any agreement at all with reality in view of the wide range of species to which they apply: we hope that they may contribute to a better understanding of some nutritional principles.

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Comparative nutrition in pregnancy and lactation

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A comparative study of any aspect of the nutrition of mammals must be based upon recognition of the fundamental similarities which exist within the group. We assume that each animal will have certain measurable characteristics, which vary between members of the group, but which are related according to a basic pattern.

In this study we are looking for measurements which describe in general terms the course of pregnancy and lactation. Special adaptations by particular groups of animals can then be distinguished by their deviations from the general pattern.

The growth and nutrition of the foetus

Perhaps the first suggestion of a common pattern of foetal growth was made by Rubner (1908), who plotted the birth weights and gestation times of a number of species and showed that all the points lay on a smooth curve, with the exception of those for man. It is now recognized that man is not a single exception, but, together with the other primates, forms a separate group whose birth weights are low in relation to the gestation times (Huggett & Widdas, 1951; Payne & Wheeler, 1967*a*).

The general pattern of foetal growth is of a lag period after conception, followed by a phase of growth, which is best described by an equation of the form

$$W = a(t-t')^3, \tag{1}$$

where W is the weight of the foetus at any time, t, after conception, and a and t' are constants. The low birth weights of primates could be due either to low values of the rate constant, a, or to an extended lag period, t'. In order to decide between these alternatives, it is necessary to establish the values of these constants for a number of species. Table 1 shows the values of a and t' which have been determined for a number of eutherian mammals and for three other species. In most instances t' lies within the range 20–25% of the total gestation time, and the slow growth of the two primates is accounted for by the low values of the constant a, which is related to the net inflow of nutrient material per day per cm^2 of effective exchange surface of the growing foetus (Payne & Wheeler, 1967*a*). It is of interest that the chinchilla, which is the only member of the hystricomorph rodents apart from the guinea-pig for which we have foetal weights, has a very low value of the constant a. These animals are noted for their long gestation periods. The values for the kangaroo cover the period between birth and first emergence from the pouch (Sharman & Pilton, 1964).

Table 1. *Values of constants in the growth equation* $W=a(t-t')^3$ *for foetuses of several species*

Species	$a\times 10^6$	t' (days)
Dog (*Canis familiaris*)	7·0	23
Rabbit (*Oryctolagus cuniculus*)	6·0	11
Cow (*Bos taurus*)	3·2	56
Rat (*Rattus norvegicus*)	3·0	11
Pig (*Sus scrofa*)	1·0	18
Mouse (*Mus musculus*)	1·0	8
Guinea-pig (*Cavia porcellus*)	0·6	15
Rhesus (*Macaca mulatta*)	0·3	29
Man (*Homo sapiens*)	0·2	36
Chinchilla (*Chinchilla laniger*)	0·08	24
Trout (*Salmo fario*)	0·001	4
Chick (*Gallus domesticus*)	4·0	1
Red kangaroo (*Megaleia rufa*)	0·3	0

The nutritional demands of pregnancy

The relation between the total weight of offspring at birth and the size of the mother has been studied by Leitch, Hytten & Billewicz (1959), who describe this relationship by the equation

$$nW_b = 0{\cdot}5408\ W_m^{0{\cdot}8323},$$

where n is the number in the litter, W_b the mean birth weight and W_m the mother's weight, the weights in this instance being expressed in grammes. As the weights of the adult females increase, the weights of the offspring produced also increase, not, however, in direct proportion to the mother's weight, but more nearly in relation to her metabolic body size ($W_m^{0{\cdot}73}$).

This allometric relationship takes no account of gestation time, and any consideration of the metabolic stress of pregnancy must include an estimate of the growth rate of the offspring rather than its absolute weight. It is a useful property of equations of the form (1) that the growth velocity at any time is given by $3W/(t\text{-}t')$, and thus we can use the ratio (W_b/t) of birth weight to gestation time as a measure of growth rate at birth; the rate of gain of the whole litter will be proportional to nW_b/t (Payne & Wheeler, 1967*b*). Fig. 1 shows this ratio plotted against mother's weight. Since the exponent of W_m is very much less than unity for both the lines, we can say that the metabolic stress of pregnancy is relatively greater for animals of small size. It is a feature of the success of many species of small animals that they produce large numbers of offspring in a short space of time.

