THE ALLOMETRY OF PRIMATE REPRODUCTIVE PARAMETERS
RUDDER, BENJAMIN CHARLES COLLYER
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The Allometry of Primate Reproductive Parameters

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PhD

University College London

The Allometry of Primate Reproductive Parameters

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This study is based on the comparison of quantitative information on the reproduction and development of individual species classified within a single mammalian order, the Primates. The main method of comparison uses logarithmic transformation of values, derived from the literature, zoological garden records and the author's observations, following the established analytical approach commonly known as interspecific allometry. The interrelation of rates, ages, and sizes of the average species members at different periods in the life cycle are examined principally in terms of energy flow. Since there is some confusion in the literature concerning the value of such analysis, attention is also given to questions of theory and method.

The three results sections deal in turn with:
1) the foetal growth period; discussion includes associated relations in placental morphology, the growth of brain and body and the energetic stress on the mother
2) the postnatal growth period; discussion includes the associations of seasonality with the relatively rapid postnatal growth of strepsirhine infants, and of maternal milk production to haplorhine infant growth
3) the reproductive potential of the species; discussion includes the relation of body size and ecology with the potential for population growth. The primates are established as the most efficient users of energy for the maintenance of living tissue for their size.

The discussion of both theory and the found results elaborates on thermodynamic concepts of life. Not only do primates have great complexity in their physiology and ecological relations but this complexity is expressed in the ability of these living forms to preserve both physiology and population structure from the random disruptive effects of the environment. A short section is included on the evolution of *Homo sapiens*.

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During the period of the studentship, one month was spent visiting the Department d'Ecologie, of the Musée d'Histoire Naturelle at Brunoy, Paris, in France.

This study, more so than many others, exists only through the work of literally thousands of students of biology, living and dead, to these the author owes the greatest debt.

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CHAPTER I - INTRODUCTION

General Introduction to study.

Section a) Course of study.

This study was commenced in the latter part of 1975. The title of the research topic has remained unchanged since that time, though the direction of the research changed during the study period, largely in response to more recent publications and some theoretical problems that were encountered in the interpretation of results (see p. 37 et sqq). The author had a prior interest in comparative studies of primates, but the exact area of study was proposed by the author's supervisor. He was aware of the relatively large amount of previously uncollated information on reproduction and also the value of comparative studies such as those of Leutenegger (1973), Sacher and Staffeldt 1974) and Payne and Wheeler (1967a, b 1968). These studies used logarithmically transformed average values of such reproductive parameters as litter weight, neonatal brain weight, gestation period and adult female body weight for separate species. The authors then analysed both the bivariate and multivariate distributions of these species mean values. This method reveals what has come to be known as the 'interspecific allometry' of these parameters within particular taxa (e.g. all primates, all homoiothermic animals, depending on the nature of the parameters, see further discussion p. 29 et sqq).

At the outset of the research period the aims of the project were summarised as follows (Rudder 1977):

1) The formulation of hypotheses on the basic physiology of reproduction with the aid of analysis of interspecific allometry.

2) The use of the 'allometric method' (see p. et sqq) to distinguish specific adaptations away from any general trend within the order Primates.

3) The prediction of reproductive parameters in species of primate not yet discovered empirically.

4) The compilation of reliable data for reference,

and 5) The evaluation of the use of 'allometry' in comparative studies.

In fact it is only those aims 2) and 5) that are realised to any extent in this dissertation. It is not that areas of the topic have been abandoned but rather, seen in retrospect, that the early proposals were misconceived. So as to give a perspective on the early outline they are discussed further.

1) The formulation of hypotheses......In general it was found that the analytical method is too crude to imply particular physiological features beyond those of rates or thresholds associated with gross energy or material exchange. In addition to the problems of precision in interpretation, essentially a product of the variety in nature, publications issued during the study period revealed considerable differences in the allometries of reproductive parameters between different mammalian orders (in particular Case, 1978, on growth rates and Western, 1977, on ecological and life history parameters). It seems that all but the most fundamental interspecific allometries show some variability between orders. The notion that a study of a single order would reveal intricate relationships naturally extendable to other orders was somewhat undermined. Most of the allometries revealed in the early analyses seemed thus to be nothing more than empirical 'laws' peculiar to the primates. This feature of most of the results determined earlier in the study was in stark contrast to a few

correlations in the literature, in particular the interspecific allometry of basal metabolic rate in mammals which has the property of an empirical 'law' for all mammals regardless (generally speaking) of taxonomic affinity (see p. 21 et sqq).

