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Food consumption, assimilation and metabolic rate in six species of shrew (Sorex and Neomys)

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Average daily metabolic rate M (J/h), measured as CO_2 production, was related to body fresh weight W(g) as $\log M = 2.66+0.58 \log W$ in *Sorex minutissimus* (average wt 2.5 g), *S. minutus* (2.7 g), *S. caecutiens* (4.9 g), *S. araneus* (8.9 g), *S. isodon* (11.1 g) and *Neomys fodiens* (17.8 g). The scaling factor 0.58 is significantly different from 0.75. Gravimetric measurements of metabolic rate gave unbiased but inaccurate estimates (experimental period 15 h).

Shrews' food utilization efficiency (assimilation minus urine production divided by consumption, all in carbon) is high (70 to 85 %) on ant pupae and sawfly cocoons but low (45 to 60 %) on beetles, which have a high proportion of indigestable chitin. Assimilation efficiency (assimilation/consumption) peaks in medium-sized species and was especially low in *S. minutissimus,* one of the smallest extant mammals. Body size constrains the size of the digestive tract. The lower size limit of shrews could be set by the maximum food processing rate of the digestive tract, achieved by optimizing between assimilation efficiency and throughput time.

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1. Introduction

Northern shrews *Sorex* have an exceptionally high metabolic rate (Vogel 1976) but relatively small energy reserves (Vogel 1980) and hence starve within a few hours (Crowcroft 1954). Consequently, questions about foraging assume a great significance in shrew ecology. Three observations, which may be controversial, exemplify the kinds of problems shrews face and their behavioural and physiological responses.

Firstly, it is not uncommon to find apparently unharmed young shrews that have died in summer, many of them probably having starved to death (Crowcroft 1957), perhaps because they had failed to establish a feeding territory. Unfortunately, nobody has attempted a serious study of this phenomenon.

Secondly, in food shortages, small shrews tended to increase but large ones to decrease their activity (Hanski 1984), which is presumably related to the smaller energy reserves of small shrews. And thirdly, to consider another time scale, Dehnel's phenomenon (Brambell 1935, Dehnel 1949), the fact that the body size of northern shrews decreases in winter (in Finland by c. 35 % in *S. araneus*; Hyvärinen 1983) has been attributed to the need to minimize energy expenditure at the time of low food availability (Mezhzherin 1964, Mezhzherin & Melnikova 1966). Reduced activity in winter may serve the same purpose (Churchfield 1982a), though this is a controversial issue in Soricinae which lack torpor (Genoud 1981).

For purposes of evaluating the amount of food available for shrews in their natural environments (e.g. Randolph 1973, Churchfield 1982a), as well as for detailed foraging studies, one needs to know the utilization efficiency of shrews with regard to quantitatively important food items, mostly arthropods (Judin 1962, Churchfield 1982a and many others) but also lumbricids (Rudge 1968, Okhotina 1974, Pernetta 1976) and slugs and snails (Whitaker & Maser 1976). Insufficient information exists on this point in the literature (though see Buckner 1964, Barrett & Stueck 1976, Pernetta 1976, Churchfield 1982b), most metabolic studies having been conducted with artificial diets. The present study reports food utilization efficiencies for shrews feeding on two types of food: heavily chitinized beetles and lightly chitinized insect pupae. I also present data on metabolic rates, measured as CO_2 production, in the six species of shrew occurring in Finland: *Sorex araneus, S. isodon, S. caecutiens, S. minutus, S. minutissimus* and *Neomys fodiens*.

2. Material and methods

Forty-four individuals, both young and overwintered, of six species of shrew, were studied in 116 experiments in 1982 and 1983 (Table 1). Shrews were trapped in southern and eastern Finland, and had been in captivity from one week to six months before any of the experiments.

These data are insufficient to analyse differences between young and overwintered animals (for metabolic rate see Gebczyński 1965, 1971). For the present purposes discrimination at the species level is sufficient.