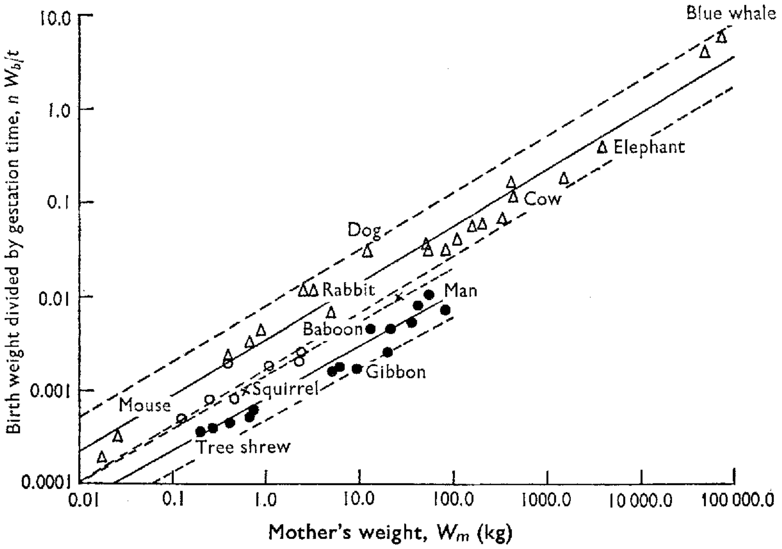

Fig. 1. The relationship between maternal weight, W_m, and the metabolic stress of pregnancy, represented by the ratio of total birth weight: gestation time (W_b/t). The values are collected from a number of sources, details of which can be supplied on request. △, non-primates $\frac{nW_b}{t} = 0{\cdot}00355\,W_m^{0{\cdot}60}$; ●, primates $\frac{nW_b}{t} = 0{\cdot}00084\ W_m^{0{\cdot}56}$; ○, hystricomorphs.

The primates as a group are again clearly distinguished from most of the other mammals by this treatment, in that the metabolic stress of pregnancy imposed upon the primate mother is much less than for a non-primate of similar weight, as indicated by the values for the intercepts of the two regression equations. The slow growth of the primates at birth is succeeded by their slow postnatal growth, and may also be a consequence of their adaptation to arboreal life. We have little information about tree-dwelling non-primates, but our single example, the grey squirrel, does in fact lie within the primate range in Fig. 1.

The hystricomorph rodents cannot be definitely assigned to either group (B. J. Weir, 1967, personal communication). They are non-arboreal, burrowing animals whose adaptation is in the direction of the production of a small number of mature young.

The lower demands of pregnancy in the primates furnish an explanation of the fact that an intake of protein or calories which would produce an adverse effect on the offspring of other mammals often appears to be adequate for man. However, in man, as in several other species, it is possible by dietary means to reduce the size or number of offspring. Table 2 shows that in a primate and a non-primate it is possible to demonstrate a reduction of birth weight consequent on a low intake of protein and/or calories by the mother.

Table 2. *The effect of variations in maternal protein and calorie intake on birth weight*

Species	Information on maternal diet	Mean total birth weight (g)
Man:		
New Guinea*	Staple = banana	2950 (all)
	Staple = sago	2630 (all)
India†	2760 kcal, 86 g protein/day	3072 (primiparae)
		3127 (others)
	1920 kcal, 48 g protein/day	2827 (primiparae)
		(2918 (others)
West Holland, 1944–5‡	1100 kcal, 34 g protein/day	3200 (all)
	2550 kcal, 78 g protein/day	3500 (all)
Dog (beagle)§	NDpCal 10%, 1060 kcal/day	1925
	NDpCal 7%, 900 kcal/day	1358

*Venkatchalam (1962); †Bagchi & Bose (1962); ‡Smith (1947);
§E. F. Wheeler (1968, unpublished).