These considerations only emphasized the lack of a theoretical perspective for such comparative studies despite almost a century of enquiry into interspecific allometry. The theoretical inadequacies do not lie especially with analytical technique. Rather they are due to the lack of any unified theoretical perspective of the nature of life in the published studies of interspecific allometry. Whilst this omission is entirely understandable in restricted and specialised research it is a severe hindrance to comparative studies which seek to generalize, such as those of interspecific allometry. It is not that such general theoretical approaches are unavailable (Bernal 1967, Bertalanffy 1968, Pirie 1937, Schrodinger 1945, Shannon and Weaver 1949, Weiner 1961) but rather that they have not been introduced to studies of interspecific allometry. Such studies have, as a result, remained essentially descriptive with the exception of only a few (in particular Bertalanffy 1957, and Sacher 1959, 1967, 1976). This conclusion of the author's was reached during the study period and accounts for the inclusion of a chapter, the second, devoted to general theory. The relevance of this chapter may at first appear a little obscure in relation to the following three chapters on results (Chapters 4, 5 and 6). However, it is hoped that this apparent incongruency is eliminated in the discussion (Chapter 7).

As far as the more technical considerations of theory are concerned, these fall into two areas. Firstly those of general interpretation of results, a subject that is excellently tackled by Gould (1966, 1970, 1971, 1977), to whom much reference is made later in this chapter. Secondly, the statistical methods employed in comparison, a subject of much discussion (see p. et sqq). The essential issue in most of the literature concerns a basic problem, the application of statistical techniques devised for controlled experiments to the 'uncontrolled' product of planetary history and natural selection. The refinement and sophistication of these techniques has been an important development in the study of allometry, although it has been argued that some students have made an idol of sophisticated statistics whilst ignoring the underlying problem mentioned above (Gould and Lewontin, in press). This problem is discussed in more detail later (see p.109 et sqq), sufficit to say at this point that statistical techniques available are considered perfectly adequate for this study, in view of the data to which they are applied.

One particular issue concerning analytical method and the formulation of hypotheses is also worth mentioning here. During the study period it was often pointed out to the author that the data pool could be profitably submitted to multivariate analysis, rather than simply to a series of bivariate analyses. Whilst not disagreeing with this suggestion, it was decided that the presentation of bivariate analysis alone in this dissertation might be viewed as a preliminary proceedure of familiarization with the data, before the more complex use of multivariate statistics. In retrospect the author believes that this approach was correct in view of the major problem of interpretation of not only bivariate analyses but espec-multivariate analyses. A more detailed exposition of this problem is given in the discussion chapter (the seventh) with particular reference to the results chapters. Meanwhile some of the data, submitted to multivariate techiques, has been presented elsewhere (Clutton-Brock, Harvey and Rudder 1977, in prep.),and the author by no means dismisses the value of such techniques. (see p. 109 et sqq).

3) The prediction of reproductive parameters...... (p. 16). There is little doubt that for most practical purposes useful and accurate predictions of reproductive parameters may be made for unresearched species. Even with limited information on taxonomic provenance and body size many empirical predictions are possible, as may be inferred from close correlations of bivariate data from studied species given later in this study. Such empirical predictions are reported by Rudder (1978), and Hunter, Martin, Dixon and Rudder, (in press). The lack of such specific predictions in this study is due to the authors desire to concentrate on less empirical concepts, though the value of such prediction is not in doubt, and they may be of great help in the preparation of breeding experiments and colonies with largely unknown species. Predictions that are made in this study refer to more general tendencies, expected from the analyses, which may be tested by comparative rather than specific research.

4) The compilation of reliable data......(p.16). This preliminary aim is not realized here for practical considerations. Most of the data used in analysis is already published and it was thought that such unoriginal material would be better presented elsewhere (Clutton-Brock, Harvey and Rudder in prep, Rudder, in prep).

As mentioned earlier, (p.16), two of the initial aims are at least partially covered in this disseration, although they have not assumed the form expected.