The shrews were maintained at 17 ± 1° C, 70-% relative humidity and constant dim light, each animal in its own plastic container measuring 60 by 40 cm. The containers had a soil layer of 5 to 10 cm, dry hay, moss and twigs. Animals were fed twice a day with fresh fish, usually perch, occasionally supplemented with insects. Mortality amongst the captive animals was usually low, except during the first two weeks in captivity, when many died. Most *Sorex araneus* kept in 1983 were killed by an unidentified intestinal disease. Sick animals were not used in the experiments.

Before each experiment, the animals were kept in a small plastic container without food for 1.5 h. Most experiments lasted for c. 15 h. The metabolic chamber, made of plexiglass and measuring 50X30X5 cm (7.5 l), was connected to a system described by Silvola & Heikkinen (1979) to monitor the CO_2 concentration in the air flowing through the chamber (60 to 100 l/h). No temperature regulated room was available for the experiments, but air temperature could be maintained at 23±2° C throughout the experiments.

The bottom of the metabolic chamber was covered with a plastic mat to facilitate cleaning. The chamber was loosely filled with nylon rope to simulate the structure of the shrews' natural environment. A small plastic nest frame loosely filled with dry hay was provided, as well as drinking water in a small cup.

The food given at the beginning of each experiment was weighed (or counted in the case of beetles), and the food remaining and the faeces produced by the end of the experiment were weighed after drying at 60° C for 50 h. Reference material was weighed before and after drying to determine the food water content. The amount of food given was usually c. 5 g fresh weight (more for *Neomys*), which was occasionally completely consumed by the larger species. Four types of food were tested in 1982: beetles (*Sphaeridium*, Hydrophilidae), ant pupae, sawfly cocoons (*Neodiprion sertifer*) and fresh fish (perch in 1982). In 1983 ant pupae were given to *Sorex* and fish (herring) to *Neomys*.

Table 1. Numbers of shrews and experiments.

	Exp.	Individuals				Body fresh weight (g)
		1982		1983		
		juv	ad	juv	ad	mean ± *SD*
S. minutissimus	4	-	-	2	-	2.5 ± 0.2
S. minutus	16	1	1	-	4	2.7 ± 0.4
S. caecutiens	16	-	1	-	4	4.9 ± 0.3
S. araneus	50	3	5	1	10	8.9 ± 1.5
S. isodon	20	-	2	1	1	11.1 ± 1.1
N. fodiens	10	-	-	8		17.8 ± 2.7

