

Bioenergetics of British Shrews in Grassland

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Some aspects of shrew energetics are discussed in the light of field and laboratory experimentation. The daily consumption, faecal production and throughput rates of *Sorex araneus* (Linnaeus, 1758) *Sorex minutus* (Linnaeus, 1766) and *Crocidura suaveolens cassiteridum* (Hinton, 1924) were measured in the laboratory. Part of the variation in stated consumption/day in the literature was shown to be due to the variable water contents of the artificial diets. The assimilation efficiency of *C. suaveolens* was measured (89%) and found to be similar to quoted values for other shrews. This efficiency was found to increase when the animals were deprived of water. A diagram of energy flow through shrew populations in Wytham grassland is based on dietary analysis of 244 and 130 snap trapped *S. araneus* and *S. minutus* respectively. Finally annual consumption and production figures for the two species are presented and reasons for the high P/C ratios suggested.

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INTRODUCTION

The work reported here formed part of a larger study of the ecology of British shrews, and extensive use is made in this paper of the data on field diets and population biology of *Sorex araneus* and *Sorex minutus* (Pernetta, 1973, 1976). In view of the current interest in bio-energetics and the relative dearth of such information for small insectivores it was felt that a combination of the above data and details of the daily food intake, faecal output, assimilation efficiency and calorific measurements obtained in the laboratory would produce an interesting picture of the ecological energetics of these animals.

MATERIAL AND METHODS

The field diets of *Sorex araneus* and *Sorex minutus* were determined by analysis of 244 and 130 snap trapped individuals of each species respectively. This snap trapping was carried out over 18 months in *Brachypodium pinnatum*

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dominated grassland on the Oxford University Estate at Wytham. Data on the densities of these species in a similar habitat, was obtained by means of a concurrent mark, release, recapture programme using Longworth live traps. These data are more fully reported elsewhere (Pernetta, 1973, 1976).

Details of the daily food intake were obtained from laboratory maintained individuals which had been in captivity for at least 30 days. Daily faecal output was determined by total collection in the case of *Crocidura suaveolens* and by extrapolation from four hour observation periods in the case of *S. araneus* and *S. minutus*. The calorific value of the food and faeces of *C. suaveolens* were determined using a Philipson microbomb calorimeter and the assimilation efficiency of this species calculated.

RESULTS

1. Metabolic Expenditure

Table 1 presents values taken from the literature of the body weight, daily food intake and ratio of food intake to body weight for various shrew species. A regression analysis was performed on these data using the equation: $\text{Log}(\text{ratio food intake:body weight}+1)=0.4773-0.0141(\text{Body weight})$.

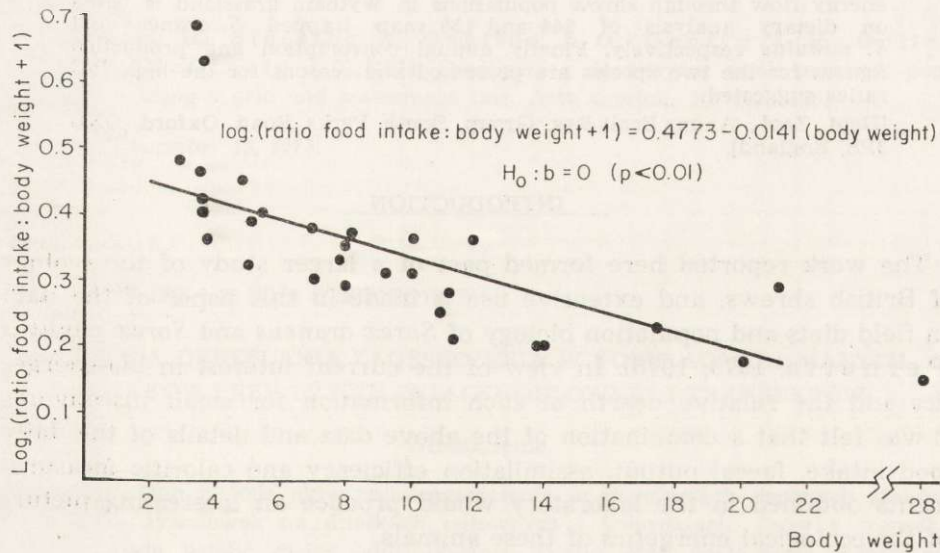


Fig. 1. Regression analysis of the ratio of food intake to body weight on the body weight of various shrew species; data from Table 1.

The resulting regression line (Fig. 1), when tested against the null hypothesis that, the ratio of food intake to body weight is constant for increasing body weight, is found to differ significantly ($p < 0.01$). Such a negative correlation might be expected from the decreasing ratio of surface area

to volume, and hence one presumes a decreasing proportional heat loss. This regression line can be used to calculate the daily food consumption where the weight of the animal is known.

