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# The Energy Cost of Nesting Growth in the European Pine Vole

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Gębczyński M. & Gębczyńska Z., 1984: The energy cost of nesting growth in the European pine vole. Acta theriol., 29, 18: 231-241 [With 6 Tables]

Metabolizable energy requirement during the gestation period in the European pine vole, *Pitymys subterraneus*, is 18% higher than those of non-breeding females. During the last 6 days of gestation this increase reaches 53%. Costs of lactation and care of the young in litters of three offspring are proportionally higher than in litters of two young only. Rearing single young, although costing less energy in comparison with larger litters, when converted to 1 g of offspring body gain is 34% more demanding. The rate of body weight increase in young pine voles is similar during the initial three weeks after birth, only litters of one individual growing significantly more rapidly between the 7th and 11the day of life. It was calculated from data for *P. subterraneus* and five other rodent species that parental energy effort is 9.6 kcal (40 kJ) per 1 g of offspring body gain in the nest.

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#### 1. INTRODUCTION

Energy allocation has recently been emphasized as an important component of reproductive strategy in animals (Ricklefs, 1974). The amount of energy going into reproduction compared to energy used for maintenance illustrates a part of parental effort, i.e. the increased risk followed by reproductive activity (Calow, 1979) is more difficult to analyze quantitatively.

Energy costs of pregnancy and lactation have been studied in some rodent species, e.g., Clethrionomys glareolus (Kaczmarski, 1966; Gębczyński, 1975), Microtus arvalis (Trojan & Wojciechowska, 1967; Migula, 1969), Mus musculus (Myrcha et al., 1969), some Peromyscus species (Millar, 1975, 1976; Stebbins, 1977), Sigmodon hispidus (Randolph et al., 1977; Mattingly & McClure, 1982) and Microtus pinetorum (Lochmiller et al., 1982). The results obtained justify the statement that gestation in a female rodent causes, as pregnancy advances, a gradual increase in energy requirements. Lactation, however, intensifies the increase in energy requirements to a greater degree. Its costs increase with growth of nesting young and the maximum occurs during the period before the start of independent feeding by the young.

The purpose of our studies was to calculate energy requirements in another species of rodent — the European pine vole, *Pitymys subterraneus*. Measurements were made of the value of energy requirements in a non-breeding female and male kept together, a pregnant female also

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kept with a male, and a pair of parent rodents rearing their young up to the 21-st-22nd day of life.

Attempts were also made to arrive at an index which would make it possible to calculate lactation costs without the necessity for carrying out direct laborious measurements. A knowledge of changes in the body weight of young during the period of their dependence on their parents would form an adequate basis for such calculations. We therefore also aimed at analyzing lactation costs in the species so far examined, in order to determine whether it was possible to introduce an index common to all rodents.

### 2. MATERIAL AND METHODS

The European pine vole, *Pitymys subterraneus* (de Sélys-Longchamps, 1836) is a species which has the smallest number of young in a litter of all the *Arvicolidae*; the average figure is 2.3 to 2.7, depending on the biotope (Pelikán, 1973; Schröpfer, 1977), while their reproduction period lasts longer than in other *Arvicolidae* and often occurs during the winter period (Wasilewski, 1960) when by far the great majority of rodents of the temperate zone are non-breeding.

No. of	Avg. body	~	Coeff. of digestibility	Coeff. of
exp.	weight, g	Sex	Mean SD	assimilation
1	19.2	F1	87.4 5.2	86.4
2	14.1	F	89.2 5.4	88.7
23	17.9	M	88.6 2.0	88.8
4	19.0	F	90.1 2.3	89.6
5	17.2	M	90.4 2.4	90.0
6	20.5	F 1	90.1 0.9	87.1
Mean	18.0		89.2 3.4	88.4

### Table 1 Coefficients of digestibility and assimilation in Pitymys subterraneus.

Experiments were conducted in metabolic cages for 8 days. Calorific

value of urine was calculated jointly for the whole experimental period.

<sup>1</sup> Lactating females.

