from 4.1 to 11.2% for winter and autumn, whereas in the summer it falls between 4.9 and 16.1%. This indicates the great homogeneity of the character, i.e., of the caloric value per gram dry weight and the good representativeness of this number of samples.

2. Caloric Value per Gram Ash-Free Weight

If the ash content is taken away from the energy value of the whole dry matter, the remainder is the so-called caloric value per gram ash-free weight. This value is comparable and fairly constant in the animal kingdom (Slobodkin, 1961). In the species of rodents and shrews under study the ash made up 10.22—13.71% of the dry weight of body. All through the year it was the highest for the yellow-necked field mouse and common vole, somewhat lower for the bank vole and the lowest for the striped field mouse and the shrew.



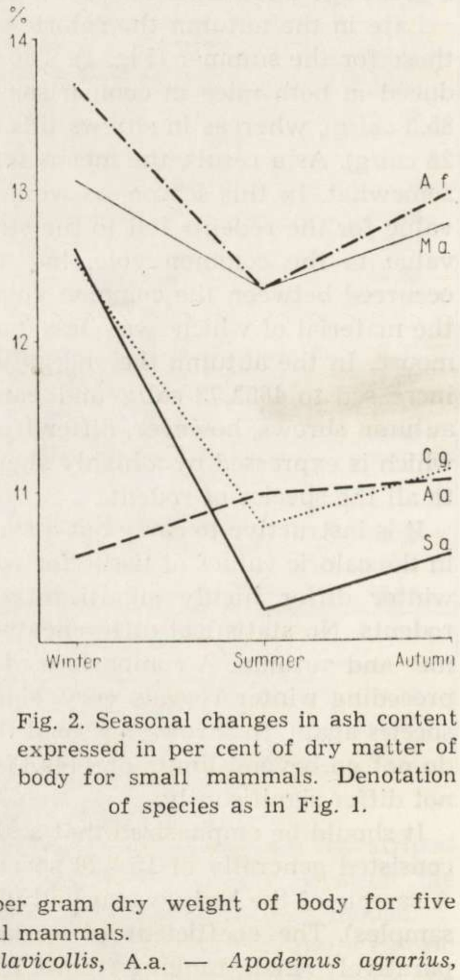


Fig. 2. Seasonal changes in ash content expressed in per cent of dry matter of body for small mammals. Denotation of species as in Fig. 1.

Fig. 1. Seasonal changes in energy values per gram dry weight of body for five species of small mammals.

S.a. — *Sorex araneus*, A.f. — *Apodemus flavicollis*, A.a. — *Apodemus agrarius*, C.g. — *Clethrionomys glareolus*, M.a. — *Microtus arvalis*.

Figure 2 and Table 2 sum up the values of the ash content determined in the bomb calorimeter for the late winter and prevernal season, summer, and late autumn. The average of percentage ash from the three seasons is 12.70 for voles, 12.35 for yellow-necked field mice, 11.50 for bank voles as well as for shrews, and 10.80 for striped field mice.

Similar values were obtained from combustions of whole animals in the electrical furnace at mid-winter. At that time the yellow-necked field mouse and the common vole had the highest proportion of mineral parts (12.85% and 13% respectively). The bank vole came second with its 12.22%, and the lowest per cent was revealed by the shrew (11.77%) and

Table 2.

Energy values per gram ash-free weight for small mammals.

Season	Content of ash (%) Mean ± S. D.	Value cal/g ash — free weight		
		Mean ± S. D.	Coefficient Variation (%)	S. E. of Mean
		Sorex araneus		
WINTER *)	12.60 ± 1.13	5137.18 ± 193.71	3.7	61.86
SUMMER	10.22 ± 1.90	4988.11 ± 828.30	16.6	180.70
AUTUMN	10.58 ± 2.39	5215.34 ± 332.49	6.3	143.36
		Apodemus flavicollis		
WINTER	13.71 ± 3.78	5044.89 ± 312.13	7.1	98.70
SUMMER	12.36 ± 2.18	6085.81 ± 483.60	7.9	108.13
AUTUMN	12.98 ± 1.45	6043.14 ± 255.31	4.2	55.71
		Apodemus agrarius		
WINTER	10.57 ± 2.48	5403.20 ± 529.50	9.7	167.40
SUMMER	10.99 ± 1.67	6070.82 ± 232.07	3.8	58.01
AUTUMN	11.09 ± 1.40	5886.39 ± 257.38	4.3	57.55
		Clethrionomys glareolus		
WINTER	12.53 ± 3.03	5138.60 ± 186.21	3.6	58.88
SUMMER	10.78 ± 1.39	5798.92 ± 614.50	10.5	137.42
AUTUMN	11.12 ± 1.37	5813.13 ± 358.28	6.1	86.15
		Microtus arvalis		
WINTER	13.10 ± 2.06	5020.08 ± 298.83	5.9	62.83
SUMMER	12.35 ± 1.34	5817.11 ± 567.70	9.7	163.98
AUTUMN	12.82 ± 1.57	5837.15 ± 247.29	4.2	66.09