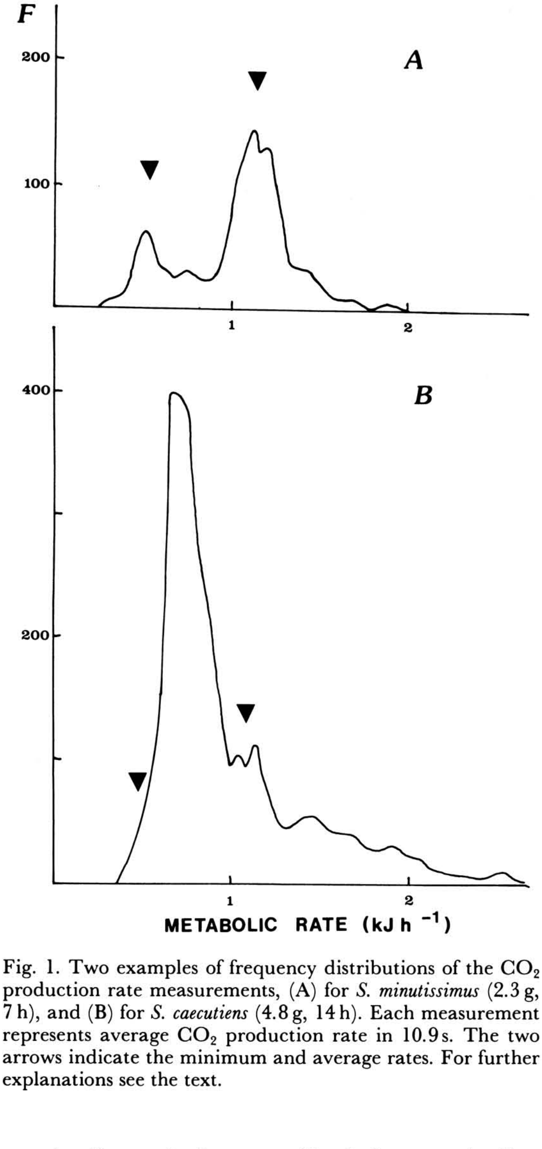

Fig. 1. Two examples of frequency distributions of the CO_2 production rate measurements, (A) for *S. minutissimus* (2.3 g, 7 h), and (B) for *S. caecutiens* (4.8 g, 14 h). Each measurement represents average CO_2 production rate in 10.9 s. The two arrows indicate the minimum and average rates. For further explanations see the text.

CO_2 concentration was measured with an infra-red gas analyser (Silvola & Heikkinen 1979) and the results were recorded with a microcomputer as average values for periods of 10.9 s. CO_2 concentration in the incoming air was measured once or twice an hour for 1 min, and the CO_2 production by the food material (if any) was assessed experimentally. These values were subtracted from the gross CO_2 production.

Carbon content in food and faeces was determined using the method developed and described by Salonen (1979).

Average and minimal rates of CO_2 production, and the total amount of carbon released in respiration were calculated for each experiment. The minimal rate was taken as the 100th

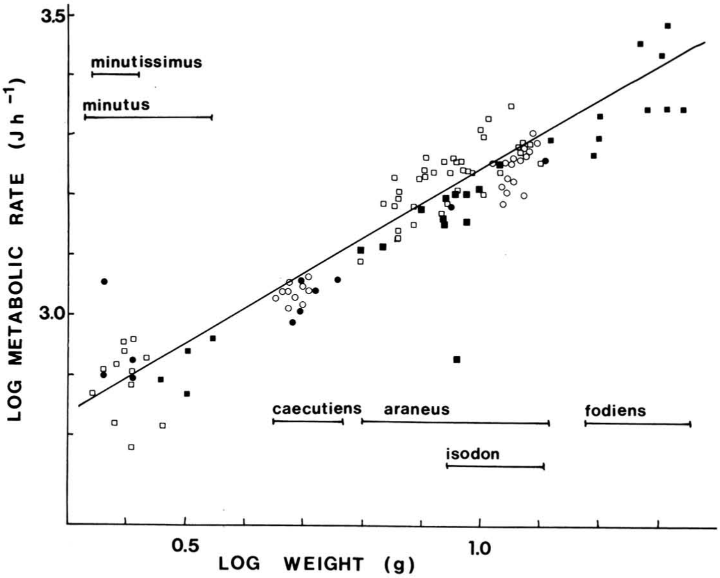

Fig. 2. Metabolic rate versus body weight in six species of shrew (note log-transformed data). The two highly deviant points (*S. minutissimus* and *S. araneus*) are discussed in the text and were omitted from the regression line: y = 2.66 + 0.58x. Open symbols are results from 1982 and closed ones from 1983. *Sorex minutissimus, S. caecutiens* and *S. isodon* are represented by circles, and *S. minutus, S. araneus* and *Neomys fodiens* by squares.

smallest value amongst the c. 5000 average values recorded in each experiment (Fig. 1). More sophisticated analyses of these results are unwarranted because several factors, including the position of the animal in the chamber, affect short-term fluctuations in the CO_2 concentration as measured here.