The European pine voles used for the experiments were laboratory bred animals. Oat grain, carrot and parsnip were used as food for both breeding and experimental purposes. Water was supplied *ad libitum*. Energy requirements during gestation, lactation and care of their offspring were defined by the food balance method (for details see Migula, 1969; Gębczyński, 1975). Separate experiments were made to determine digestibility and assimilation coefficients, including those for reproducing females. In the second series of experiments the energy requirements for non-breeding pairs were defined. The third series of experiments consisted in determining the amount of food consumed by parents possessing offspring, from the time of the latter's birth up to the attainment of complete independence by the young animals. The experiment was continued for a full three weeks after birth, since although juvenile pine voles consumed small quantities of solid food at 13—16 days old (Gębczyński, 1980) and ate substantial quantities at 17—18 days old, they were not weaned until they were about

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20-22 days old (Schröpfer, 1977). In addition calculation was made of body weight increase and energy consumption by gestating females, also kept in pairs with males. In all the experiments, with the exception of those in which digestibility and assimilation was determined, the animals had access to nesting material (cotton).

All the experiments were carried out at a temperature of  $17-19^{\circ}C$ , relative-humidity 70%, and photoperiod 12L:12D.

Food was placed in the cages every day and uneaten food and faeces were alsocollected daily. Samples of food and faeces were oven-dried for 48 hours at  $70^{\circ}$ C<sup>-</sup> to determine dry matter intake. The coefficient of digestibility and urine production (Table 1) made it possible to calculate metabolized energy intake. Energy equivalents of oat grain, carrot and parsnip were determined, using an adiabaticoxygen bomb calorimeter (Type KL - 3).

#### 3. RESULTS

Energy requirements in non-breeding European pine voles kept in pairs were compared with those of single, sexually inactive females. The data obtained on food consumption were converted to the value of metabolizable energy, using coefficients of digestibility and assimilation obtained in separate experiments (cf. Table 1). Energy requirements: expressed per unit of body weight, is about  $9.5^{0}/_{0}$  greater in females

Table 2

Metabolizable energy requirement in non-breeding European pine voles kept in pairs and alone during measurements.

No. of		1	Paired			Single <sup>1</sup>	
exp.	Duration	Body wt.,	kcal/g	day	Body	kcal/g	day
	of exp., days	F+M, g	Mean	SD	wt. g	Mean	SD
1	6	39.8	.603	.032	19.0	.719	.097
2	6	39.4	.519	.131	14.4	.698	.148
2 3 4 5 6 7 8 9	6 6 8	33.0	.721	.122	17.3	.707	.126
4	8	33.7	.624	.061	19.6	.739	.082
5	8	29.6	.596	.146	17.2	.801	.112
6	8	26.8	.633	.054	20.4	.636	.074
7	4	31.2	.535	.188			
8	4	29.3	.713	.129			
9	16	23.4	.662	.050			
10	16	24.5	.626	.091			
Mean/Total	82	29.3	.629	.120	18.0	.713	.116

<sup>1</sup> Measurements lasted for 8 days each.

kept singly than in animals kept in pairs. As parental care is exercised by both female and male European pine voles and the male remained in the nest with the young animals even longer than the female (Gębczyński, 1980), the value of energy consumption proper to these animals kept in pairs, was taken for calculating costs of rearing young in the nest (Table 2).

Body weight in gestating females increases with successive periods-

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of gestation. The greatest increase is in body weight during the last six days of pregnancy, i.e., from the 16th-21st day after fertilization, and on an average is 53% for this period (Table 3) Energy requirements also increase, but not only on account of increasing body weight. Calculation

#### Table 3

Body weight changes and metabolizable energy requirements in pregnant females (n=11) of P. subterraneus.

A female was kept together with a male and measurements of food consumption started as soon as the female was visibly pregnant, usually 7 days before parturition. In calculating energy requirement for females 1 to 7 days of pregnancy, it was assumed that their metabolic rate is the same as in non-breeding females. Metabolic level for the females in the second period of pregnancy (8-15 days) was

assumed to be intermediate for non-breeding and highly pregnant. Body weight of females in the last day of pregnancy was  $22.2\pm0.65g$  (SE), n=11.

Item		Pre		Period	of pregnan	cy, days	Postp turiti	
Item		Mean		1—7	8—15	16-21 1		SD
Body weight,	g %	14.2 100.0	1.9	15.0 105.6	16.7 117.6	19.8 139.4	17.2 121.1	1.8
Energy requirement, kcal/g day kcal/female		.629 8.93		.629 9.43	.659 11.0	.689 13.64		
0/0		100.0		105.6	123.2	152.7		

<sup>1</sup> It was assumed that pregnancy lasts 21 days (Langenstein-Issel, 1950; Schröpfer, 1977).