*) Winter + prevernal season

the striped field mouse (10.45). The amount of ash depends chiefly on the massiveness of the skeleton, and this is more delicate in the shrew, striped field mouse and bank vole than in the yellow-necked field mouse and the common vole.

The ash content has a similar course of seasonal changes in all species. The animals caught in the winter had the largest amount of mineral parts, those from the autumn somewhat less, and the specimens from the summer had decidedly the least (Fig. 2). The age structure of the population may be responsible for this fact. In the summer there are many young animals with weak skeletons, whereas in the late autumn most animals are completely grown up. The seasonal fluctuations discussed above are not intense. In rodents their amplitude lies between 0.4 and 1.8 %, and for the shrew it reaches as much as 2.4 %. These differences in shrews may be of the nature of seasonal-and-age changes (Borowski & Dehnel, 1953). At the end of winter and in the prevernal season, shrews reach the age of old adults. In the high summer the population of shrews consists of young animals and old adults, whereas late in the autumn it is composed nearly completely of young adults born in the same year. The differences in the ash content between species are not very great, they are of the order of 1.9% between the means from the values of the whole year. Since the specific and seasonal variation of the per cent ash is not very great, and, therefore, the general distribution of the caloric values per gram ash-free weight is similar to the course of the caloric values per gram dry weight discussed above.

The caloric value per gram ash-free weight is correspondingly higher, on the average by 10.22—13.71% than the caloric value per gram dry weight (Table 2, Fig. 3).

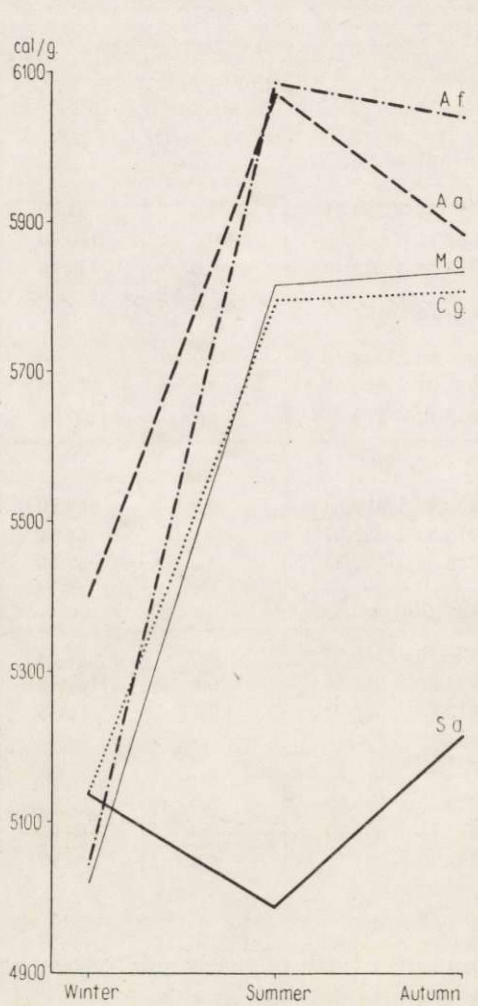


Fig. 3. Seasonal changes in energy values per gram ash-free weight for small mammals. Denotation of species as in Fig. 1.

In the winter the striped field mouse has the highest caloric value (5403.20 cal/g), which varies from the other species with their values grouped between 5020.08 and 5138.60 cal/g. The differences between species, however, do not attain statistical significance. It is striking in this season that the specific differences in the caloric values of body of small mammals do not depend mainly on the ash content. The energy values per gram ash-free weight (Fig. 3) stand only slightly more closely to each other than the caloric values per gram dry weight including the ash content (Fig. 1). For example, the striped field mouse has the lowest ash content and the highest caloric value per gram ash-free weight. On the other hand, however, the species with the similar per cent ash, the bank vole and the shrew (12.53 and 12.60), are marked for almost identical caloric value of ash-free tissue (5138.60 and 5137.18 cal/g).