Subtraction of the amount of food remaining from the amount of food provided gives total consumption during an experiment (calculated in carbon). Carbon excreted in urine was not measured but was estimated from Buckner's (1964) work as 0.425 mg C g^{-1} fresh wt h^{-1}. Food utilization efficiency was then calculated as $1-(F+U)/C$, where F, U and C stand for the carbon defaecated, urinated and consumed during an experiment. Food utilization efficiency as defined here is always less than assimilation efficiency (digestability), $1-F/C$.

3. Results

3.1. Metabolic rate

Metabolic rate versus body weight

Energy liberated in metabolism was calculated on the assumption that 12.56 Joules correspond to 1 mg of CO_2 produced (Petrusewicz & Macfadyen 1970). Thus calculated, average metabolic rate is given by $\log M = 2.66 + 0.58 \log W$, where the units of M and W are J/h and g fresh wt (Fig. 2).

Vogel's (1976) results for Soricinae (*S. araneus, S. minutus* and *Neomys fodiens*) yielded $\log M = 2.53 + 0.65 \log W$, which gives 8 to 21 % lower values than the present equation for the relevant size range from 2 to 20 g. Vogel (1976) also cites results from other sources (4 studies) giving the equation $\log M = 2.72 + 0.52 \log W$. These parameters give values differing by less than 11 % from the ones predicted by the present equation for Soricinae weighing from 2 to 20 g. These small differences are expected as there were differences in the experimental methods used, in the species studied, their age, time in captivity, etc. Vogel (1976) for example measured the rate of O_2 consumption during 20 to 30 min while the animal was active, and at a slightly higher temperature (25° C) than used here (23 ± 2° C). Note that the regression coefficient obtained here (0.58) is close to the mean of the above two values (0.59). It differs highly significantly (t=9.94, P<0.001) from 0.75, the modal value for mammals (n=146; Peters 1983). McNab (1979, 1983) has cogently questioned the universality of the scaling factor 0.75.

The largest deviation in Fig. 2 deserves comment. A *Sorex araneus* male trapped on May 24, 1983 and tested on June 15 and July 8 had an exceptionally low metabolic rate, 837 and 933 J/h (experimental periods 16 and 8 h; the latter is not shown in Fig. 2). The former figure is only 51 % of the predicted value (for a shrew weighing 9.1 g). Gravimetrically calculated metabolic rate (see below) was 213 % of the directly measured one, i.e. close to "normal". Apparently, this individual had a severe metabolic disorder, though it behaved normally, and large amounts of carbon were excreted in the urine.

The minimum metabolic rate as defined and measured here (Section 2 and Fig. 1) represents the lowest level of CO_2 production in sleep. The equation of the minimum rate is $\log M = 2.47 + 0.52 \log W$. Metabolic rate predicted by this equation is c. 60 % of the average rate.

The minimum values cited by Vogel (1976) from Buckner (1964) and Pearson (1948) hover around $\log M = 2.54 + 0.53 \log W$. These parameters give 20 % higher minimum rates than the ones measured here. But again there are important differences in the experimental methods. Buckner (1964) for example carried out his measurements at 9 to 14° C, at which temperatures more energy is used for thermoregulation.

Four experiments with *Sorex minutissimus* gave the results shown in Fig. 2. The one very high value is due to an individual which was exceptionally active in a relatively short experiment (7 h, see also Fig. 1a). Otherwise the results do not show any difference between *S. minutissimus* and small individuals of *S. minutus*. Buckner (1964) found nothing special in the metabolic rate of *Sorex hoyi*, another small Soricinae, and Frey (1980) concludes that the very small size of *Suncus etruscus* (Crocidurinae) does not influence its torpor in any particular way.

Direct versus gravimetric measurements of metabolic rate

Respiration R, as measured with the infra-red gas analyser, should equal assimilation $A=C-F$ minus urine production U, all expressed as carbon (Table 2 gives the constants of transformation). If the body carbon content changes during the experiment ($\Delta B \neq 0$), a correction should be made for this. A change in the body carbon content must be estimated from change (if any) in body fresh weight, which gives at best a very inaccurate estimate of ΔB. Therefore, R was compared with both $A-U$ (assuming no change in body carbon content) and $A-U-\Delta B$ (assuming a linear relationship between body carbon content and fresh weight).

