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Production efficiency in small mammal populations

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Summary. The data used to analyse the relationship between production (P) and respiration (R) in small mammals (Grodziński and French 1983) are reanalysed and different conclusions are drawn. Differences in production efficiency cannot be attributed to any particular trophic class, but in the higher taxonomic categories the murids have higher production efficiency than the rest. However examination of numerous populations of the same species shows that production efficiencies of congeneric species sometimes differ significantly and show differences which exceed those between higher taxa. The same applies to trophic classes. The low slope described for the regression of P on R for Insectivora is due to an aberrant set of data for *Sorex araneus*. Production efficiency is directly related to litter size in rodents and inversely to survival of adults. This result conflicts with much earlier work and is discussed at length.

Introduction

Plotting annual production (log P) of animal populations against annual respiration (log R) produces a straight line allometric relationship (Engelmann 1966; Golley 1968; Hughes 1970; McNeil and Lawton 1970; Lévêque 1973; Grodziński and French 1974, 1983; Humphreys 1979). Such lines may be used, within the statistical bounds of the regression, to predict the unknown value from either P or R.

Attention has focused on the slopes and elevations of the regression lines. A departure of the slope from unity implies that production efficiency (P/R, or P/A where $A = P + R$) varies with the magnitude of P (or R; McNeil and Lawton 1970; Humphreys 1979). Lines which are parallel but displaced along the abscissa show that production efficiency differs between the classes considered. Several attempts have been made to distinguish statistically between classes, using different criteria for subdivision (e.g. habitat, taxa and trophic habit), to obtain more accurate predictive equations (McNeil and Lawton 1970; Shorthouse cited in Humphreys 1979; Grodziński and French 1974, 1983; Humphreys 1979).

Grodziński and French (1983), from an analysis of 102 populations of small mammals belonging to 30 species, concluded that:

1. Insectivora had lower P/A than rodents.
2. Insectivora had a lower slope (0.628) than rodents (1.008).

3. Within rodents there was no effect on P/A of taxonomic position.

4. Within rodents, trophic habit influenced P/A giving, in rank order insectivores < granivores < herbivores (respective P/A% = 0.7, 2.3, 2.6 and 3.4).

They recommended the use of different regressions for Insectivora and rodents, and for trophic classes within the rodents.

Grodziński and French's paper analyses a much larger set of data, more rigorously defined, than those previously considered. Their conclusions do not support previous empirical and theoretical generalizations (Humphreys 1979; Lavigne 1982). The slope of their Insectivora equation ($b = 0.628$) implies a change in P/A by a factor of ≈ 2.4 for each order of magnitude change in R.

Population densities of Insectivora often fluctuate by an order of magnitude within seasons (range 1.8 to 18.5; French, Stoddart and Bobek 1975). Assuming that P/A, through its influence on reproduction (P_r), has selective consequences, then, normal population fluctuations in Insectivora should lead to, through the effect on production efficiency, substantial changes in fitness (all other things being equal). This being so the Insectivora would be prime candidates for an examination of the relationship between density changes, production efficiency and fitness.

These results are such that I present here a reanalysis of Grodziński and French's (1983) data and incorporate some demographic measures.

Methods

Source of information

I analyse the data in the Appendix of Grodziński and French (1983). Additionally I extract data, for the species concerned, on various demographic measurements from French, Stoddart and Bobek (1975). For each species all values of a given parameter were averaged; the limits of ranges were treated as separate estimates. Body weight and length were taken from Hall and Kelson (1959) and Brink (1976) using mean values if ranges were given (Appendix).

Statistical treatment

The data are treated in their entirety or, where the different numbers of populations per species may bias class data, as the average value of all populations per species (see Grodziński and French 1983).

Regressions were calculated between log R and log P (dependent variable) for various subsets of the data. Analy-

sis of covariance was used to test whether the slopes were not parallel. If parallel they were tested for similarity of the intercepts. If the intercepts were not similar, statistical separation of particular regression lines was achieved using an unplanned multiple comparison test (SNK procedure).

Mean values of production efficiency were analysed using ANOVA for unequal sample size followed by an unplanned multiple comparison test (GT2 procedure).

Demographic data were combined with energetic data for the same species and the relationships examined by regression.

As body weight is rarely reported in the taxonomic literature, body weight (log) where available, was regressed against log (total length – tail length)³. The slope was 1.06 and the regression accounted for 97% of the variance ($N=10$). Hence for all animals the body length (L) was scaled as L^3 and used, as it is routinely available, in place of weight.