In summer, rodents reach the highest energy value per gram ash-free weight. At the same time this value for shrews attains the minimum of the annual cycle (4988.11 cal/g). It is for this reason that the differences between all the rodents and the shrew are highly significant. The caloric values per gram ash-free weight are very similar for both of the mice in the summer (6085.81 and 6070.82 cal/g), but they exceed the values for voles by about 270 cal/g ash-free weight. Thus, this difference is not connected with the ash content but with the degree of fatness.

In the autumn the energy value per gram ash-free weight drops somewhat (by about 185 and 43 cal/g) for both the mice and rises slightly for voles. The most evident autumn rise in the caloric value occurs in shrews. In this period they reach 5215.34 cal/g, which is the highest value in their annual cycle, though still lower than the value for rodents, on the average, by 730 cal/g and so differing from it significantly.

It is instructive to analyse the seasonal changes in the caloric values per gram ash-free weight. There are highly significant differences in all the species of rodents, but not in shrews, between the winter and the summer values as well as between the values for the autumn and those for the preceding winter. The summer and autumn values do not differ significantly except for the striped field mouse.

The variation in the caloric values per gram ash-free weight is very similar to that calculated for the caloric value per gram dry weight. The coefficient of variation is comparatively low. It amounts to 3.6—9.7% in the winter and autumn, to 3.8—10.5% in the summer, and to as much as 16.6% for shrews (see Table 2).

3. Caloric Value of Biomass

From the ecological point of view the caloric value of biomass is the most important and it is used in all bioenergetic convertions. It is obtained from the caloric value per gram dry weight, taking into account the water content.

The percentage water for the species under study is offered in Table 3 and also illustrated by Fig. 4. As will be seen from the graph, the water content is a character which is rather uniform in the species examined and has a fairly similar course in the annual cycle. In the winter, rodents and shrews contain the smallest amount of water in their bodies (64.79—69.88 %). During the summer the water content increases somewhat and ranges from 69.10 % in shrews to 71.87 % in bank voles. A drop in the

Table 3.
Energy values of biomass of body for small mammals.

Season	Body weight Mean ± S.D.	Content of water (%) Mean ± S.D.	Value cal/g biomass		
			Mean ± S.D.	Coeff. Variat. (%)	Avg. value for whole animal
		Sorex araneus			
WINTER *)	6.11 ± 0.52	64.79 ± 1.58	1577 ± 29.4	5.9	9639.1
SUMMER	7.65 ± 2.35	69.10 ± 1.98	1369 ± 212.8	15.5	10472.8
AUTUMN	6.03 ± 0.58	66.94 ± 1.95	1547 ± 110.5	7.1	9328.4
		Apodemus flavicollis			
WINTER	25.46 ± 3.70	68.27 ± 2.13	1391 ± 17.7	1.2	35414.9
SUMMER	23.26 ± 9.45	71.12 ± 2.81	1552 ± 233.6	15.5	36099.5
AUTUMN	24.06 ± 7.70	72.28 ± 1.69	1408 ± 201.1	14.2	33876.5
		Apodemus agrarius			
WINTER	17.35 ± 2.65	65.42 ± 3.34	1693 ± 336.1	19.8	29373.5
SUMMER	25.94 ± 7.03	71.40 ± 2.70	1543 ± 181.0	11.7	29580 0
AUTUMN	17.44 ± 3.58	68.49 ± 1.35	1671 ± 143.8	8.6	27638.6
		Clethrionomys glareolus			
WINTER	16.51 ± 2.82	68.04 ± 1.45	1434 ± 101.4	7.0	23675.8
SUMMER	20.40 ± 5.92	71.87 ± 2.05	1450 ± 170.5	11.7	29580.0
AUTUMN	18.70 ± 3.60	71.33 ± 1.63	1478 ± 114.6	7.7	27638.6
		Microtus arvalis			
WINTER	22.56 ± 4.64	69.88 ± 2.77	1301 ± 183.3	14.0	29508.5
SUMMER	19.23 ± 3.28	69.27 ± 3.90	1586 ± 342.6	21.6	30498.8
AUTUMN	13.63 ± 2.62	69.84 ± 2.43	1518 ± 185.2	12.2	20690.3

*) Winter + prevernal season

percentage water can be observed in most species in the autumn. Considering the data for the whole year, we find that bank voles and yellow-necked field mice are "better hydrated" than the other rodents. Shrews have the lowest water content all through the year, though they do not differ principally from rodents in this respect.