The means of $100\ [(A-U)-R]\ /\ R$ and $100\ [(A-U-\Delta B)-R]/R$ are close to their expected value, zero (Table 2; the two years do not differ significantly). Direct and gravimetric measurements of metabolic rate give similar results on average, though in individual experiments a substantial difference (±30 %) can occur. Such variation is expected because of the relatively short experimental period (c. 15 h) and the impossibility of estimating changes in body carbon content with any accuracy. In the one much longer experiment (48 h, *S. minutissimus*), the difference was only 1 %. These results refute Gebczyński's (1965) suggestion that the gravimetric method is biased towards higher values when used with small mammals like shrews.

Table 2. Comparison between direct (infra-red gas analyser) and gravimetric measurements of CO_2 production (mean ± *SD*). $n=$ number of experiments. See text for further explanations.

	Direct	Gravimetric	n
1982	- 5.9 ± 24.2	- 4.3 ± 24.7	77
1983	15.7 ± 27.4	12.4 ± 24.4	31
Pooled	0.3 ± 26.9	0.5 ± 25.7	108

Constants for transforming the original measurements to carbon. —Respiration: 1 mg CO_2 = 0.273 mg C (=12.56 J). — Biomass: 1 mg fresh wt = 0.175 mg C (assuming that body water content is 65 %, Churchfield 1981, and dry matter carbon content is 50 %). —Food: beetles (*Sphaeridium*, Hydrophilidae) 50.2±2.1 % (n=11, mean±*SD*, of dry wt), sawfly cocoons (*Neodiprion sertifer*) 56.3±1.9 % (n=5), empty sawfly cocoons 51.8±3.2 % (n=8), ant pupae 49.1=2.0 % (n=7), fish 53.3±0.5 % (n=4). — Faeces (when fed with ...): (beetles) 45.6±1.7 % (n=11), (sawfly cocoons) 41.2±3.3 % (n=16), (ant pupae) 39.8±3.8 % (n=12) and (fish) 31.0±5.6 % (n=4).

Comparison between two years

As experiments were run in two years, the results were analysed with two-way ANCOVA, species and year being the two factors and log body weight an independent variable. *Sorex minutissimus* and *Neomys fodiens* were excluded because no measurements were made in 1982 (Table 1).

Body weight has always the overridingly important effect on metabolic rate (Fig. 2) but the two years differed highly significantly ($P<0.001$), and differences between the species were significant at the 5 % level. Estimates of the main effects suggested that differences between the species are due to *S. araneus*. The above analysis was run for the remaining species, and now species and year had nonsignificant effects. In one-way analyses species had a highly significant effect on metabolic rate in 1982 ($F=7.06$, $df=3.72$, $P<0.001$) but a nonsignificant effect in 1983, *S. araneus* having a positive and the remaining species a negative effect in 1982 (see Fig. 2).

Table 3. Food utilization efficiencies (see below) in six species of shrew fed with four types of food (mean ± *SD*, *n* in brackets).

	Fish		Sawfly cocoons		Ant pupae		Beetles	
S. minutissimus	-		-		73.0 ± 4.2	(2)	-	
S. minutus	93.0	(1)	85.2 ± 2.9	(5)	83.3 ± 1.8	(6)	61.7 ± 6.1	(3)
S. caecutiens	93.0	(1)	85.3 ± 1.2	(3)	83.0 ± 2.3	(6)	54.2 ± 9.8	(4)
S. araneus	90.2 ± 1.0	(4)	80.1 ± 6.7	(18)	74.5 ± 3.5	(24)	47.0 ± 3.6	(3)
S. isodon	86.0	(1)	76.5 ± 4.3	(6)	70.7 ± 1.4	(6)	46.8 ± 2.9	(6)
N. fodiens	86.7 ± 4.0	(7)	-		71.0 ± 1.4	(2)	-	