The generally high food intake in shrews has lead many authors to the conclusion that the daily metabolic rate of these animals must be

Table 1
Food consumption and ratio to body weight, for various shrews.

Species	Body wt. g	Food wt. g	g food/g body wt/day	References
<i>Cryptotis floridana</i>	5.0	5.5	1.1	Springer, 1937
<i>Diplomesodon pulchellum</i>	10.0	10—17	1.3	Hepner, 1939
<i>Microsorex hoyi</i>	3.5	6.5	1.86	Buckner, 1964
<i>Blarina brevicauda</i>	20.1	10.1	0.5	"
	18.0	—	0.3—0.5	Hamilton, 1930
	—	—	0.7	Babcock, 1914
	21.0	—	0.96	Morrison <i>et al.</i> 1957
	23.0	—	0.42	"
	—	—	0.9	Shull, 1907
	15.8	—	1.16	Tupikova, 1949
<i>Neomys fodiens</i>	14.1	8.2	0.58	Hawkins & Jewell, 1962
	13.8	8.0	0.58	"
	17.6	12.7	0.72	"
	11.1	9.9	0.89	"
	10.9	8.4	0.77	"
<i>Crocidura suaveolens</i>	8.0	7.4	0.93	"
	5.1	—	1.33	Tupikova, 1949
<i>Sorex cinereus</i>	3.6	11.7	3.3	Blossom, 1932
	3.6	5.8	1.61	Buckner, 1964
<i>Sorex arcticus</i>	5.4	8.2	1.52	"
<i>Sorex minutus</i>	3.6	5.4	1.5	Hawkins & Jewell, 1962
	4.8	8.9	1.85	"
	3.0	—	2.03	Tupikova, 1949
<i>Sorex</i> sp.	3.66	—	1.27	Morrison <i>et al.</i> 1957
	3.35	—	3.84	"
<i>Sorex araneus</i>	6.5	6.5	1.0	Hawkins & Jewell, 1962
	8.0	9.9	1.24	"
	11.8	15.2	1.29	"
	7.8	8.9	1.14	"
	9.2	9.7	1.05	"
	11.0	6.8	0.62	Rörlig, 1905
	8.33	—	1.42	Tupikova, 1949
	8.43	4.3	0.543	Wolk, 1969
	—	—	2.5	Svihla, 1934
<i>Sorex palustris</i>	10.0	10.3	1.03	Conaway, 1952

high (Morrison *et al.*, 1957; Gębczyński, 1965). Hawkins & Jewell (1960) have shown that the resting metabolic rate is the same as that for white mice of the same size. Even if this is correct the overall energy expenditure per day is likely to be greater than that of rodents since the activity of shrews is higher (Crowcroft, 1954; Gębczyński-

s ki, 1965). More recent and comprehensive work V o g e l (1976) suggests that a very real difference exists between shrews of the subfamily *Soricinae* and other mammals in terms of their basal metabolic rates, that of the shrews being much higher. He further shows that the *Crocidurinae* have a basal metabolic rate lower than that of the *Soricinae* and approaching that of other mammals.

If *Sorex minutus* is assumed to have a mean weight of 4 g then the average heat loss per day becomes 7.2 kcal/animal. This value is somewhat higher than the 5–6 kcal/animal/day quoted by G ę b c z y ń s k i (1971) for pre-winter juveniles, but agrees with the mean of values presented in his earlier paper, G ę b c z y ń s k i (1965). The assumption of an annual mean weight of 4 g for *S. minutus* is based on the work of C r o w c r o f t (1957), S h i l l i t t o (1960) and B o r o w s k i & D e h n e l (1953). C r o w c r o f t (1957) presents data with a mean weight of 3.5 g and range of 2.6 g–5.6 g, values which are somewhat lower than those of this species. A mean of their monthly means is 4.6, range 2–5 g. ~~of this species. A mean of their monthly means is 4.6, range 2–5 g.~~ ^{the workers Borowski and Dehnel (1953) presents the mean} monthly weights for large samples representing two separate generations of this species. A mean of their monthly means is 4.6, range 2–5g. Elsewhere in the present paper a mean weight for *S. araneus* is taken as 7.5 g, following C r o w c r o f t (1954) and in close agreement with B o r o w s k i & D e h n e l (1953), 7.6 g and 8 g being the annual means of their samples. This annual mean weight for *Sorex araneus* corresponds to an average daily heat loss of 9.9 kcal/animal/day which agrees well with the individual values determined by G ę b c z y ń s k i (1965) of 9.2 kcal/animal/day.