All statistical algorithms were taken from Sokal and Rohlf (1981).

Results and discussion

Methodological check

My procedures gave the same equations and, despite different follow up statistics, similar probabilities as those in Grodziński and French (1983; their Tables 2 and 3; save line 8 where my $a = -2.005$ in place of -1.994).

Influence of weight on P/A

Where available L^3 (i.e. scaled to weight) was correlated with mean species P/A for various subsets of the data. The entire set shows significant correlation (Table 1) but this is due to Insectivora having exceptionally low P/A and, as shown later, should be treated separately. Rodent P/A is not correlated with L^3 . No trophic subset of rodents exhibited significant correlation but one taxonomic category did (mice = Cricetinae + Muridae + Heteromyidae). The murids are later shown to have distinct production efficiency so the correlation is spurious.

The various subsets show no consistent trend indicating a relationship between weight and production efficiency and I do not consider weight in the subsequent analyses.

Table 1. Correlations between mean species P/A and $3 \times$ (log body length) for various groups of small mammals

	r	n	P
1. All small mammals	0.406	26	<0.05
2. 1 minus <i>P. semispinosus</i>	0.518	25	<0.05
3. Insectivora	0.761	4	NS
4. All rodents	0.271	22	NS
5. 4 minus <i>P. semispinosus</i>	0.400	21	NS
6. Sciuridae	-0.638	5	NS
7. 'mice' ^a	0.851	8	<0.01
8. Microtinae	0.410	8	NS
9. All insectivores	0.545	5	NS
10. granivores	-0.522	5	NS
11. omnivores	0.591	8	NS
12. herbivores	0.368	7	NS

^a Includes Muridae, Heteromyidae and Cricetinae

Table 2. Regression equations and ANCOVA describing the relationship between log R (x) and log P (y) within various small mammal species. Probabilities are for the significance of the slope from zero. I insectivores, H herbivores, O omnivores, G granivores

A Species	b	a	r^2	n	P	
<i>Sorex minutus</i>	1.058	-2.460	0.929	7	0.0002	
<i>S. araneus</i>	0.249	1.799	0.332	9	0.099	
<i>Clethrionomys glareolus</i>	0.843	-0.800	0.837	18	<10 ⁻⁸	
<i>Microtus agrestis</i>	0.843	-0.820	0.958	9	<10 ⁻⁶	
<i>M. arvalis</i>	0.931	-0.722	0.857	6	0.0045	
<i>Apodemus sylvaticus</i>	0.645	0.348	0.622	9	0.009	
<i>A. flavicollis</i>	0.962	-1.293	0.888	14	<10 ⁻⁷	
ANCOVA excluding <i>S. araneus</i>						
	F_s	d.f.	P			
slopes	0.568	5,51	0.724			
intercepts	36.49	5,56	<10 ⁻¹⁵			
SNK tests on the regressions excluding <i>S. araneus</i> . Lines include species not different at $\alpha=0.05$.						
B Trophic type I	H	O	G	G	H	
Species ^a	<i>S.m.</i>	<i>M. agrestis</i>	<i>C.g.</i>	<i>A.f.</i>	<i>A.s.</i>	<i>M. arvalis</i>
adjusted \bar{x} log P	2.85	3.46	3.49	3.54	3.73	4.13
$\pm 95\%$ C.I.	0.163	0.162	0.110	0.137	0.167	0.257
	insectivora	micro-tine	micro-tine	murid	murid	micro-tine
C Rodent genera only						
Trophic type genus	O <i>Clethrionomys</i>	H <i>Microtus</i>	G <i>Apodemus</i>			
adjusted \bar{x} log P	3.52	3.62	3.75			
$\pm 95\%$ C.I.	0.087	0.103	0.091			

^a Exclusion of *Sorex* spp. from the analysis shows that *A. sylvaticus* and *M. arvalis* are significantly different from each other and both from the other 3 species. Comparison of all *Sorex* spp. with the above rodents gives parallel lines with *Sorex* spp. separate from all rodents

Species specific relationship between P and R

Sufficient populations of 7 species are available to examine the within species relationship between P and R (Table 2). The regression for *Sorex araneus* ($b=0.249$) is not significant and is excluded from consideration. Exclusion of the *S. araneus* data (assuming aberrant data) results in parallel and displaced lines (Table 2A) with *S. minutus* clearly separated from rodents. Additionally there is taxonomic separation within the genus *Microtus* and separation within the same trophic type (Table 2B).