#### Table 4

Body weight (g) increase in the European pine vole during initial weeks of life, depending on litter size. Mean values, standard deviation and numbers of measurements (in brackets) are given.

Litter size 1, n=111, r=0.921, y=1.580+0.376xLitter size 2, n=471, r=0.891, y=1.248+0.277xLitter size 3, n=880, r=0.881, y=1.522+0.316x

Age,			Litter	size			
days	1		2		3		Mean
Birth wt.	1.64	.14	1.56	.24	1.57	.13	1.58
	(14)		(24)		(21)		(59)
1-3	2.0	.3	2.0	.4	2.0	.4	2.0
	(18)		(68)		(110)		(196)
4-6	3.1	.6	2.9	.6	3.0	.4	3.0
	(15)		(68)		(120)		(203)
7-9	4.4	1.0 1	4.1	.6	3.9	.51	4.0
	(13)		(67)		(120)		(200)
10-12	5.5	1.1 1	4.9	.91	4.7	.81	4.8
	(13)		(64)		(120)		(197)
13-15	6.2	1.4	5.8	1.0	5.7	1.0	5.8
	(13)		(60)		(126)	Core .	(199)
16-18	7.0	1.6	7.0	1.3	7.2	1.4	7.1
	(13)		(60)		(133)		(206)
19-22	9.0	.8	8.3	1.2	8.5	1.6	8.5
	(12)		(60)		(130)		(202)

<sup>1</sup> Statistically significant differences, Student t test,  $P \le 0.05$ .

Table  $\hat{5}$  Cost of lactation and nesting growth in P. subterraneus, in litters of different size.

		Energy	require-		Juvi	Juveniles		
size	Body wt., F+M, g Mean SD	ment of and off Mean	ment of parents and offspring Mean SD	Mean litter wt., g	Mean off- spring body gain/day	kcal/ litter per day	kcal/g of body gain Mean SD	g of gain SD
First week of	off							
1		26.38		2.8	0.31	4.44	14.32	
2 14		26.29	2.45	5.4	0.28	5.50	9.82	1.62
		28.42	3.43	8.1	0.28	7.19	8.56	1.96
Second week	0							
		26.20		5.4	0.31	4.65	15.01	
2	12 33.0 2.8	27.17	1.98	9.8	0.28	6.38	11.40	2.01
3		29.92	3.16	14.1	0.26	8.75	11.22	1.58
<b>Third week</b>	off							
1 2	33.8	27.00		7.3	0.43	5.71	13.27	
2		29.01	4.11	14.4	0.36	8.29	11.51	2.34
	33.8	36.46	2.82	21.9	0.40	15.17	12.64	1.95

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was made of food consumption and consequent energy requirements for the last six days of gestation. When converted to unit of body weight this requirements increases by  $9.5^{\circ}/_{\circ}$ , and after taking into consideration increase in weight of females this means that these animals must assimilate  $53^{\circ}/_{\circ}$  more energy than a non-breeding female.

It is also necessary to know the rate of increase in body weight in order to calculate growth costs in nesting young. Young European pine voles weigh, a few hours after birth, i.e., less than one day old, from 1.2 to 2.0 g. The value for mean body weight for individuals from litters of one is almost the same as for litters consisting of two or three young (Table 4). Rate of increase in body weight up to the 6th day of life in litters of different size is not significantly different (Student t test). It is not until the age of 7—9 days that single young significantly increase their weight, but only in comparison with litters composed of 3 young. Single pine voles 10-12 days old are, however, significantly heavier than those of the other groups. Differences are not significant in any of the older groups (Table 4).

Food consumption in parents rearing young increases successively as the young grow. It is lowest during the first week of life of the young animals. Irrespective, however, of the period of nest development of the young, the greatest differences in energy consumption are connected with the number in the litter. The value of energy consumption calculated for different litters is a good illustration of this fact (Table 5). Production cost of 1 g of body weight in young animals is similar in litters of 2 or 3 individuals. It is only in young reared singly that this costs seems to be higher during the first two weeks of life in comparison with larger litters (Table 5).