2) The use of the 'allometric method' to distinguish specific adaptations......(p. 16). It had been hoped that indices of deviation for particular species from general tendencies would be a feature of this study. However, the low number of species with available data to provide a full complement of variables led the author to concentrate on the general trends revealed. The use of such indices is however profitable and instructive where circumstances permit (see Bauchot and Stephan 1969 for example, giving indices of encephalization). Major deviations seen in certain species for several correlations are noted, but a systematic use of the method is lacking here. There are also the problems of interpretation of such indices, it may be only a matter of speculation as to the significance of a particular deviancy of a species to its natural history. This problem is discussed further in relation to multivariate methods (p. 109 et sqq, p. 345 et sqq.).

5) The evaluation of the use of 'allometry'...... (p. 16). Whilst issues of interpretation and method are discussed throughout the dissertation and in particular in the discussion chapter (p. 304 et sqq.), it has been concluded that the method requires little defence. In the author's experience there are students who protest, for example, against the use of average values for a species on the grounds that it cannot adequately describe the species (an argument that might just as well be levelled against the use of statistics in entirety). However, the real value of a scientific concept lies not in the nicety of its abstraction but in the facility it lends to the interpretation and generalization of the movement within

an infinitely complex universe. That allometric tendencies may be reported or denied on insubstantial evidence, or that the significance of such tendencies may be under or over estimated is unfortunate (though no doubt inevitable). But such studies cannot detract from, for example, the powerful generalization of Kleiber's (1947, 1961), that the Basal Metabolic Rate of adult homoiothermic animals may be estimated by the allometric relationship,

$$M = 70W^{\frac{3}{4}}$$

where M is the metabolic rate in KCal per day, and W the body weight in Kilograms. This relationship has been and will be a highly significant conceptual, and practical tool in the work of modern biologists, farmers, veterinary surgeons and all those dealing with living animals. It is in this manner that the real value of such generalizations is demonstrated.

Furthermore, in the authors opinion, the method of generalization through studies af allometry will prove to be the only method of identifying not only the relative proportions of rates, sizes, and periods in living systems (the principal use of the method to date) but also of the evolutionary and physically necessary absolute values of parameters of living systems. In other words, taking Kleiber's findings (above) as an example, not only does the allometric relationship 'explain' why heavier mammals consume relatively less energy per unit weight, but it also begs the question, why the values 70 and $\frac{3}{4}$? (see discussion p. 67).

Section b) Revision of early approach.

Having briefly discussed the problems associated with the initial formulation of the study topic, the final form of the dissertation may be introduced. As described earlier (p. 17), the author felt it necessary to find a unified framework within which to proceed with the analysis, and this was found in the concepts of Entropy and its opposite Negentropy. As very general concepts applicable to the motion of all forms of matter (be they 'living' or 'dead') they are well established in the literature since their first introduction to the biological sciences by Schrodinger (1945). Since, in the authors knowledge, with the outstanding exception of Sacher (1959, 1976), a discussion of these important concepts has never been taken up in the very suitable subject of interspecific allometry, and certainly not to studies of mammalian reproduction, it was felt that some elaboration of these concepts should be central to the thesis. It might be expected on a theoretical basis that the replication of living objects (reproduction) is closely linked with the thermodynamic aspects of energy flow described by the generalized concepts of entropy and negentropy, and this issue is dealt with in the discussion chapter. The discussion in the results chapters (4, 5 and 6) deals with the more particular interelations of aspects of the reproductive and developmental cycle as they affect the growth of the foetus (Chapter 4) the postnatal growth of the individual (Chapter 5) and the reproductive potential of the population (Chapter 6). The form of the dissertation requires that the introduction of the general theory, (not expressly discussed until Chapter 7) is given in Chapter 2. This is not a great disadvantage since the importance of energy flow in living systems (described theoretically in Chapter

2) emerges in the results chapters without direct reference to general theory. Also, the inclusion of this theoretical discussion early in the dissertation emphasizes the author's concern with such basic generalization rather than any purportedly exhaustive or complete analysis of primate reproduction.

It should be said that consideration of general theory arose in part from limitations imposed by the available data which are not distributed evenly between species, and lack the precision required for very specific analyses. It must also be stated that the results given in the study undoubtedly imply many relationships not seen by the author, and the the data may well, without further addition, disclose important information under different methods of analysis.