2. Daily Food Intake

Some of the confusion surrounding the magnitude of the variation in the daily food intake in single species of shrews may be due to the shrews initial behaviour in captivity. When first brought into the laboratory individuals feed at a higher rate than later, and put on weight (C r o w c r o f t, 1957) or may, during their captivity exhibit rapid increases and decreases in body weight (P u c e k, 1964).

The nature of the artificial diets upon which assessments of daily intake are based, may also contribute to the variation observed by different workers. For example the very high ratio of food intake to body weight quoted by M o r r i s o n *et al.* (1957) for *Sorex* sp. (Table 1) is based on measurements taken from animals fed on a diet of earthworms whereas the smaller value is taken from animals fed on rat liver. The low values of W o ł k (1969) are due to the fact that she fed her shrews on partially dried meat. (For this reason the values are not included in the regression calculation for Figure 2). It would appear from this that the water content

of the diet (as might be expected) affects the daily food intake when expressed in wet weights.

During the present work it was noted that when shrews were fed on a diet consisting solely of fly larvae the daily intake of food (wet weight) was greater than that obtained when the animals were fed on a diet of last instar *Tenebrio molitor* larvae. The calculated daily intake for these two diets in terms of dry weight was however approximately equal (Table 2). The degree of chitinisation of items in the diet might

Table 2

Daily food intake of *C. suaveolens* and *S. araneus* expressed in dry and wet weights. (Mean based on 2 days testing on 10 individuals of each spp.)

Food	<i>C. suaveolens</i> wet wt., g		Intake/day dry wt., g	<i>S. araneus</i> wet wt., g		Intake/day dry wt., g
	mean	range		mean	range	
<i>T. molitor</i> last instar larvae	6.2	4.5—8.4	2.7	5.8	4.0—7.2	2.5
<i>Musca</i> sp. pre-puparial larvae	11.2	8.5—14.7	2.5	19.5	8.0—16.0	2.4

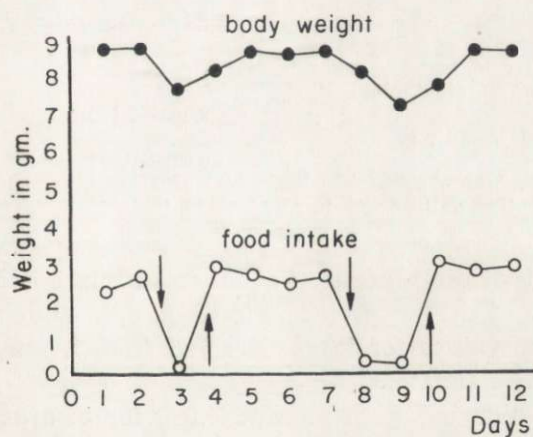


Fig. 2. The effect of drinking water on food consumption and body weight of *C. suaveolens*. Arrows indicate water removed or replaced.

also affect the daily food intake; a shrew might be expected to have a higher daily intake when feeding on highly chitinised invertebrates than when feeding on lightly chitinised ones; due to the indigestibility of chitin; further investigations are necessary to elucidate this point.

In addition to the two factors mentioned above the daily food intake was found to vary in the presence or absence of free water for the animals to drink. When *Crocidura suaveolens* was deprived of water the

daily food intake dropped dramatically and the body weight of animals subjected to a variable regime of water presence and absence fluctuated in phase with the fluctuations in intake (Fig. 2). This suggests that an external water source is vitally important to these animals and that in its absence body fats may be rapidly metabolised to provide metabolic water. Indeed experience in keeping shrews has shown that both *S. araneus* and *S. minutus* die within a few days of being deprived of water. The only occasion on which *C. suaveolens* was observed to feed direct from the rectum (as described by Crowcroft, 1957 for *S. araneus*) occurred when the animals were deprived of water (8 observations).

In attempting to assess the daily food intake in the field one can do little more than accept a value based on laboratory determinations, accepting that many of these values are not in fact directly applicable

Table 3
Wet weight of the gut contents of field snap trapped
S. araneus and *S. minutus*

	<i>S. araneus</i>	<i>S. minutus</i>
Number	244	130
Mean wt. food in stomach, g	0.1277	0.09
Range, g	0.000—0.425	0.000—0.125
Mean wt. food in gut, g	0.480	0.139
Range, g	0.090—0.902	0.054—0.800
Total wt. food, Mean, g	0.608	0.229
Percentage of the daily food intake	6.1%	2.3%

to field diets. In that the regression equation in Fig. 1 is calculated using data for a variety of shrew species maintained on a wide variety of diets by many workers, values for intake derived from it may be considered the »best possible« estimate.