Lactation

Brody (1945) presented findings for three species suggesting that maximum daily energy production in milk is related to metabolic body size of the mother. We have collected some additional values which are shown in Fig. 2. In most instances, the figures given are for maximum milk production. In the same way as the relationships between birth weight and body size indicate that the stress of pregnancy is greater for smaller animals, so this figure shows that the same applies to the stress of lactation.

Brody estimated that the net efficiency of milk energy production is around 60% for the rat, the goat and the cow. Using this figure, we can calculate the total energy requirement during lactation as 312 kcal per day per kg$^{0.73}$, that is, about four times the basal energy requirement. Using mean values of 23 and 9 protein-calories % for

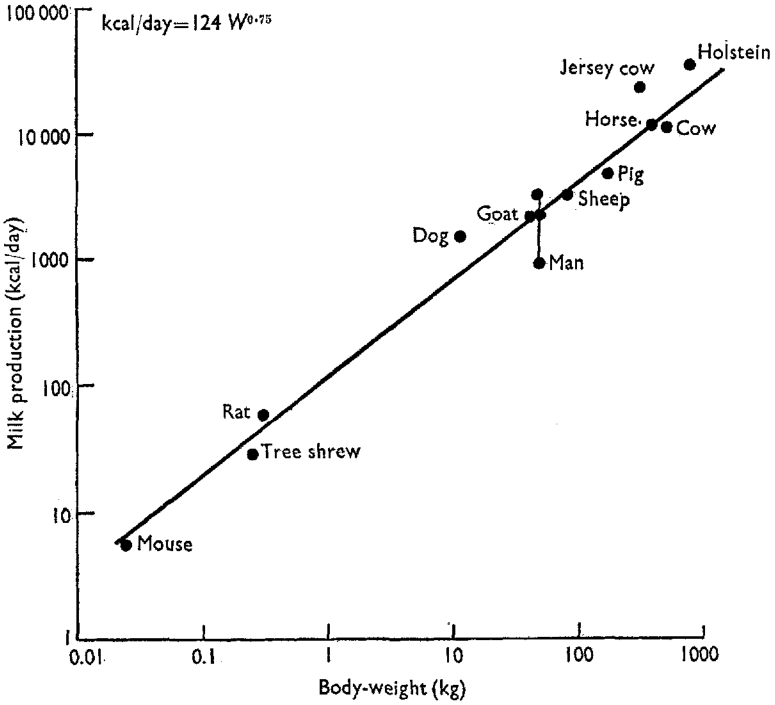

Fig. 2. Maximum milk energy production in relation to maternal body size.

the milks of non-primates and primates (see pp. 135, 136), we have calculated total net protein needs during lactation as being 8·7 and 4·7 g of net protein per day per kg$^{0\cdot73}$ respectively. For both these calculations, the figures for minimum maintenance energy and protein needs suggested by Miller & Payne (1963) have been used. Combining the figures for calorie and protein requirements, it seems that diets suitable for lactation should provide 11 or 6% of their total calories in the form of protein which is fully utilizable for anabolic purposes, i.e. they should have net dietary-protein calories (NDpCal) of 11 and 6%. This latter figure is in accordance with recent estimates of human protein needs during lactation, and is slightly higher than estimates of needs during pregnancy.

Thus it seems that these two groups of mammals, while having similar maintenance requirements (approx. 5 NDpCal %), have markedly different needs for the reproductive period. However, the dietary factor which appears to exert the most effect on milk production is the level of energy intake (Dean, 1951; Blaxter, 1964).

Milk composition and the growth of the young

Bunge (1898) suggested that growth rates of young animals, when represented by the times taken to double birth weight, were directly related to the protein concentrations in the milks. Blaxter (1964) pointed out that these figures could equally well be interpreted as meaning that the smaller animals needed a more concentrated