The caloric values of biomass fall within a range of 1301—1693 cal/g for all the species and seasons (Fig. 5, Table 3). This important value is fairly compact and does not show any regular seasonal changes or interspecific differences. If the values for all the rodents and shrews are added up within seasons, the mean for the winter and prevernal season will be 1497 cal/g, for the summer 1500 cal/g, and for the autumn 1524 cal/g. Thus the most general mean annual value for all the species is about 1500 cal/g. The

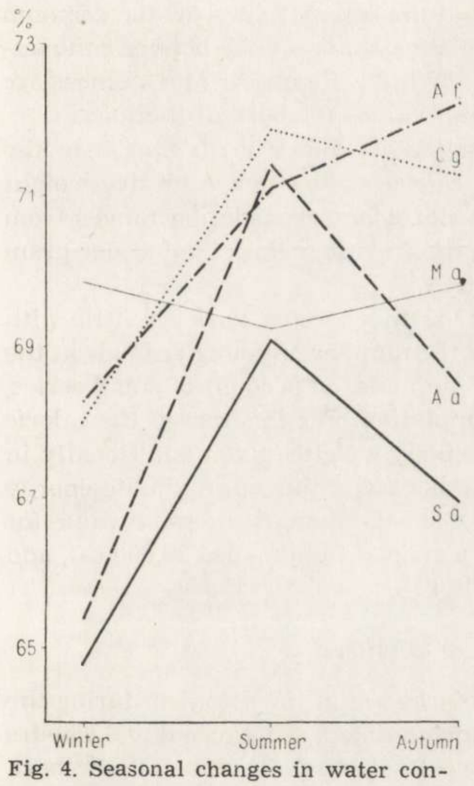


Fig. 4. Seasonal changes in water content expressed in per cent of fresh weight of body for small mammals. Denotation of species as in Fig. 1.

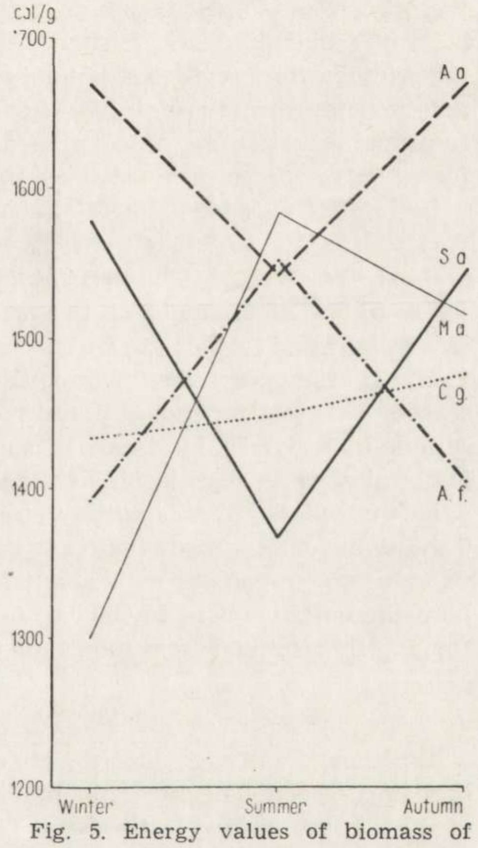


Fig. 5. Energy values of biomass of body for small mammals in the annual cycle. Denotation of species as in Fig. 1.

mean annual values for various species are 1450 cal/g for the yellow-necked field mouse, 1454 cal/g for the bank vole, 1468 cal/g for the common vole, 1498 cal/g for the shrew, and 1636 cal/g for the striped field mouse. At first sight only the striped field mouse varies evidently from the other animals. However, a statistical analysis of differences between the species and seasons does not allow the free listing of the above-presented means.

In the winter the striped field mouse differs highly significantly from the remaining rodents, and the shrew from the common vole and the yellow-necked field mouse, whereas the common vole differs significantly from the bank vole. In the summer the statistically significant differences were revealed only between the shrew and the common vole as well as both the mice. In the autumn the highly significant differences in the energy values of biomass occur only between the striped field mouse and the other rodents. Also seasonal intraspecific differences often exceed the level of accidentalness. There are highly significant differences between the winter caloric values of biomass and the summer ones for the common vole and the shrew and, in the case of the common vole, between the autumn values and those of the preceding winter. Significant differences are found between the summer and autumn values for both of the mice.

Individual variation in this character is somewhat higher than the variation of the previously discussed caloric values per gram dry weight and ash-free weight. The percentage coefficient of variation ranges from 1.2 to 21.6%, for it includes the variation of the caloric value per gram dry weight and that of the water content.