Substituting body weights of 7.5 and 4.0 g for *S. araneus* and *S. minutus* respectively, into the equation one obtains values for consumption of 10 g for *S. araneus* and 6 g/day for *S. minutus*. In the case of *S. araneus* this value is 5% larger than one obtained by taking a mean of the values in Table 1, but in the case of *S. minutus* a mean taken from the values in Table 1 is 20% greater than the present one.

Table 3 presents the approximate weights of the gut contents of snap trapped shrews from grassland. Such values are highly suspect being obtained by the difference in weight between empty and full guts; which are affected by the extent to which the stomach and gut are adequately dried (an impossible factor to keep constant) before each weighing. The results do serve to indicate the order of fullness, which represents

approximately 5% of the daily food intake. This in itself suggests that these animals are rarely in a state of repletion in the wild and supports the observations on field activity which suggest that these animals spend much of their time searching for food (Crowcroft, 1957; Gębczyński, 1965; Buchalczyk, 1972; Pernetta, 1973).

3. Through Put Rate

On the basis of the values for the weight of food found in the gut of field trapped animals it is possible to calculate a theoretical value for the rate at which food passes through the gut. If on average any animal in the field at any instant in time has 5% of the daily ration in its alimentary tract, then there must be total replacement of this material every 72 minutes.

Table 4
Rate of movement of various items through the gut
of *S. araneus*

Shrew No.	Specimen	Time of Appearance, Minutes	
		First	Last
1	<i>Philoscia</i>	20	180
2	<i>Philoscia</i>	24	150
3	<i>Philoscia</i>	40	180
4	<i>Philoscia</i>	32	167
5	<i>Philoscia</i>	18	100
6	Lumbricid	42	200
7	Lumbricid	50	191
8	Lumbricid	67	280
9	<i>Arion</i>		(71) ¹
10	<i>Arion</i>		(91)

¹ Time of appearance of radula

An attempt was made during the present study to test this theoretical value in the laboratory. Captive animals were fed solely on a diet of one species (usually fly larvae) and then presented with a different item. The times of first and last appearance of parts of this item were then recorded by faecal collection and examination (Table 4).

It became apparent as the trials proceeded that the results would be difficult to interpret conclusively and that the amount of labour required to quantify them sufficiently to produce average throughput rates for even the major items would be prohibitive. They were therefore not pursued. However, in conjunction with the studies of Rudge (1968) for *Sorex araneus* and Kostelecka-Myrcha & Myrcha (1964) on *Neomys fodiens* they indicate several observable tendencies. (a) Smaller items with brittle exo-skeletons pass through more rapidly than larger

tougher items such as *Arion*. (b) That the rate of passage is between 30 minutes and 3 hours. (c) That each item becomes so mixed with the total gut contents that its total egestion time is extended over a long period.

Whilst the results are somewhat inconclusive in themselves they do serve as additional information supporting the contention that shrews are rarely in a state of repletion in the field, in that the theoretically derived time of total replacement of gut contents lies midway between the times of first and last appearance of items in the trials above.

4. Faecal Production

Observations made during the above and other behavioural experiments indicate the rate and quantity of faecal production. The time of production of the first faecal pellet after introduction to an experimental arena is highly variable, and depends upon the state of the animal. The minimum time for production of the first pellet was 4 minutes, the maximum 180 minutes ($n=62$), the average 22 minutes. In the majority of cases at least one food item was eaten prior to defecation, and once feeding had commenced defecation continued at a fairly regular rate. The results are summarised below:

S. minutus: 6 observation periods, total 10½ hours. Pellets produced approximately every 10 minutes giving a daily production of 144.

S. araneus: 24 observation periods, total 96 hours. Pellets produced approximately every 18 minutes giving a daily production of 80.

C. suaveolens: 47 observation periods, total 160 hours. Pellets produced approximately every 15 minutes giving a daily production of 96.

In attempting to collect the faecal pellets and determine the weight produced during a full 24 hour period it was found that animals kept in small, or uniform smooth sided polythene containers which permitted total collection failed to behave normally. The daily food intake fluctuated wildly and the animals level of activity was extremely high. Although this was the case with both *Sorex* species, *C. suaveolens* appeared to behave normally. The number of faecal pellets produced by this species averaged 120/day ($n=20$).

This value is some 20% higher than the value determined on the basis of the observation periods quoted above. The values quoted for the other two species on the same basis may also be underestimates, resulting from the short periods of observation over which the collections were made.

5. Assimilation Efficiency of *C. suaveolens*

Since food intake and faecal production were measured for this species in the presence and absence of drinking water an estimate of the assimilation efficiency under both conditions can be calculated, Dr. R.