#### 4. DISCUSSION

Determination of costs of gestation, lactation and rearing young in rodents leads to the question as to whether measurements should be carried out on females kept singly after fertilization, or females kept with males. The majority of the measurements were made on single females during pregnancy, then with the litter after birth (e.g. Kaczmarski, 1966; Myrcha et al., 1969; Migula, 1969; Millar, 1975; Randolph et al., 1977; Lochmiller et al., 1982). This approach is the result of the conviction that rodents are species with a polygynous type of mating, which would suggest that the female takes the main burden of the care of progeny (Ralls, 1977). Our knowledge of the mating system of voles under natural conditions is slight and the first proofs, e.g. in *Peromyscus polionotus* (Foltz, 1981), indicate that they may live in long-term monogamy. Observations of laboratory-bred *Pitymys subterraneus* show (Gębczyński, 1980) that the male warms the young more intensively than the female does. For these reasons definition of reproduction costs in the European pine vole was made on animals kept in pairs.

Lactating female pine voles have a food digestibility and assimilation coefficient similar to that in non-breeding females. This has been observed in other rodent species — the bank vole (Kaczmarski, 1966), the common vole (Migula, 1969), the laboratory mouse (Myrcha *et al.*, 1969, the cotton rat (Randolph *et al.*, 1977), and the American pine vole (Loch-miller *et al.*, 1982).

The average body weight of newborn pine voles is 1.6 g (Table 4), and thus is the same as the weight of pine voles from Czechoslovakian populations (Šterba, 1976). The pine vole from western Europe weighs 1/5 more at birth, average weight being 1.95 g (Schröpfer, 1977). The American pine vole *Microtus (Pitymys) pinetorum* weighs 2.0 g at birth, but birth weight does not depend on litter size, as is the case with the European pine vole.

Increase in body weight in the pine vole is several times more rapid during the initial three weeks of life than during the subsequent period (Schröpfer, 1977). Increase in body weight during the initial 21 days of life is four times as great, but there are no distinct differences depending on litter size in the body weight of pine voles leaving the parent nest (Schröpfer, 1977; see Table 4). In many other species of rodent the body weight of individuals in large litters is smaller than in small litters, for instance the body weight of a 20-day-old bank vole from litters of 3—5 young is  $45^{0}/_{0}$  higher per vole than those from litters of 6-9 (Korabelnikov, 1972). In the cotton rat weight at birth also depends on litter size (Randolph *et al.*, 1977).

The significant increase in energy requirements during the last days of gestation found in pine voles is also observed in many other species — the bank vole (Kaczmarski, 1966), the common vole (Migula 1969), the laboratory mouse (Myrcha *et al.*, 1969), the white-footed mouse (Millar, 1975). This is undoubtedly due to the uneven growth of embryos during gestation. There are no data on prenatal changes in the body weight of pine voles, but in the bank vole this increase is 10 times greater during the week immediately preceding birth (Ożdżeński & Mystkowska, 1976). Observations of the ossification of the skeleton point to similarly accelerated growth during the final phase of gestation in *P. subterraneus* (Šterba, 1976).

In some of the rodent species examined, e.g. Peromyscus maniculatus, however, gestation was not found to cause perceptible increase in energy requirements (Stebbins, 1977). Many authors have stated (cf. comparison of 5 species by Randolph *et al.*, 1977) that female rodents during gestation increase energy consumption by an average of  $28^{\circ}/_{\circ}$ . A female pine vole needs  $18^{\circ}/_{\circ}$  more energy during this period, which is certainly due to the fact that litters are small. Increase in consumption during lactation and rearing young has been demonstrated in all the rodent

Species	Litter size	Birth weight, g	Wt. at the end of cal- culation period <sup>1</sup>	Calculation period <sup>1</sup> , days	kcal/g of offspring body gain	Reference
Clethrionomus glareolus	5.0	1.6	9.6	18	9.79	Kaczmarski, 1966
C. alareolus. winter	3.1	1.9	9.1	14	10.83	Gebczyński, 1975
. glareolus. spring	3.3	1.9	11.5	14	8.98	Gębczyński, 1975
Microtus arvalis	4.3	17	9.9	16	10.27	Millar, 1978
Peromyscus leucopus	4.9	1.8	8.9	13	8.92	Millar,1978
Microtus pinetorum	2.2	1.9	1.7	18	8.84	Lochmiller et al., 1982
Pittymys subterraneus 2	2.5	1.6	5.7	14	10.25	this study
Microtus occonomus	4.6	2.5	7.4	12	9.28	Gębczyński & Gębczyńska,
						in preparation
Sigmodon hispidus	5.0	6.5	16.3	12	5.26	Randall et al., 1977
Sigmodon hispidus	5.0	6.6	17.1	12	4.92	Mattingly & McClure,1982

Table 6

Energy cost of parental investment in different species of rodents.