The average body weight (biomass) of the species varied a little with season. This was dependant mainly on the number of young animals in the sample material. The presence of such animals, on account of small series, is not always representative of the population. For this reason the caloric values of whole animals with average body weights given additionally in Table 3 are only approximate. As can be seen, the approximate energy value of a common shrew is about 10,000 cal, whereas the same value for both the voles is about 27,000 cal, for a striped field mouse 29,000 cal, and for a yellow-necked field mouse 35,000 cal.

4. Caloric Values of Litters

The energy values of litters were determined in the summer, during the breeding season. The litters of new-born animals not exceeding 12 hours of life were examined in this way. The cal/g dry weight value of new-born animals was lower than that of adults by 200—1200 cal/g in this period. For the bank vole, common vole, and yellow-necked field mouse it amounted respectively to 4746.72, 4894.63, and 4181.91 cal/g. The new-born animals have also somewhat less ash in their bodies than their parents. In the litter of a yellow-necked field mouse the ash formed 10%, in the bank vole 10.6%, and in the common vole as much as 12.21%. The caloric value calculated per gram ash-free weight is the lowest for new-born yellow-necked field mice (4650.04 cal/g), higher for common voles (5578.42 cal/g), and intermediate for bank voles (5307.58 cal/g). The percentage water in the body of new-born rodents is, naturally, higher than in adult animals, ranging approximately from 73 to 85. The energy value of biomass depended to a high degree on the water content and, for this reason, is considerably lower than in adult rodents. New-born common voles which were hydrated the most, had an extremely low caloric value of biomass — 742.44 cal/g. They are followed by new-born bank voles (1030.39 cal/g) and yellow-necked field mice (1139.20 cal/g) with the lowest water content.

The weight of the litter of the bank vole, composed, on the average, of 4.5 new-born animals, was 5.4 g; it amounted to 5.8 g for the litter of yellow-necked field mice (5 young ones) and 7.12 g for common voles (4 young ones). The energy value of such new-born litters is calculated and amounts respectively to 5564.4, 6607.4, and 5286.2 cal. This makes from 17.3 to 18.8% of the caloric value of an adult rodent in the same season (Table 3). These figures, however, do not include placentae and foetal membranes, which also constitute some expense of energy at reproduction.

The data offered above for the litters of three rodential species are only approximate, as they are based on a very small number of specimens (4 litters — 18 new-born animals).

IV. DISCUSSION

1. Energe Value of Small Mammals

The caloric value of tissue of small mammals has hitherto been determined for only three species of rodents. Golley (1959, 1960) studied samples from 4 specimens of *Microtus pennsylvanicus* (Ord) and established their average caloric value equal to 4650 cal/g dry weight. He (Golley, 1959; Davis & Golley, 1963) presented also the energy value for white mice (*Mus musculus* L.), amouting to 5675 cal/g. Next, Golley (1961) used the mean value calculated from both these species, 5163 cal/g. Sharp, 1962 (after Davis & Golley, 1963) determined the caloric value of tissue of *Oryzomys palustris* Harlan as equal to 5840 cal/g. These American data are based on poor materials; it is, however, worth while to compare them with the results offered in this paper.

The caloric value of *M. pennsylvanicus* from Michigan resembles that for the European member of this genus, *M. arvalis*. The value for *M. pennsylvanicus* (4650 cal/g) is lower only by about 200 cal/g than the average annual value for *M. arvalis* (4857 cal/g) and lies just between the values from the autumn and the end of winter (5090—4364 cal/g). The data for *Mus musculus* and *Oryzomys palustris*, however, diverge considerably from the present annual averages for both field mice (*Apodemus*), which were characterized by the highest energy values (5175 and 5002 cal/g). In the case of white mice this difference may be due to the intense fat deposition in these animals in the laboratory.

The caloric values per gram dry weight have been lacking for mammals. All such values presented by Slobodkin & Richman (1961) and by P a i ne (1964) for various types of invertebrates lie within a range of 5185—6675 cal/g. The values calculated for five species of small mammals in this study are fairly uniform. The caloric value per gram ash-free weight for these animals ranged from 4988 to 6086 cal/g in various seasons. This corroborates S l o b o d k i n's opinion (1962) that the caloric value per gram dry weight after taking away the mineral parts is similar in different types of animals. On the other hand, differences in the values within the same group, i.e., small mammals, are nearly independent of the ash content.

2. Variation of Energy Values

Seasonal changes in the caloric values of mammals under study are more essential than the differences between species. The causes and nature of both seasonal and specific differences can perhaps be explained using the caloric value per gram dry weight as an example.