Table 3A. Production efficiency (%) for various taxa calculated from the mean value for each species

Taxa	P/R			P/A		
	mean	s	N	mean	s	N
Insectivora	1.185	0.893	4	1.163	0.867	4
Sciurids	1.923	0.571	6	1.883	0.545	6
'mice' ^a	2.599	2.142	9	2.493	1.965	9
microtine	3.495	1.553	10	3.347	1.426	10

None of these values differ significantly from each other

ANOVA

For P/R $F_{3,25} = 2.502$ $P = 0.082$

^a Includes Cricetinae, Muridae and Heteromyidae

Table 3B. Comparison of regression lines for groups of rodents with >5 measurements of P and R

	Slope	Intercept	n	r ²	t _s	P
Sciuridae	0.980	-1.680	6	0.99	18.78	<10 ⁻⁵
Cricetinae	1.300	-3.161	8	0.97	9.54	<10 ⁻⁵
Microtinae	1.084	-1.993	42	0.92	21.85	<10 ⁻²⁴
Muridae	0.914	-0.999	23	0.81	9.40	<10 ⁻⁹

ANOVA	F _s	d.f.	P
slopes	2.085	3,71	0.110
intercepts	5.865	3,74	0.0012

SNK test: Line includes groups not differing at $\alpha = 0.05$

	Sciuridae	Cricotinae	Microtinae	Muridae
Adjusted \bar{x} log P	3.43	3.52	3.58	3.78
$\pm 95\%$ C.I.	0.194	0.166	0.077	0.107

Combining the data into genera (Table 2C) results in non-parallel lines. Excluding *Sorex* gives statistical separation of *Clethrionomys* and *Apodemus* and of omnivores from granivores (Table 2C). The ascending rank order of trophic types differs from that in Grodziński and French (*ibid*; Table 4) which is granivores < omnivores < herbivores.

Hence congeneric species (or the same trophic category) may separate, according to their production efficiency, more than do genera or higher taxonomic categories (Microtinae and Muridae; *C. glareolus* and *Apodemus* respectively). Conversely taxa or feeding types may have similar efficiencies (*Apodemus* spp.; Table 2C). *Microtus* ranks middle place because the two species lie at opposite ends of the range of production efficiencies considered.

Higher taxa

Analysis of the higher taxonomic groupings for rodents shows that murids have higher production efficiency than the sciurids, cricetines or microtines which themselves do not differ (Table 3A, B). Excluding the data from the Insectivora which cause the different slope (*Sorex araneus* and

Table 4. Comparison of the relationship between P and R in rodents of 3 trophic types. The data used are those specified in Grodziński and French (1983; Table 2, rows 6-8)

	Slope	Intercept	n	t _s	P
Granivores	0.853	-0.815	30	10.00	<10 ⁻¹⁰
Omnivores	1.002	-1.621	26	15.33	<10 ⁻¹³
Herbivores	1.092	-2.005	25	15.52	<10 ⁻¹²

ANOVA	F _s	d.f.	p
slopes	2.754	2,75	0.070
intercepts	2.283	2,77	0.109

	Omnivores	Granivores	Herbivores
Adjusted \bar{x} log P	3.527	3.642	3.660
$\pm 95\%$ C.I.	0.0822	0.0852	0.0962

Table 5. The relationship between production efficiency ($\sin^{-1} \sqrt{P/R}$) and trophic class in small mammals. None of these classes is statistically separable from any other single class despite the significant overall ANOVA

	\bar{x}	S.D.	N
Insectivores	5.98	1.83	5
Granivores	8.59	2.59	8
Omnivores	9.14	2.78	9
Herbivores	10.70	2.45	7

ANOVA	F _s	D.F.	P
	3.49	3,25	0.031

Barlett's test for homogeneity: $\chi^2 = 0.80$, N.S.

Neomys fodiens) leaves the Insectivora with lower production efficiency than all other groups in Table 3B.

Trophic type

Grodziński and French (1983; Fig. 2 and Table 3) showed granivorous and herbivorous rodents had regressions of P or R which were not parallel and had different intercepts. These data are biased by the differing numbers of populations in each species so they calculated the mean species production efficiencies and calculated class means (*ibid*; Table 4). No further statistical tests were conducted so the implied significance of trophic type on production efficiency is derived from the regression analysis. Note that their regression lines are not parallel and intersect near the mid-range of values considered. Hence for R values below the intersection P/R for granivores < herbivores, while for R values above the intersection herbivores > granivores.