Taking these results at their face value, *Sorex araneus,* but not the other species, had an elevated metabolic rate in 1982. Tested alone, *S. araneus* demonstrated a highly significant difference between the two years (F=15.4, df=1.47, P<0.001), the average metabolic rate being 17 % higher in 1982 than in 1983 (Fig. 2). A separate analysis for the other species is unwarranted, as only one or two individuals were studied in 1982 (Table 1). Buckner (1964) found a marked difference (c. 25 %) in the metabolic rates of individuals originating from low and high density populations, but whether this factor plays a role here is not known.

Metabolic rate and food type

The influence of food type on metabolic rate was studied in 1982. Two-way ANCOVA with log body weight as an independent variable and food type and shrew species as the two factors slightly improved the squared multiple correlation of a regression model; the interaction term had a significant though not a large effect. *Sorex araneus* had a positive and beetles a negative main effect. Major differences in food utilization efficiency (below) between the food types are due to beetles (Table 3).

Individual variation in one species was analysed with four adult *S. araneus,* tested repeatedly with three food types. No significant differences were found.

3.2. Food utilization efficiency

Carbon assimilation is defined as the carbon consumed (C) minus the carbon excreted in faeces (F). In calculating food utilization efficiency I have subtracted the carbon excreted in urine (U) from assimilation to give the carbon available for maintenance and growth.

Table 3 summarizes the utilization efficiencies $1-(F+U)/C$ for the six species feeding on four types of food. ANCOVA for species, food type and body weight revealed only the obvious difference between the food types: efficiency is low when shrews eat beetles (Table 3). A separate analysis for ant pupae, for which much data exist, gave no significant effect for species or year, but body weight had a significant effect (t=3.22, df=33, P<0.01; *S. minutissimus* and *N. fodiens* excluded).

Differences between the species are in fact explicable by differences in body weight, small species being more efficient than large ones (Table 3). *Sorex minutissimus* is an exception, two measurements with ant pupae giving efficiencies of 70 and 76 %, much lower values than in the two other small species, *S. minutus* and *S. caecutiens* (Table 3). These measurements for *S. minutissimus* refer to two individuals and two long experiments (17 and 48 h).

Fig. 3 summarizes previous and the present estimates of assimilation efficiency $1-F/C$ of shrews feeding on insect pupae (ants, sawflies, flies). Assimilation efficiency, as food utilization efficiency, peaks in medium-sized species, *S. minutissimus* having a particularly low efficiency. It should be recollected that, if measurements are in carbon or energy unit, assimilation efficiency is necessarily higher than food utilization efficiency, because the former includes energy liberated in protein catabolism, an important energy sink in shrews (Buckner 1964, Barrett 1969).

4. Discussion

4.1. Assimilation efficiency and the morphology of the digestive tract

Animals eating poorer quality food should have larger digestive tracts, other things being equal (Sibly 1981). Larger species of shrews generally eat poorer quality food (e.g. whole earthworms, low caloric content) than smaller

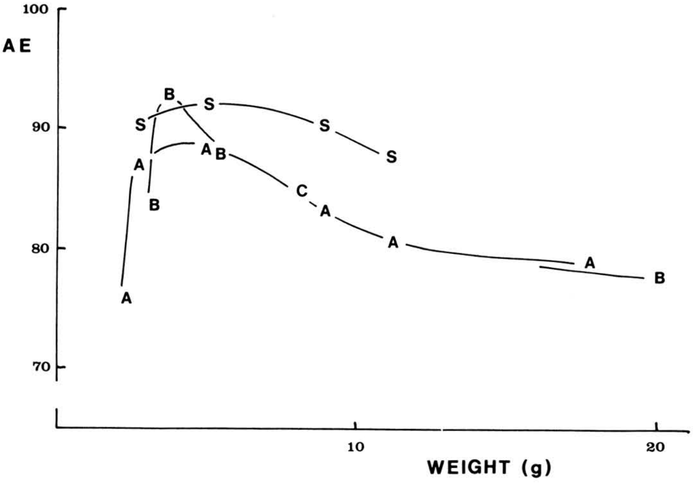

Fig. 3. Assimilation efficiency AE versus body weight in 9 species of *Sorex, Neomys fodiens* and *Blarina brevicauda* feeding on ant pupae (A, present study), sawfly cocoons (S, present study; B, Buckner 1964) and carrion fly pupae (C, Churchfield 1982b).