It may be useful to bring to mind the general nature of this variation in rodents and shrews, using statistically significant differences (Fig. 1, Table 1). In all the rodents the caloric values for the winter differ highly significantly from the values for the summer. Similar differences occur also between the values for the autumn and those for the preceding winter, whereas the statistical differences between the species of rodents are observed only in the winter between the striped field mouse and both the common vole and the yellow-necked field mouse. Shrews differ in this respect significantly from all the rodents in the summer and autumn. Variation in the caloric value per gram dry weight depends perhaps on changes in the fatness or in the ash content. This last may be responsible only to a low degree for the variation of the caloric value of small mammals. The seasonal courses of the caloric values per gram dry weight and per gram ash-free weight hardly varied from species to species (Figs. 1 and 3). Fluctuations in the ash content in various species and seasons were also small (Table 2, Fig. 2). It was to be expected, as the rodents and shrews examined represented a uniform type of skeletal structure. If animals dealt with have very various types of exo- or endoskeleton and contain 8—58% of ash in their bodies, their differentiated caloric value per gram dry weight depends chiefly on the ash content (S l o b o d k i n & R i c h m a n, 1961; P a i n e, 1964).

Everything points to the fact that the variation of the caloric values in small mammals is closely connected with the fat content of their bodies. The energy value of fats determined in the bomb calorimeter is 9.3—9.5 Kcal/g, whereas the caloric value of proteins in the body is nearly half that value (S p e c t o r, 1956). Hence, a small change in the fatness of an animal can change its caloric value considerably.

The information on the fatness of rodents is scanty and refers to animals from different climatic zones. Changes in fatness in the annual cycle may depend, e.g., on changes in the environmental temperature (Sealander, 1951), food supplies of the environment (Connell, 1959 after Golley, 1962), density of the population (Hsia Wu-ping & Sun Chung-lu, 1963), as well as on the age and hibernation of animals (Jameson & Mead, 1964). It is difficult to make up a uniform picture of these changes on the basis of such different data. The curve of fatness, established by Connell (1959, after Golley, 1962) for *Peromyscus polionatus* Wagner from the southern states of the U.S.A., has two evident peaks, one in the summer and one in the winter. Sealander (1951) holds that *Peromyscus leucopus* Davis and *P. maniculatus* Coues in the central northern States have the highest fat content in the winter. Hsia Wu-ping and Sun Chung-lu (1963) found the greatest fatness of *Clethrionomys rutilus* Pallas from China in April, and they referred it to the density of population, which was the lowest at that time. So far there are no data on the fatness of Central-European rodential species. The dissections of many animals and preparation of samples for the calorimeter as well as the knowledge of the nutritional conditions (Drożdż, in litt.) make it possible only to imagine the probable cycle of seasonal changes in fatness. At Ojców, where most of the animals used for this study were collected, the year 1964 was characterized by a retardation in the arrival of spring and fairly good crops of beechmast in the autumn. The end of the winter and the prevernal season are a critical nutritional period for rodents in a deciduous forest (Grodziński, 1961, 1963; Górecki & Gębczyńska, 1962). And so all the rodents had the lowest caloric value in the year in the period (Figs. 1 and 3, Tables 1 and 2). Out of these only striped field mice were more fatty, which may have been due to their synanthropic ways of life in the winter. In the spring and early in the summer the ground cover of the beech forest develops very rapidly (Rajchel, 1965). It provides rodents with a plenty of available and readily taken food (Drożdż, in litt.). This explains a rapid growth of the caloric value of the body for rodents in the spring. Late in the summer and in the autumn the fatness and caloric value of rodents should be the highest in the annual cycle. The autumn of 1964 was favourable to rodents because of these abundant beechmast crops. In spite of that, the caloric value of the body of rodents hardly changed in the period from summer till autumn. The shrew holds an exceptional position, as its caloric value per gram dry weight is maintained at nearly the same level throughout the year (4449.17—4682.73 cal/g), being evidently lower than the value for rodents. Probably this distinctness of shrews may also be explained by their fatty conditions.

Shrews feed mainly on small invertebrates such as insects, myriapods, and snails as well as on seeds (Borowski & Dehnel, 1953; Kisielewska, 1963). The amounts of available insects on the floor of a forest in the winter (benumbed insects in the litter, fauna of groundlings) and in the high summer are alike (Grodziński, 1961). Consequently, the food supplies for shrews do not change during the year as essentially as the suplies for phytophagous rodents do. On the other hand, in view of shrews' very intense metabolism and diurnal activity (Gębczyński, 1965), the deposited fat could not be maintained in their body for a long time. Shrews develop a fairly great fatness of body only in captivity (Pucek, 1964).