Abel of this department performed the calorimetric measurements on a Phillipson micro-bomb calorimeter.

Calorific value of the food (<i>T. molitor</i> larvae)	=6.441 kcal/g
Calorific value of the faeces (with external water)	=4.812 kcal/g
Calorific value of the faeces (without external water)	=4.276 kcal/g

(All values based on at least 2 replicates)

Calculated dry weight intake (with external water)	=2.81 g (n=20)
Calculated dry weight intake (without " ")	=0.63 g (n=6)
Faecal production dry weight (with " ")	=0.40 g (n=20)
Faecal production dry weight (without " ")	=0.03 g (n=6)

(Faecal dry weights and intake dry weight equivalents determined by drying in a vacuum oven at 60°C)

Assimilation Efficiency in the presence of external water =

$$\frac{\text{Consumption} - \text{Faeces}}{\text{Consumption}} = \frac{18.1 \text{ kcal} - 1.92 \text{ kcal}}{18.1 \text{ kcal}} \times 100 = 89.4\%$$

Assimilation Efficiency in the absence of external water =

$$\frac{\text{Consumption} - \text{Faeces}}{\text{Consumption}} = \frac{4.06 \text{ kcal} - 0.13 \text{ kcal}}{4.06 \text{ kcal}} \times 100 = 97.8\%$$

Both of these values are extremely high, but comparable with those of Buckner (1964). An explanation of this high efficiency is difficult to produce but may lie in the low proportion of indigestible chitin in the artificial diet provided. Almost certainly assimilation efficiency in the field will be lower since the natural diet includes a high proportion of small items and hence a higher proportion of indigestible chitin. In order to determine the magnitude of this effect it would be instructive to maintain shrews in the laboratory on diets of small invertebrates, and conduct a more detailed study of this aspect of shrew bio-energetics.

The difference in the assimilation efficiency in the presence and absence of a free water source for the animals to drink (although not statistically proven) may result from the observed tendency for rectal feeding in the absence of water. Examination of the above figures shows that faecal production in the absence of water is disproportionately lowered, suggesting either, that the material is being recycled by rectal feeding on a large scale or that the rate of passage through the alimentary tract is considerably slower, or both. Assuming that the dry weight of faeces produced per day should remain in the same proportion to the food intake, with or without water, then; with water present 0.40 g faeces are equivalent to 2.81 g food. Without water present 0.03 g faeces are equivalent to $(0.03 \times 2.81) : 0.4 = 0.21$ g. However the measured intake was 0.63 g, therefore 0.42 g (dry wt.) of food remain in the gut. This is approximately equivalent to 1.5 g of food by wet weight, a value three times

greater than the average value for the wet weight of food contained in the gut of field trapped animals (Table 3). Thus one may conclude that the gut is indeed being maintained in a full condition, by the operation of one or other of the processes suggested above, and hence the hunger drive itself is being suppressed.

6. Annual Consumption on Upper Seeds, Wytham, Berkshire

Table 5 presents figures for the annual consumption of *S. minutus* and *S. araneus* in terms of the dietary composition, densities and daily intake

Table 5

Density and annual consumption by *S. araneus* and *S. minutus* in *Brachypodium pinnatum* grassland, Wytham, near Oxford.
All consumption values expressed in g/ha.

Months	J.F.M.	A.M.J.	J.A.S.	O.N.D.
<i>S. araneus</i>				
Density/ha	5.3	5.6	8.0	6.3
Consumption/individual (wet. wt.)	873	883	892	892
Total cons/ha	4,627	4,945	7,186	5,620
Consumption of:				
<i>Lumbricidae</i>	1,147	924	2,021	2,636
<i>Enchytraeidae</i>	190	—	36	1,001
<i>Mollusca</i>	37	178	121	118
<i>Opiliones</i>	870	460	1,307	175
<i>Aranae</i>	606	361	429	203
<i>Coleoptera</i> Adults	1,051	2,224	2,220	1,265
Larvae	292	747	485	68
Others	433	40	521	156
<i>S. minutus</i>				
Density/ha	4.0	6.7	9.9	4.5
Consumption/individual (wet. wt.)	540	546	552	552
Total cons/ha	2,160	3,658	5,465	2,484
Consumption of:				
<i>Opiliones</i>	315	413	1,475	1,093
<i>Aranae</i>	145	867	1,251	132
<i>Coleoptera</i> Adults	1,043	1,262	2,131	1,160
Larvae	564	823	333	57
Others	93	293	275	42

(the latter calculated from the regression line in Fig. 1 as described above). Dietary composition and densities were taken from the major study referred to (Pernetta, 1973). The figures for consumption are presented in wet weights. To calculate the energy consumption of the shrew populations, values for the daily intake in dry weight (Table 2) were used, this assumes a water content for the diet as a whole of 75%. Since the diet was assessed quantitatively the calorific contribution of

each prey group to the maintenance of the shrews can be assessed. Such values are presented in Table 6.