Whilst other comparable studies have looked at many of the interspecific relations examined here, none has attempted to deal with the whole reproduction cycle, rather they consider in isolation the allometry of such parameters as postnatal growth rate (Case 1978), newborn litter weight (Leutenegger 1973, 1976), foetal growth rates (Sacher et al. 1974, Payne et al. 1967a), milk nutrition at birth (Payne et al 1967b, 1968) and captive lifespan (Sacher 1959).

Whilst such studies often include information from several orders the results are difficult to interpret without a perspective on the whole reproductive cycle, and in particular the energetic relations of the reproducing population. This problem is exemplified in Case's (1978) study of postnatal growth rates, where it is demonstrated that the lowest postnatal growth rates are shared (relative to adult body size) by possibly the two most disparate mammalian groups, the marsupials and anthropoid primates. It might have been expected that some trend in either higher or lower relative growth rates would characterize the differences in values between the more primitive mammalia and the more advanced. The apparently confusing results of Case assume a more 'expected' form when further features of the reproductive cycles of these different mammalian taxa are taken into account. Case has however, in the author's opinion, identified the principal factor in this disrupted pattern, the low metabolic rate of marsupials (Dawson and Hulbert 1969) though this is a contradictory effect.

The study deals with only a single order, a feature which whilst obviously a hindrance to certain types of comparison, has permitted an essentially novel approach in the use of the concept of allometry. In addition to this, rather than compare categories of data as they initially appear in a static and fixed form, an attempt has been made to examine the processes moving through these categorical relationships.

The study topic of reproduction is one that requires not only a method which attempts to incorporate the whole cycle but also a general conception of the three united flows in the maintenance and generation of living tissue; the flows of matter, energy and information (see Engelgardt 1978 and chapter 2). It is in this attempt to establish a method and general theoretical conception that the author feels that the originality of the study lies. The primates are an interesting order in this respect since they are generally considered as an advanced order of living species (Martin 1975b), and the expression of this 'advancement' in the reproduction process is revealing. This view was not conceived at the instigation of the study but arose during the study period, and not without many dead end enquiries not reported here due to lack of space.

Allometry, a general introduction.

Section a) General description.

In this part is the introduction the comparative concept of allometry, upon which the analyses are based. The author has had little reason to enquire independently into the history and development of the concept and its application since the papers of Gould (1966, 1970, 1971, 1977) are both extensive and exhaustive. In these papers Gould has extracted the general principles and also many of the misapplications and problems associated with the interpretation of quantitative biological data under the allometry concept. It is to Gould that most modern studies of allometry owe their terminology and their general conceptual framework, and most of this section is based on his work.

To quote Gould (1966 p. 629): 'Allometry is defined as the study of proportion changes' (this author would prefer 'differences', see below) 'correlated with variation in size of either the total organism or the part under consideration. The variates may be morphological, physiological or chemical; the size differences may arise in ontogeny, phylogeny or the static comparison of related forms differing in size; the term is not confined to any one form of mathematical expression, such as the power function'.

This broad definition might be further stretched to include the ecological variates employed by Milton and May

(1976) and Clutton-Brock and Harvey (1978). The term allometry would then refer to those difference in proportion of any variate associated with some size parameter of biological tissue. This association of the term 'allometry' with size seems reasonable, since it allows the discrimination of two sorts of difference in proportion; those associated with differences in size - allometric in nature, and those independent of size - expressing a difference in the 'level' of the proportionality (see p. 29 et sqq). This distinction is followed in published studies and is followed here.

The note on the word 'changes' in Goulds definition (above) is simply to allow the definition to cover the static comparisons mentioned later in his definition. In the static comparison between extant species for example, it is clear that the proportional differences in size and another variate which may be found will not be due to 'changes'of one species into another. This may appear to be a small point, but it eliminates any confusion between the allometric trends in a lineage or individual over time,Evolutionary and Ontogenetic and the static comparative allometry between contemporaneous organisms.