species (Judin 1962, Okhotina 1974). Okhotina (1974) has shown that, up to a limit, the relative intestine length increases with body size in shrews, which supports the above prediction.

There is a caveat to this observation. Sibly's (1981) model assumes maximization of the net rate of obtaining energy. It is far from clear that this is true for most shrews in most situations.

Apart from the very smallest species, assimilation efficiency increases with decreasing body size (Fig. 3). One possible explanation is the difference in the diet of small and large shrews in the wild. Small species feed mostly on small arthropods, from which a greater proportion of energy may be assimilated economically than e.g. from earthworms and large beetles, important components of the diet of large shrews. It is possible that the shrews' digestive processes cannot respond optimally to meal-to-meal changes in food quality, and hence the observed difference in assimilation efficiency on the same diet.

Ecological factors may favour an increase in assimilation efficiency, especially in small species which mostly forage above ground. It may be more important to minimize foraging time (to minimize predation risk) than to maximize energy gain, in which case high assimilation efficiency would be selected for. Availability of small arthropods may have large temporal variance; if this limits ingestion rate more energy is gained by increasing throughput time and thereby assimilation efficiency (Sibly 1981).

In the two smallest species, *Sorex minutissimus* studied here and *S. hoyi* studied by Buckner (1964), assimilation efficiency again decreases, which poses another problem: the above considerations do not suffice to explain this. I do not know the explanation but suggest that the very smallest shrews may in fact need to maximize net energy gain to compensate for their high metabolic rate per unit weight. A decrease in throughput time is then selected for even though assimilation efficiency would decrease if the end result is an increase in net energy gain (cf. Sibly's 1981 model). This however assumes that ingestion rate is not a limiting factor.

The rate of food processing and absorption per surface area of the gut wall must have an absolute maximum, or at least the cost of these processes increases rapidly with high absorption rates. The intestine length and hence the surface area across which food is absorbed is constrained by body size. If the smallest shrews maximize net energy intake by optimizing between assimilation efficiency and throughput time, as suggested above, their digestive tract operates at the highest economical level. In other words, the claim is that *S. minutissimus* approaches a size limit below which it becomes impossible to assimilate food fast enough to compensate for high metabolic rate —part of which is the cost of assimilating almost twice the body weight food in 24 h. One can see here the potential for a deleterious positive feed-back.

Sorex minutissimus has the most elongated stomach and the relatively strongest development of the stomach mucous membrane amongst all the studied species of *Sorex* (Myrcha 1967), which is consistent with the idea that its intestine works continuously at a maximum or near maximum rate. A large stomach is needed to store food for

Table 4. Food requirements of shrews in 24 hours. Daily food consumption (g dry weight) has been calculated from average metabolic rate and by making an allowance for carbon (energy) in faeces and urine. Relative consumption = g dry weight food / g dry weight shrew. Measurements were made at 23° C.