If the lumbricid, enchytraeid and molluscan fraction of the diet is assumed to have a calorific value of 5.00 kcal/g dry weight, and the rest of the diet a value of 5.82 kcal/g dry weight, following Gibb (1957) and Kitchell & Norris (1969, unpublished, quoted in Kuminis & Wuycheck, 1969) then the energy entering the two shrew populations can be calculated. In the case of the common shrew this value is 31,912 kcal/ha/annum, and in the case of the pigmy shrew 20,031 kcal/ha/annum. If the assimilation efficiency of the two species is assumed to

Table 6

Some energetic parameters of *S. araneus* and *S. minutus* populations.
All values in kcal/ha unless otherwise stated.

Months	J.F.M.	A.M.J.	J.A.S.	O.N.D.
<i>S. araneus</i>				
Biomass, g	47.7	50.4	72.0	56.7
Consumption (dry wt., g)	1193	1274	1840	1449
Calorific contribution of earthworm, enchytraeid and molluscan diet fraction	1944	1427	3338	4970
Calorific contribution of mixed insect diet fraction	4663	5771	7176	2623
Total consumption	6607	7198	10514	7593
Faecal loss	661	720	1051	759
Heat loss	5710	6100	8810	6948
Total loss	6371	6820	9861	7702
Total production	+236	+378	+653	-114
<i>S. minutus</i>				
Biomass, g	16.0	26.8	39.6	18.0
Consumption (dry wt., g)	540	915	1366	621
Total consumption	3143	5323	7951	3614
Faecal loss	314	532	795	361
Heat loss	2590	4390	6558	2981
Total loss	2904	4922	7353	3342
Production	+239	+401	+598	+272
Annual Consumption (C)	Annual Production (P)		P/C	
31,912 kcal/ha	1,153 kcal/ha		0.03 <i>S. araneus</i>	
20,031 kcal/ha	1,509 kcal/ha		0.08 <i>S. minutus</i>	

be the same as that for *C. suaveolens* in the presence of water (i.e. 90%), then it can be seen that contributions to the decomposer chain via faeces will be 3,191 kcal/ha/annum and 2,003 kcal/ha/annum in the case of common and pigmy shrews respectively.

If the average heat loss per day from the common shrew is taken as 1.33 kcal/g and that for the pigmy shrew as 1.8 kcal/g, the annual heat losses per hectare may be calculated; these are 27,568 kcal in the case

of the common shrew and 16,519 kcal in the case of the pigmy shrew. Although these figures are only approximate they do enable one to gain an estimate of the total annual production of shrew populations; 1,153 kcal/ha/annum and 1,509 kcal/ha/annum for the common and pigmy shrews respectively.

No account is taken in these figures of urine production and the figure represents total production in terms of growth, production of new individuals, lactation, moult (which occurs at least twice annually in Britain, Pernetta, 1976; three times in Poland, Borowski, 1973) and other epidermal losses.

If the ratio of production to consumption is calculated it is found to be 0.03 and 0.08 for the common and pigmy shrew respectively (Table 6). Both of the values are higher than similar ratios in other species, which tend to fall around 0.02. This suggests either that the figures for annual consumption are higher than expected on the basis of the available information or that the figures for respiratory losses should be higher, or that urinary losses are appreciable. It would seem likely that any errors can be attributed to the two latter reasons since no account is taken of the urinary losses, and field respiratory losses are likely to be higher than those measured in the laboratory, since activity is greater in an unrestricted environment.

DISCUSSION

Figure 3 shows the fate of energy entering and leaving the shrew populations each year. One of the problems associated with these animals is that they cannot be easily assigned to any single trophic level since their energy requirements are drawn from diversified sources. If the opiliones, spiders and adult coleoptera are arbitrarily assigned to the secondary consumer level, the earthworms, molluscs, enchytraeids and larvae to the decomposer cycle, we can see that the annual consumption in the case of the common shrews is based on the secondary consumers and decomposers, in the proportion 3:2. In the pigmy shrew however the decomposers play a minor role. Such an arbitrary assignment is obviously a gross oversimplification in that many of the larvae are predatory, and many of the adult coleoptera are either primary consumers, or tertiary consumers which themselves may be based at least in part on decomposer organisms. As a broad generalisation however this picture displays the inherent difficulties in the practical application of the trophic dynamic concept of ecology in determining the position of the shrews, whilst at the same time giving an indication of the shrew's position.