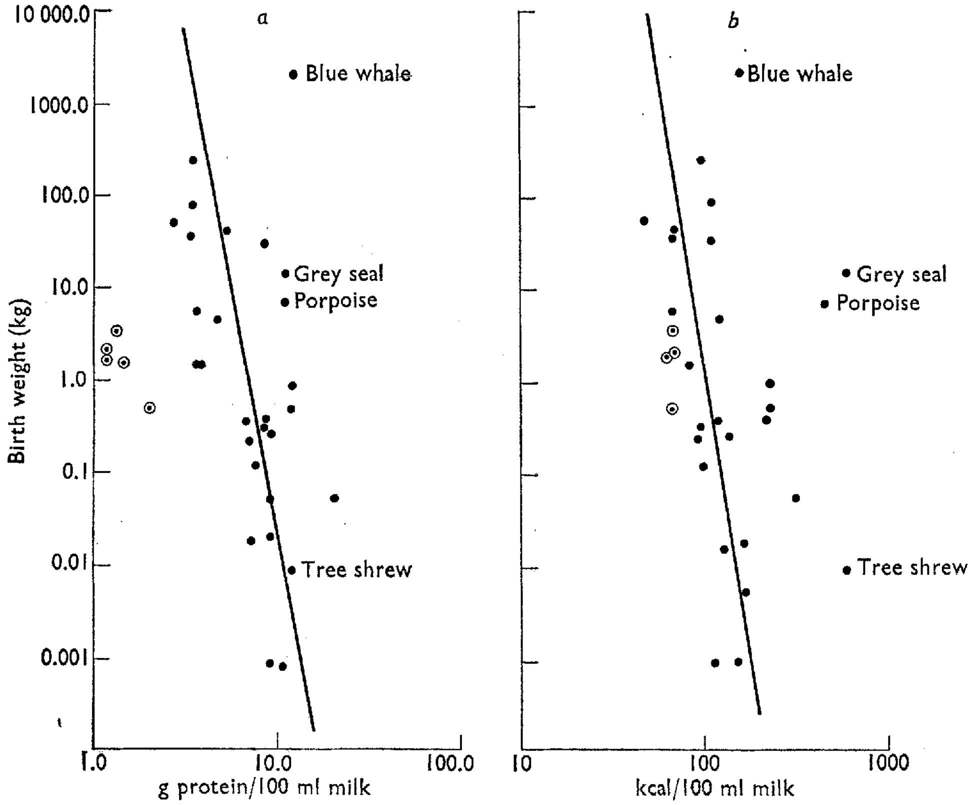

Fig. 3. (*a*) Protein and (*b*) calorie contents of milks related to birth weight.

supply of nutrients. Fig. 3*a* shows birth weights of a number of species plotted against the calorie contents of their milks. With some exceptions, the points are grouped around a line whose negative slope indicates that in general the smaller animals receive more concentrated milk. If energy needs are proportional to body-weight$^{0\cdot73}$, and the volume of milk intake is directly proportional to body-weight, then the calories/100 ml of milk should be proportional to body-weight$^{-0\cdot27}$; the observed slope of the line, −0·28, is of the expected sign and approximate magnitude. The aquatic mammals have exceptionally high milk energy contents, and this may be associated with the high heat losses to be expected in species adapted to aquatic life. Certain small mammals, such as the rabbit and tree shrew, also have high-energy milks, and this is almost certainly related to the fact that they are suckled infrequently. For example, the tree shrew is fed by the mother for 5 min every 2 days; at birth a 9 g *Tupaia* is able to ingest 6 g of milk (Martin, 1966). The primates are not distinguished in any way by the calorie content of their milk.

Fig. 3*b* shows birth weights for the same animals, plotted against the crude protein content in g/100 ml of the milks, and the form of the relationship is very similar to that between calorie content and birth weight. However, those species which constituted the exceptions in Fig. 3*a* now conform to the general mammalian pattern, whereas the five primates clearly form a separate group whose milk protein contents are much less than would be expected on the basis of body size alone, and probably reflect the very slow growth rates of primates (see Fig. 4).