	Body fresh weight (g)	Metabolic rate		Daily food consumption			
		J/h	g C/24 hrs	Beetles		Ant & sawfly pupae	
				g	relative	g	relative
S. minutissimus	2.5	778	0.41	-		1.14	1.30
S. minutus	2.7	813	0.42	1.36	1.43	0.94	0.99
S. caecutiens	4.9	1148	0.60	2.21	1.28	1.35	0.78
S. araneus	8.9	1626	0.85	3.60	1.15	2.08	0.67
S. isodon	11.1	1845	0.96	4.09	1.05	2.19	0.56
N. fodiens	17.8	2427	1.26	-		3.61	0.58

the short periods of sleep, which never exceeded 30 min in the experimets, and were usually shorter (Hanski unpubl.). According to Skarén (1978), throughput time varies from 12 min to 1 h in *S. minutissimus*; throughput time varies from 30 min to 3 h in *S. araneus*, depending on the diet (Pernetta 1976).

Finally, what little is known about the litter size in *S. minutissimus* indicates it to be clearly smaller (4-5) than in other species of *Sorex* (average 7-8; Judin 1962). While many factors could contribute to the difference, which still needs to be confirmed, *S. minutissimus* females are possibly limited by their incapacity to feed more young.

4.2. Food requirements in shrews

These results allow one to estimate the daily food requirements of shrews feeding on two contrasting but natural diets: beetles and insect pupae (Table 4). The difference between the two lies in the proportion of indigestable cuticle, which is high in beetles but low in ant and sawfly pupae.

Pernetta (1976) has summarized previous estimates of food consumption in shrews. Much scatter in the literature data is caused by variable water content in the mostly artificial diet used in the experiments. Any results, including the present ones, clearly do not apply to environmental conditions very different from the ones studied, e.g. consumption is likely to be different in winter and summer (Churchfield 1982a) because of changes in metabolism (Randolph 1973, Genoud 1981), though assimilation efficiency may remain more constant (Randolph 1973, Churchfield 1982a). The present measurements were made at 23° C, and are probably slight underestimates of consumption (and metabolic rate) in fluctuating summer temperatures. According to Gebczyński (1965, 1971) metabolic rate changes by 15-20 % between 15 and 25° C in *Sorex araneus* and *minutus* in summer.

The highest food requirements per body weight are found in the smallest species (Table 4). In one experiment lasting 48 h, a *S. minutissimus* individual weighing 2.6 g and having been in captivity for one week ate 2.6 g dry wt of ant pupae. Assuming that the shrew's water content is 65 % (Churchfield 1981), this individual consumed, in terms of dry weight, 1.43 times its body weight in 24 h. In terms of fresh weight the ratio is 2.17, agreeing well with two previous estimates (Kaikusalo 1967, Skarén 1978) but being much lower than two other estimates: 4.2 (Blagosklonov 1957) and 4.6 (Okhotina 1974). In the experiment lasting 48 h, gravimetrically measured metabolic rate differed by only 1 % from the one measured directly, which increases confidence in these results.

Although it is not within the scope of this paper to make detailed comparisons between the daily food requirements of shrews and the amount of food available in their natural environments (see e.g. Randolph 1973), one example demonstrates the kind of calculations one can make. In Churchfield's (1982a) study *Sorex araneus* ate mostly small staphylinid beetles, with an average length of 5 mm. The figure cited by her (Churchfield 1979, 1982a) as the daily food requirement, 2.5 g dry wt, appears too low for beetles, though the value arrived at here, 3.6 g dry wt (Table 4), may be too high for small beetles. But let us assume that, when feeding on small staphylinid beetles in summer, *S. araneus* consumes 3.6 g dry wt per 24 h. An average prey length of 5 mm corresponds roughly to 2 mg dry wt (Koskela & Hanski 1977). In 24 h a common shrew would need to eat 1800 such beetles. The handling time of this prey is c. 5 s (Tuominen & Hanski unpubl.), which means that the shrew would have to use 2.5 h for eating, exlusive of searching, finding and killing the prey. How this figure fits the time budget of free roaming common shrews remains an open question.

When good data on the availability of different food items become available (some already exist), questions relating to shrews' habitat selection and intraspecific and interspecific competition can be discussed meaningfully. As a prelude, several authors have shown that numbers of shrews and numbers of their prey are positively correlated (Judin 1962, Butterfield et al. 1981).

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