Such a complexity in the trophic position of shrews suggests that the

insectivorous habit should be treated as ecologically distinct from the carnivore habit; the anatomy, behaviour and ecology of the two life styles resulting in different selection pressures.

If the assimilation efficiency quoted in this paper and those of Buckner (1964) are correct then it may be that the production/consumption ratio is indeed considerably higher than that of carnivores. Several reasons may be advanced in support of this; firstly shrews have a short life span, maximum 12—14 months (Michielson, 1966; Pernetta, 1973; Shillito, 1965); and secondly their food source is much less stable than that of most carnivores. Although it is well known that many small mammal populations fluctuate in numbers in a cyclic

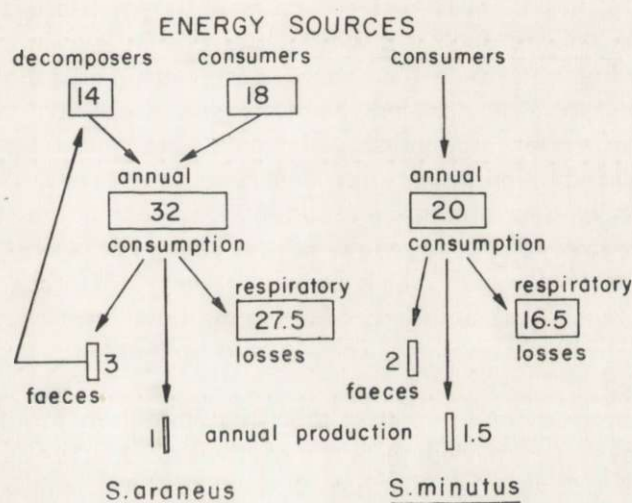


Fig. 3. Energy pathways in Wytham shrew populations. Values given in thousands kcal/ha/annum; to the nearest 500 kcal.

fashion (Elton, 1942) and in doing so cause similar though delayed fluctuations in their predators, little is known concerning the effect of unpredictably fluctuating food sources on vertebrate populations. Other vertebrate insectivores include predators of winged insects such as the bats, which hibernate over the winter period of food shortage; swifts swallows martins etc., which migrate to warmer climates; and in other geographic areas, specialists on particular insect groups such as termites, ants, etc. Many passerine birds in the temperate zones for example use insects as a high protein food source for the nestlings thus using them for only part of the year. Moles, which are closely related to shrews both in their taxonomic and phylogenetic position specialise on soil invertebrates

particularly earthworms, their adaptation to a subterranean existence enables them to follow the movements of prey in the soil. Shrews on the other hand are directly affected by fluctuations both in numbers of prey and their availability, the effect of earthworm availability on the remainder of the diet of the common shrew has been well demonstrated (Pernetta, 1973). The work of Tupikova (1949), Rudge (1968), Yudin (1962), Lavrov (1943), Mezherin (1958), Folitarek (1940) has shown that the nature of shrews diets are largely determined by invertebrate prey availability, itself a reflection of season, habitat and geographic location. To what extent the often rapid and violent fluctuations observed in many invertebrate populations affect the shrews is unknown; what is known is that the density, distribution and abundance of small insectivores varies from year to year, locality to locality and season to season. Such a mosaic pattern of shrew abundance would suggest that fluctuations in food sources are continually altering the relative favourability of different habitats and areas. It could well be argued that a vertebrate under such conditions would be expected to have a high production to consumption ratio to ensure survival of the population. Selection pressures on individuals for successful breeding must be extremely great in view of the short life span; their reproductive biology suggests (Tarkowski, 1956; 1957) that they are in fact geared to the maximum production of new individuals, any mechanism which increases this success would undoubtedly be selected for, hence the high P/C ratio.

One further point of interest is the negative figure for production in *S. araneus* over the period October to December. This is very likely correct since it is well known that the body weight, length, and weight of the internal organs of these animals decreases over winter (Borowski & Dehnel, 1953; Crowcroft, 1957; Pucek, 1970). In fact it is known that the body length decrease results from regression of the inter-vertebral discs (Hyvärinen, 1969). Such changes in morphometric parameters are well known to occur in many species, which would suggest that the production figures for *S. minutus* are too high. In both species however peak production occurs during the summer months, corresponding to the period of peak production and growth of young animals.