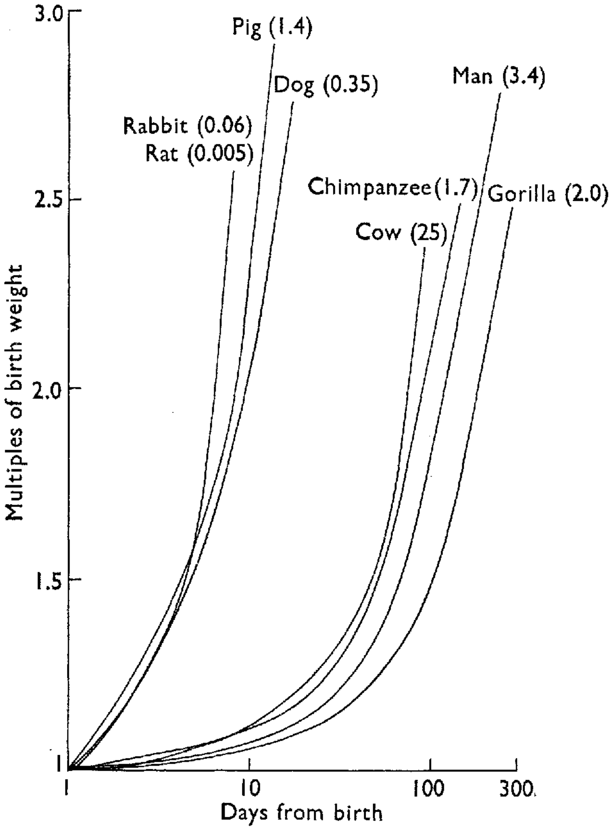

Fig. 4. Growth of young animals expressed as multiples of birth weight (birth weights (in kg) are given in parentheses).

One might expect that growth rate would be better correlated with protein calories as a percentage of total calories in milk than with protein concentration. We have therefore tried to compare growth rate in g per day per unit of metabolic body size with the protein-calories percentage of milks. Figures for early growth rates are available for very few species, and as a measure of growth rate at birth we have used the ratio of birth weight to gestation time (W_b/t) as described earlier. Fig. 5 presents the values of protein-calories percentage in the milks of ninety-six species (Ben Shaul, 1962; Evans, 1959; R. D. Martin, 1968, personal communication). The mean values for the milks of non-aquatic, non-primate mammals are

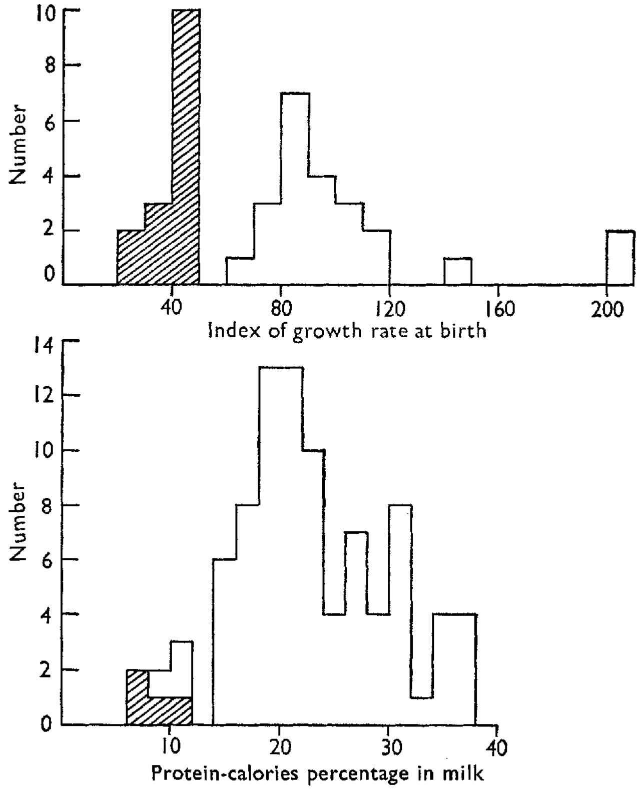

Fig. 5. Distribution of growth rates, expressed as g per day per unit metabolic body size $((W_b/t)/W_b^{0\cdot73})$, and protein to calorie ratios of milks in a number of species. Hatched areas, primates.