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species so far examined. There is also agreement as to consumption being markedly greater than gestation costs. Lactation costs were calculated either by means of food consumption balance or by measurement of oxygen consumption. The ways in which increased energy requirements were expressed were more varied. Generally it was shown in percentages how much more energy a female must consume during the whole lactation period, or in the various phases of this period, in order to feed and rear its progeny. This method makes it necessary to establish both the metabolism level of the given species and the introduction of corrections for litter size, since larger litters require greater amounts of energy outlay than smaller ones (e.g. Lochmiller et al., 1982). The next component element of the calculations must be rate of growth and development in the nest, since rapidly growing species have different energy requirements from those of the slow-growing species (cf. Randolph et al., 1977). For these reasons we carried out calculations (Table 6) in order to determine whether there is an index unifying costs of lactation and rearing young in the rodents examined. It was found that parental investment expressed in 1 g of body weight increase of the young is  $9.64 \pm 0.27$  (SE) kcal of metabolizable energy. It was only in Sigmodon hispidus that this index is half this value (Randolph et al., 1977; Mattingly & McClure, 1982). The difference between S. hispidus and the other listed rodent species may be explained by the higher body weight at birth (6.5 g versus 1.5-2.5 g).

Therefore if index 9.6 kcal per 1 g of body growth in offspring is. correct for other rodent species with the low birth weight, then the bioenergetic parameters of lactation may be calculated from changes in the body weight of young during the period of their dependence on their parents in the nest.

The period of complete dependence of young rodents is divided from. the independence period by 3-5-day phase of partial reliance on parental care. Energy investment increases during this time (e.g., Stebbins, 1977; Millar, 1978; this paper). This must be due to increase in the young animals' activity, leaving the nest more often and for longer at a time, sucking their mothers but also independently additionally consuming the food laid out. Under natural conditions such additional eating undoubtedly takes place outside the nest without further expenditure on the part of the parents. It would thus appear that acceptance of the calculated value of 9.6 kcal assimilated energy per 1 g of offspring body gain during the nest period accurately describes the parental effort in rodents during the period when the parents care for their young. It does not, however, represent the whole of parental investment, since apart from increased energy consumption aimed directly at production and maintenance of the young, the parents are exposed to increased risk. Such risk may involve weakening of vitality and condition, increased susceptibility to disease and parasites, possibility of being injured, etc.

Unfortunately we do not as yet know how to calculate this part of parental expenditure in comparable units.

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## ENERGETYCZNY KOSZT WZROSTU DARNIÓWKI W GNIEŹDZIE Streszczenie

Zapotrzebowanie energetyczne jest w okresie ciąży (Tabela 3) u darniówki, Pi-tymys subterraneus (de Sélys-Longchamps, 1836) wyższe o 18% w porównaniu do nierozradzających się samic (Tabele 1, 2). W ostatnich sześciu dniach ciąży zapotrzebowanie to wzrasta o 53% (Tabela 3). Koszty laktacji i wychowu młodych w miotach złożonych z trzech młodych są proporcjonalnie wyższe niż w miotach składających się z dwóch osobników. Wychowanie pojedynczych młodych, choć energetycznie mniej kosztowne w porównaniu do liczniejszych miotów, w przeliczeniu na 1 g przyrostu masy ciała potomka, wymaga o 34% więcej nakładu energetycznego ze strony rodziców. Tempo wzrostu ciała młodych darniówek jest podobne w początkowych trzech tygodniach po urodzeniu, tylko mioty pojedyncze rosną istotnie szybciej między 7. a 12. dniem życia (Tabela 4). Na podstawie danych dla *P. subterraneus* i pięciu innych gatunków gryzoni obliczono, że nakład energetyczny rodziców wynosi 9,6 kcal (= 40 kJ) na 1 g przyrostu masy ciała młodych w okresie gniazdowym (Tabela 6).

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