Taking a calorific value of 5 kcal/g biomass for *S. araneus* and *S. minutus* body material (Myrcha, 1969) it is possible to calculate the theoretical number offspring produced/ha if total production from April to September went into the production of offspring. This is 32 in the case of *S. araneus* and 16 in the case of *S. minutus*, representing 12 young/female for the former species but 30/female for the latter. Whilst the figure

for *S. araneus* is reasonable representing just under two litters/female/year that for *S. minutus* is not, which further suggests that the figures for production in *S. minutus* are too high. An increase in an individual's daily heat loss of 5% (=0.1 kcal/g/day) or a decrease in food intake of 6% (0.4 g/animal/day, wet weight) gives an annual production of the order of 600 kcal/ha annum and hence a *P/C ratio* of 0.028 for this species. This illustrates the difficulties inherent in the use of the energetic approach to ecology, in that laboratory measurements are necessary to complete the equations for energy flow, and a small error in such measurements may alter the resultant picture quite dramatically.

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BIOENERGETYKA RYJÓWEK ZAMIESZKUJĄCYCH MURAWY

Streszczenie

W warunkach laboratoryjnych zmierzono konsumpcję dobową, tempo przechodzenia treści pokarmowej i ilość wydalanego kału u *Sorex araneus*, *Sorex minutus* i *Crocidura suaveolens cassiteridum* (Tabele 2, 4). Wykazano, że podawane w literaturze (Tabela 1, Ryc. 1) rozbieżności co do wielkości zużycia pokarmu przez ryjówki są, przynajmniej w części, powodowane różną zawartością wody w sztucznych dietach. Współczynnik strawności u *C. suaveolens* wynoszący 89% jest podobny jak u wielu innych gatunków ryjówek. Wskaźnik ten ulega podwyższeniu jeśli zwierzęta pozbawi się dostępu do wody.

Diagram (Ryc. 3) przedstawiający przepływ energii przez populację ryjówek zamieszkujących murawy kserotermiczne z *Brachypodium pinnatum* w okolicach Wytham w Anglii, oparto na analizie pokarmu u *S. araneus* (244 osobników) i *S. minutus* (130 osobników) złapanych w pułapki zabijające (Tabela 3). Przedstawiono też konsumpcję (C) i produkcję (P) roczną (Tabele 5, 6) dla obu tych gatunków i dokonano próby objaśnienia wysokiego stosunku P do C.

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gryzoniami feromonów (E. Christiansen i K. Døving) a także oddziaływaniami na hormonalną regulację rozrodu (P. Meurling i E. Nyholm).

Na wybranych przykładach *Microtus agrestis* i *Arvicola terrestris* (A. Myllymäki) oraz myszy i szczurów (M. Lund) omówiono postęp badań w zakresie poznania socjalnych stosunków w populacjach tych ssaków, interakcji międzygatunkowych i możliwości oddziaływania na te struktury i procesy populacyjne w celu ograniczenia liczebności.

Pojawianie się populacji odpornych na działanie chemosterylantów zmusza do poszukiwania innych metod, przy czym jednak użycie metod genetycznych nie jest bardziej obiecujące niż konwencjonalnych (O. Halkka, M. Rasmuson). Przegląd metod oceny liczebności drobnych ssaków (A. Myllymäki) oraz opis systemu gromadzenia danych dla celów prognostycznych (B. Hörnfeldt) zamykają tę część książki.

Końcowe rozdziały obejmują przegląd aktualnych badań, wytyczają kierunki przyszłych studiów. Za najważniejsze uważa się przy tym: (1) poznanie skutków działania człowieka w środowisku, (2) badanie odporności roślin na gryzanie przez gryzonię, (3) rola stosunków socjalnych, w tym też feromonów, behawioru i mechanizmów fizjologicznych w regulacji liczebności populacji, (4) poszukiwanie środków chemicznych skutecznych dla zwalczania gryzoni ale nie powodujących szkadeń środowiska, (5) ocena roli patogenów i pasożytów, oraz (6) wypracowanie systemu dokumentacji (szkód, prognozowania itp.).

Liczni autorzy i redaktorzy książki dają wyraz temu, że doceniają znaczenie podstawowych badań ekologicznych dla walki biologicznej ze szkodliwymi gryzoniami. Proporcje książki i zakres prezentowanego w niej materiału dobitnie jednak świadczą, że faktyczny dorobek w tym zakresie jest dotychczas raczej skromny. Książka daje przegląd istniejącego stanu badań w zakresie zwalczania szkodliwych gryzoni i owadożernych. Zasadniczym jej walorem jest kompleksowe potraktowanie problemu i skierowanie uwagi na metody walki biologicznej. Należy żywić nadzieję, iż będzie to działało stymulująco na przyszłe badania w tym zakresie.

Książka jest cenną pozycją współczesnej literatury teriologicznej, stanowi dobre kompendium wiedzy na temat zwalczania drobnych ssaków, przydatne dla studentów i wszystkich zainteresowanych tymi problemami.

Z. Pucek