Analysis of these data using multiple comparison tests following ANCOVA, rather than pairwise comparison, shows the lines for rodent trophic types are parallel but not displaced (Table 4). Analysis of the mean values for

each species shows overall significance, but follow up tests fail to distinguish between any two trophic classes at $\alpha=0.05$ (Table 5). The rank order is insectivores < granivores < omnivores < herbivores with respective mean P/R, after retransformation, of 1.08, 2.23, 2.52 and 3.45%.

While trophic type influences production efficiencies, no one trophic class can be distinguished from any other.

Demographic parameters

In Table 6 the results are mostly presented excluding Insectivora due to their low P/A. In no case does their inclusion change the outcome of the null hypothesis at $\alpha=0.05$. Despite the small sample size and averaged values from separate populations, production efficiency is positively related to population density and litter size and negatively related to monthly survival of adults (Table 6). The density data are strongly influenced by a single value and are unreliable. The regression on litter size accounts for 73% of the variance and litter size is not related to body weight ($r=0.12$, $n=13$) nor to density ($r=0.006$, $n=13$). Over the range of values considered, for litter size, production efficiency varies between 1.0% and 4.6% (Fig. 1A).

The relationship between adult survival and P/R is notable (Fig. 1B), although marginally not significant ($P=0.062$), because it is the only measure inversely related to production efficiency; this is expected as will be shown in the General Discussion. Over the range of survival considered P/R varies between 1.5 and 4.9% (Fig. 1B). Note that 2 of the 6 species are not common to the litter size analysis (Appendix).

General Discussion

The results here contrast with those of Grodziński and French (1983) in showing taxonomic differences in production efficiency at the species level and at the family level. However, no clear separation of trophic classes was detected.

The data for *Sorex araneus* are aberrant when considered at the species level. Removal of these data from the Insectivora produces a relationship between P and R not differing in slope from the rodents.

The strong direct relationship between litter size and production efficiency requires comment. Large litter size is related to intrinsic rate of natural increase (r_m) and is a correlate of the r - K selection continuum (Table 7). As such it should have the opposite slope to the relationship between P/R and survival; this is the case for the rodent data (Fig. 1).

The food habits of animals influence the basal rate of metabolism and their field production efficiencies irrespective of their taxonomic affiliation, plant feeders having higher metabolic rates and lower P/A than carnivores, with omnivores in between (Humphreys 1979; McNab 1980; Lavigne 1982). Trophic type also is related to home range size with granivores > herbivores (Mace and Harvey 1983). However, within the entire set of information analysed here, no clear distinction can be made between any trophic class, whereas within the same genus (*Microtus*) two herbivores are clearly separated according to their production efficiency with other genera and trophic classes intermediate. Indeed "the apparent correlation of ecological strategy with rate of metabolism may, in fact be quite complex" McNab (1980).

Although groups of rodents have distinctive growth constants and metabolic rates (microtines > cricetines > heteromyids; McNab 1980), it has not been possible to separate these groups on the basis of their field determined production efficiencies. Whether this results from the greater error inherent in field determinations, from different scopes of activity between species, or from other causes is unclear.

In his detailed analysis of the relationship between metabolism (respiration) and demographic parameters, McNab (1980) found the clearest separation related to the number of young per female per year. In my analysis P/R was not related to the product of number of litter per season and the number of young per litter. However, production efficiency was strongly related to average litter size (Fig. 1A) while neither was related to body weight. Within Fig. 1A there is no clear separation of taxonomic or trophic categories.

The correlation between production efficiency and litter size is the clearest relationship between field determined energetics and a field determined demographic parameter. Litter size is a correlate of the r - K selection gradient; by implication r -selected species are thus more energetically efficient than K -selected species.