$23\cdot1 \pm 6\cdot7$ (SD), for aquatic mammals 10·3 (three values) and for primates $9\cdot2 \pm 2\cdot4$. The figure also shows the indices of growth rate

$$\left(\frac{W_b}{t}/W_b^{0\cdot73}\right).$$

The mean growth index for the non-primates was 0·01064 kg per day per $\text{kg}^{0\cdot73}$, and for primates 0·00416 kg per day per $\text{kg}^{0\cdot73}$; clearly these low growth indices are associated with the low values for protein-calories percentage in milk. The aquatic mammals gave growth indices within the non-primate range, and the low protein-calories percentage of their milks is associated with their high energy content.

Although this analysis has shown that the large differences existing between the growth rates of two groups of mammals are related to the composition of their milks, it is not adequate to explain differences in growth performance within the groups. A more detailed study of a small number of species for which measured growth rates and milk intakes are available indicates that differences in growth are accounted for by differences in intake rather than in milk composition. Table 3 shows that for four species taken before their birth weight has quadrupled, the growth rate per

Table 3. *Rate of growth in relation to energy and protein intake of young animals of different species*

Species	Protein-calories % in milk	Calorie intake (kcal/day kg$^{0.73}$)	Protein intake (g/day kg$^{0.73}$)	Growth rate (g/day kg$^{0.73}$)
Rat*	22·5	136	7·6	28
Rabbit†	26·7	179	12·0	48
Ox (calf)‡	20·0	336	16·8	61
Pig§	18·5	370	17·2	76
Man‖	6·0	210	2·7	8

*Brody (1945); †Davies, Widdowson & McCance (1964); ‡Blaxter (1952); §Blair, Diack & MacPherson (1963); ‖Chilver & McCance (1967).

unit metabolic body size is directly related to the total calorie and protein intake. With the human infant, the protein-calories percentage of the mature milk taken was very low, resulting in a low total protein intake, and this, rather than the calorie intake, appeared to be the determining factor for growth. The calorie intake is within the range of those of the faster-growing species, and from this point of view is anomalously high. In relation to this, it is interesting to note that Robertson (1966) commented about the growth of 9-year-old children that 'the large appetites and food intakes (without exceptional weight gain) during periods of rapid growth remain somewhat of a mystery.'

Summary

A quantitative description of mammalian reproduction therefore includes the following features:

The growth of the foetus proceeds as a parabolic function of time, to a birth weight which is proportional to the metabolic body size of the mother. The rate of growth of the foetus rises to a maximum at the end of pregnancy, and imposes a metabolic stress upon the mother which is related to her body-weight, $W_m^{0.5}$, i.e. the stress of pregnancy increases with body size less rapidly than does metabolic rate ($W_m^{0.73}$).

During lactation, milk output is directly proportional to metabolic body size, and the concentration of the milk produced is proportional to the birth weight, $W_b^{-0.27}$. The subsequent growth of the offspring is a function of its total protein intake in the milk. Where deviations from this basic pattern occur, special circumstances can be found to account for them. These relationships can be taken into account when defining diets suitable for the reproductive period.

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Minerals in the animal body

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The minerals in the world today are those which were there when life began. As life evolved more than thirty of them have been incorporated into living matter, and these are listed in Table 1. Some elements are almost universally present in animal bodies, while others have been used by only one or two families. Some elements have known functions, others not, and their presence may be merely fortuitous. Sometimes the same element has been used to fulfil many functions, sometimes the same function has been served by two or more elements. Our own mineral metabolism is the legacy of the ages.

Table 1. *Minerals found in animal tissues*

(Roman numerals refer to group in Periodic Table)

Essential		Useful but probably not essential to vertebrates	Present in animal tissues, but no known function	
Sodium	I	Silicon IV	Lithium	I
Potassium		Fluorine VII	Rubidium	
Copper			Silver	
Calcium	II		Strontium	II
Magnesium			Barium	
Zinc			Beryllium	
			Cadium	
Phosphorus	V		Mercury	
Sulphur	VI		Boron	III
Chromium			Aluminium	
Selenium			Tin	IV
Molybdenum			Lead	
Chlorine	VII		Vanadium	V
Iodine			Arsenic	
Manganese				
Iron	VIII		Bromine	VII
Cobalt			Nickel	VIII