3. Energy Value of Productivity of Small Mammals

In order to determine the net productivity and energy flow through the populations of small mammals it is, above all, nessary to have at one's disponal the data on the caloric value of biomass. This value refers closely to the amount of water in animals' bodies. The hydration of small mammals under study changed with season and was the highest in summer, 70.55%, generally slightly smaller in autumn, 69.77%, and the lowest in the winter and prevernal period, 67.88% (Table 3, Fig. 4). The average per cent water ranges from 68.43—70.55% for rodents and amounts to 66.94% for shrews. Similar annual cycles are observed in *Peromyscus* (Sealander, 1951) as well as in *Citellus* and *Eutamias* (Jameson, Mead, 1964). Seasonal variation in the hydration of small mammals levels away the differences between the caloric values of their biomass remarkably. The cal/g dry weight value for mammals is the lowest in the winter and in the prevernal season, i.e., just when their water content is the lowest. It is considerably higher in the summer, but the rodents and shrews then examined were more hydrated. As a result, the caloric value of biomass is fairly constant for the five species under study. In different seasons it fluctuated within a narrow range of about 1.3—1.7 Kcal/g (Table 3, Fig. 5). Such a narrow range of differentiation of this important value is very convenient to all bioenergetic calculations. Golley and Sharp (Golley, 1960; Davis & Golley, 1963) presented rather uniform values for three American rodents. They established the values of 1.4 Kcal/g for *Microtus pennsylvanicus*, 1.7 Kcal/g for *Mus musculus*, and 1.9 Kcal/g for *Oryzomys palustris*. As can be seen, only this last species exceeds the values calculated for our small mammals.

Golley (1962) formulated an equation to calculate the energy flow through a population of rodents, for which it is necessary to know the caloric value of biomass to express the net productivity,

$$E_t = \Sigma\, 115.2\, (RB)_{wt} + 1.4\, (PN)_w$$

where R is the average oxygen consumption per hour (115.2 = product of caloric equivalent of oxygen, 4.8, and 24 hours), B — biomass, P — average net productivity, N — number of specimens, w — particular weight or age class, and t — temperature of environment (including the nest).

In this equation Golley applied the coefficient of caloric value of biomass for *Microtus pennsylvanicus*, i.e., 1.4 Kcal/g. This coefficient seems to be slightly too low for our wild mammals. The results of the present study make it possible to offer three different degrees of accuracy in calculations of the net productivity of populations. Naturally, the parameters suggested here refer to rodents and shrews of Central Europe.

1) The least accurate but simplest method would be to adopt only one mean value, 1.5 Kcal/g for all species and seasons. It is this coefficient (1.501 Kcal/g) that has been calculated from Table 3 for the whole material in the face of statistically significant differences, which distinguish some species and seasons. When calculated only for the four species of rodents under study, it is almost identical (1.502 Kcal/g).

2) More accurate results can be obtained, if the coefficient of caloric value of biomass for all the rodents has been differentiated for seasons, whereas in the case of shrews one value is used for all the seasons. The mean for all the rodents will be 1.455 Kcal/g in the winter and prevernal season, 1.533 Kcal/g in the summer, and 1.519 Kcal/g in the autumn (summer + autumn = 1.526 Kcal/g). The mean annual caloric value for the shrew is 1.498 Kcal/g.

3) The last and most detailed method of calculation is the adoption of distinct values for particular species of animals and, in addition, their contingent differentiation according to seasons. The annual means from the data for the species examined are 1.498 Kcal/g for the shrew, 1.450 Kcal/g for the yellow-necked field mouse, 1.636 Kcal/g for the striped field mouse, 1.454 Kcal/g for the bank vole, and 1.468 Kcal/g for the common vole. However, all these animals except the bank vole exhibit statistical differences between some of the seasons. For this reason, double means should be used in calculations: for the common vole 1.301 Kcal/g (winter) and 1.552 Kcal/g (summer and autumn), for the yellow-necked field mouse 1.471 Kcal/g (winter and summer) and 1.408 Kcal/g (autumn), for the striped field mouse 1.618 Kcal/g (winter and summer) and 1.671 Kcal/g (autumn). For the shrew the winter value amounts to 1.577 Kcal/g and that for summer and autumn to 1.458 Kcal/g. Such accuracy based on the seasonal differentiation of the values for particular species may lead to exaggeration. The individual energy values of biomass depend on local differences in the age structure and the density of population as well as on the food supplies of environment. Consequently, these values probably vary from year to year.

The results calculated from concrete materials by the three methods presented above differ from each other within limits of 3—5%. Therefore, for all less precise calculations the first or the second method is generally recommendable. Only in the case when one species is dealt with, the third, most punctilious, method may be used.