These data (Fig. 1A) are in conflict with previous work. Animals with high metabolic rates have high intrinsic growth rates (r_m) (McNab 1980) and are hence r -selected; those with low metabolic rates have low r_m and are hence K -selected. In addition reproduction *per se* increases metabolic rate several fold (Kaczmarski 1966) and litter size is directly related to metabolic rate (McNab 1980; Henne-man 1983); this despite the broad trend for mammals of equal size to have litters of the same weight irrespective of litter size (Western 1979). Animals with high metabolic rates have lower production efficiency than those with low

Table 6. Relationship between production efficiency (P/R) in small mammals and various demographic measurements. Data were extracted from Grodziński and French (1983) and French, Stoddart and Bobek (1975)

	Transformation ^b	N	a	b	r ²	F _s	P
1. Density (ha ⁻¹)	linear	15	2.33	0.008	0.34	6.705	0.0225
2. Density (ha ⁻¹) ^a	linear	13	2.66	0.007	0.34	5.74	0.0354
3. No. litters × litter size ^a	power	8	0.53	0.578	0.44	4.651	0.074
4. Litter size ^a	power	13	0.36	1.217	0.73	29.61	0.0002
5. No. litters ^a	power	9	—	—	0.08	0.571	0.47
6. Adult survivorship	log	6	1.31	-5.541	0.62	6.597	0.062

^a Excluding Insectivora

^b Form of equations: linear $y = a + bx$; log $y = a + b \ln x$; power $y = ax^b$

Table 7. Correlates of production efficiency suggested by various authorities. The state of each parameter is placed below the state of production efficiency to which it is related

Parameter	State of parameter		Authority
	low	high	
Production efficiency			
litter size	small	large	this paper
adult survival	high	low	this paper
r-K	K	r	this paper
r-K	r	K	Cody 1966
r-K	r	K	Pianka 1970
interspecific competition	high	low	Humphreys 1979
body size	=	=	Lavigne 1982
body size	=	=	Humphreys 1979
body size	small	large	Fenchel 1974
population density	low	high	Humphreys 1979
population density	low	high	Bobek 1969
population density	low	high	Grodziński and French in Humphreys 1979
age	old	young	Calow 1977
population growth	stable declining	growing	Calow 1977
trophic type	herbivore	carnivore	Humphreys 1979
trophic type	herbivore	carnivore	McNab 1980
trophic type	herbivore	carnivore	Lavigne 1982
trophic type	granivore	herbivore	Grodziński and French 1983
metabolic rate	high	low	Lavigne 1982

metabolic rates (Lavigne 1982). Indeed Lavigne concluded that production efficiency of animals is characterized primarily and fundamentally by their metabolic rate as influenced by their food habits, and thus related production efficiency to McNab's work and to broad taxonomic trends in P/A (Humphreys 1979). These relationships imply, in general, that *r*-selected animals should have low production efficiency, while *K*-selected animals should have high production efficiency. The field determined data for rodents (Fig. 1A) contradicts this as litter size is directly related to production efficiency. This is different from the trade off between metabolic rate and r_m which has been discussed elsewhere (McNab 1980, Henneman 1983).

This contradiction may be resolvable without rejecting any of the works considered or the rodent data. McNab (1980) and Lavigne (1982) draw their conclusions by considering respectively the metabolism and scaling effects of various energetic measurements on *individuals*. Their conclusions support the separation of trophic classes and broad scale taxonomic classes based on the energetics of field *populations* (Humphreys 1979). However, at the finer level of analysis, represented by the rodent data, this distinction between individuals and populations may be crucial. *r*-selected populations are characterized by having high reproduction and hence a larger proportion of young in the pop-