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WARTOŚĆ ENERGETYCZNA CIAŁA DROBNYCH GRYZONI

Streszczenie

Zbadano wartość energetyczną tkanek ciała pięciu gatunków drobnych ssaków, które dominują w naszych ekosystemach leśnych i polnych. Są to: ryjówka aksamitna (*Sorex araneus* L.), mysz leśna (*Apodemus flavicollis* Melch.), mysz polna (*Apodemus agrarius* Pall.), nornica ruda (*Clethrionomys glareolus* Schr.) i nornik zwyczajny (*Microtus arvalis* Pall.). W kalorymetrze spalono 270 próbek z 220 zwierząt, które zostały odłowione w trzech zasadniczych porach roku (późna zima i przedwiośnie, lato, jesień). Określano wartość kaloryczną suchej masy, procent wody i popiołu, a obliczano także wartość kaloryczną masy bez popiołu i biomasy.

1. Wartość kaloryczna suchej masy zmienia się sezonowo, przy czym przebieg tych zmian jest odrębny u gryzoni i ryjówek. U wszystkich gryzoni wartość ta jest najniższa z końcem zimy i na przedwiośniu (średnia 4508,44 cal/g). Potem wzrasta ona gwałtownie i w pełni lata osiąga wysoki poziom (średnio 5261,05 cal/g), który utrzymuje się w jesieni (5204,08 cal/g). Kaloryczność ciała ryjówek przez cały rok utrzymuje niską wartość od 4449,17 do 4682,73 cal/g. (Tabl. 1, Ryc. 1).

2. Zawartość popiołu w ciele drobnych ssaków zależała głównie od masywności szkieletu. Ilość popiołu u wszystkich gatunków w różnych sezonach wahała się od 10,2—13,7%. (Tabl. 2, Ryc. 2). Wartość kaloryczna wolna od popiołu przewyższa o taki właśnie procent wartość suchej masy, wykazując przy tym bardzo podobną zmienność gatunkową i sezonową (Ryc. 3).

3. Uwodnienie drobnych ssaków zmieniało się sezonowo: najwyższe było w lecie. 70,55%, nieco mniejsze na ogół w jesieni (69,77%), a najniższe w zimie i na przedwiośniu — 67,88% (Tabl. 3, Ryc. 4). Sezonowa zmienność uwodnienia drobnych ssaków niweluje znacznie różnice pomiędzy wartością kaloryczną ich biomasy. Dlatego kaloryczność biomasy jest wielkością dość stałą, dla pięciu gatunków w różnych sezonach wahała się zaledwie od 1301—1693 cal/g (Tabl. 3, Ryc. 5).

4. Kaloryczność suchej masy ciała noworodków gryzoni wynosi od 4181,91—4894,63 cal/g, to jest o 200—1200 cal/g mniej niż taka wartość dla dorosłych zwierząt w okresie rozrodu. Noworodki zawierają w swym ciele nieco mniej popiołu (10,0—12,3%), natomiast ciało ich jest znacznie bardziej uwodnione (73—85% wody). Dlatego kaloryczność biomasy noworodków jest bardzo niska (742,44—1139,20 cal/g). Wartość energetyczna świeżo urodzonego miotu można oszacować na 17—19% wartości kalorycznej dorosłego gryzonia (por. tabl. 3).

5. Zmienność sezonowa i różnice gatunkowe wartości kalorycznej suchej masy ciała drobnych ssaków zależą głównie od ich otłuszczenia, a tylko w nieznacznym stopniu od zawartości popiołu.

6. Do obliczania produktywności netto populacji drobnych ssaków można zaproponować różną dokładność parametru wartości kalorycznej biomasy: (a) Użycie wspólnej dla wszystkich sezonów i gatunków wartości średniej (1,5 Kgcal/g). (b) Zróżnicowanie tej wartości u gryzoni na różne sezony — 1,455 Kgcal/g dla zimy z przedwiośniem, 1,526 Kgcal/g dla lata i jesieni. Dla ryjówek wystarczy jedna średnia roczna 1,498 Kgcal/g. (c) Przyjęcie oddzielnych średnich dla poszczególnych gatunków (*S. araneus* — 1,498 Kgcal/g, *A. flavicollis* — 1,450 Kgcal/g, *A. agrarius* — 1,636 Kgcal/g, *Cl. glareolus* — 1,454 Kgcal/g, *M. arvalis* — 1,468 Kgcal/g) i ewentualne różnicowanie ich jeszcze w sezonach.