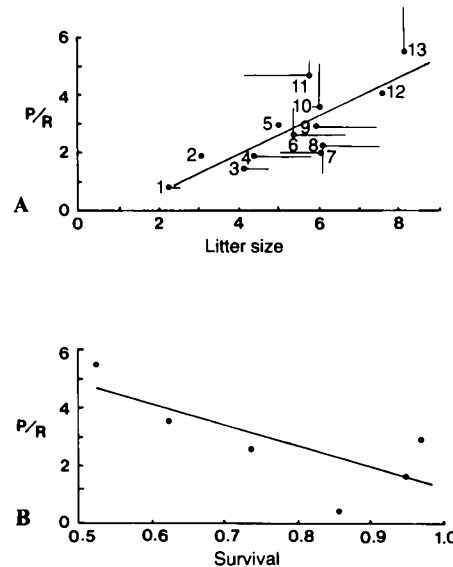


Fig. 1 A, B. The relationship between production efficiency (P/R%) in species of small mammals. The data are the means for each species collated from Grodziński and French (1983; P/R) and French, Stoddart and Bobek (1975; demographic) A P/R regressed on litter size in 13 species of rodents. The linear model is depicted where $y = 0.67x - 0.72$, $r^2 = 0.67$. G = granivores, H = herbivores, O = omnivores. Lines to points represent 1 S.D. of the mean 1 *Dipodomys meriami*; heteromyid, G. 2 *Peromyscus polionotus*; cricetid, G. 3 *Tamiasciurus hudsonicus*; sciurid, G. 4 *P. leucopus*; cricetid, O. 5 *Microtus pensylvanicus*; microtine, H. 6 *Clethrionomys glareolus*; microtine, O. 7 *C. rutilus*; microtine, O. 8 *M. agrestis*; microtine, H. 9 *Spermophilus tridecemlineatus*; sciurid, O. 10 *Apodemus flavicollis*; murid, G. 11 *Arvicola terrestris*; microtine, H. 12 *Sigmodon hispidus*; cricetid, H. 13 *Apodemus sylvaticus*; murid, G. B Production efficiency (P/R %) regressed on mean monthly survival of adults of 6 species of rodents. The linear model is shown when $y = 8.43 - 7.1x$; $r^2 = 0.56$

ulation. Young animals have much higher production efficiency than older animals (Calow 1977). Hence the age structure of populations may be sufficient to reverse the expected inverse relationship between individual production efficiency and the *r*-*K* continuum to that observed in rodent populations (Fig. 1A). Too few data are available to examine the effect of population structure in rodents on production efficiency. Indeed the relationship may be spurious resulting from examination of inappropriate ratios. Mathematical models suggest that energy balance in organisms is far more sensitive to changes in assimilation efficiency than to respiration (Majkowski and Bramall 1980) and hence production efficiency. Demographic parameters may also be more influenced by assimilation efficiency than by food quality (Rushton and Hassall 1983).

It is tempting to infer from population budgets various attributes of ecological strategies, as I did earlier. However, ecological strategies are relevant only to the individuals upon which selection acts. The integration of individual energetic data into populations may seriously bias the energetic picture of those individuals with successful strategies.

There is an alternative explanation, which I favour, which would require reappraisal of some of the generalisations discussed above. The data come from Mattingly and McClure's (1982) elegant analysis of reproductive effort

Appendix

Demographic data for small mammals, summarized from French, Stoddart and Bobek (1975) as described in Methods

Species	No. litters	Litter size	Adult survival per month	Density (ha ⁻¹)	log(L ³) ^a
1. <i>Sorex minutus</i>	3	5.97	–	7.7	5.19
2. <i>S. araneus</i>	3	6.06	–	11.8	5.58
3. <i>Spermophilus tridecemlineatus</i>	1.5	5.95	0.97	–	6.42
4. <i>Sciurus carolinensis</i>	–	–	0.95	1.2	–
5. <i>Tamiasciurus hudsonicus</i>	1.67	4.15	–	–	6.92
6. <i>Dipodomys merriami</i>	2	2.31	–	2.0	5.99
7. <i>Peromyscus polionotus</i>	–	3.1	–	15.9	5.83
8. <i>P. leucopus</i>	4.5	4.45	–	6.0	6.01
9. <i>Sigmodon hispidus</i>	–	7.6	–	5.7	6.70
10. <i>Clethrionomys glareolus</i>	5	5.38	0.74	2.87	6.03
11. <i>C. rutilus</i>	3.67	6.03	–	20	6.09
12. <i>Microtus agrestis</i>	–	6.07	–	99.7	6.17
13. <i>M. arvalis</i>	–	–	–	490	6.09
14. <i>M. oeconomus</i>	4.67	–	–	–	6.51
15. <i>M. pennsylvanicus</i>	–	5	–	140	6.23
16. <i>Arvicola terrestris</i>	2.45	5.77	–	75.3	6.69
17. <i>Apodemus sylvaticus</i>	3.5	8.2	0.53	12.6	–
18. <i>A. flavicollis</i>	–	6.03	0.63	2	–
19. <i>Proechimys semispinosus</i>	–	–	0.86	–	7.07

^a L = total length – tail length

with varying litter size. In *Sigmodon hispidus* total mass of the litter is directly related to litter size. Consumption by the mother increases directly with litter size during both pregnancy and lactation, while assimilation efficiency remains constant. Respiration rate does not differ between pregnant, lactating or non-reproductive animals (Mattingly and McClure 1982). Hence production efficiency must increase with increasing litter size and thus accords with the general relationship derived from population energy budgets (Fig. 1).

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