There is also a semantic point concerning the definition of the term 'allometry', - does it refer to the study of proportion differences or to the differences themselves as they occur in nature? Whilst in his definition Gould expressly uses the term to refer to the human activity of study, the rest of his article (1966) uses the term in reference to the relationships in nature. This dual use of the term is similar to the common use of the word 'ecology' for example, which is properly defined as the study of the ecosystem, though often used mistakenly to refer to the relationships in the ecosystem themselves. However, in this study, the term is used in the sense Gould most often employs, describing the relationships in nature rather than a technique or a method of analysis.

Gould proceeds to define the types of allometry found in nature, making the important distinction between the 'static' comparison of related forms at equivalent stages in development (Intraspecific and Interspecific types below), and those allometric alterations in form over time either in the ontogeny of an individual, or in the evolution of a lineage (Ontogenetic and Evolutionary types below). Gould's classification and terminology is based on that of Rohrs (1961) yielding the following types:

1) <u>Intraspecific allometry</u> - allometric differences between members of a single population at the same growth stage but of different sizes.

2) <u>Interspecific allometry</u> - allometric differences between (usually 'average' members of) species of a single taxon at the same growth stage but of different sizes.

3) <u>Ontogenetic allometry</u> - allometric changes in a single individual at different growth stages.

4) <u>Evolutionary allometry</u> - allometric changes between members at a similar growth stage, usually adult, of a direct line of descent.

In this study the allometric trends discussed are all of the Interspecific type (2). Further discussion in this section will refer in particular to the 'static' allometries, and especially Interspecific allometry.

Another aspect of Gould's use of the term 'allometry' (above) which may cause some confusion is his extension of the term to include mathematical approximations other than that known as the equation of simple allometry,

$$y = bx^{\alpha},$$

a power function. This generally accepted association between the term 'allometry' and the power function followed Huxley's generalization of a differential growth equation to include all types of difference in proportion associated with size, (Huxley 1924, 1932). This restraint on the term was lifted by Huxley himself (in Reeve and Huxley 1945) following Haldane's objection to the universality of the power function in all cases of differential proportionality with respect to size. Haldane had pointed out (Huxley 1932) that the sum of two power functions cannot itself yield a power function, for example total limb length could not be expected to follow the power function if two limb segments did.

The deviations from simple allometry in this case are slight, but Huxley was forced to abandon any notion of universal 'axioms' of growth requiring the universality of the power function, and to adopt the criterion of empirical utility for the equation of simple allometry. This criterion is the one assumed for the use of the power function for analysis in this study, just as it is the criterion that allows Goulds (1966) extension of allometry to include mathematical approximations other than simply the power function. This relegation of the power function from an expected axiom to an empirical approximation is considered further in the discussion (p.345 et sqq).

Section b) Application of concept to data.

Apart from the good empirical fit of the power function to many allometric trends, there are two particular features of the function that lend it an additional attraction over other mathematical models (polynomial functions for example -, $a + bx + cx^2 + \ldots$etc). The first is that it is simple, often yielding a relatively simple biological interpretation, (and also that similar relationships may be found in non-living matter see p. 34 et sqq). The second is that the power function has a property which permits the use of simple statistical techniques to evaluate the general trend of the allometry, and also its 'level'. When the equation

$$y = bx^{\alpha}$$

is rendered in logarithmic form there is a linear relationship between log y and log x;

$$\log y = \log b + \alpha \log x$$

where α is the slope or gradient of the line and log b the value of log y when log x = 0. It is this property of the power function, describing a curve between real values of x and y and a straight line between log x and log y which has led to the reference to 'allometric curves' and 'allometric slopes or gradients.' The first term applies to the real relationship and the second to the slope or gradient of the logarithmically transformed values. The term 'scaling' is also often applied to such allometric relationships, (e.g. Schmidt - Nielsen 1975). In cases where $\alpha = 1$, the variables x and y are said to be isometric (as opposed to allometric). Where $\alpha > 1$

y is said to be in positive allometry to x and where $\alpha < 1$ y is negatively allometric to x,

On the basis of an 'expected' power function the general allometric trend may be approximated by a series of techniques which will fit a straight line to the more or less scattered points in what is assumed to be a normal bivariate distribution between log x and log y (see Chapters 2 and 3). α and log b are taken as the gradient and intersection on the log y axis respectively. The value of log b is of particular interest when a series of taxa are considered yielding allometries all of slope α, but different levels (i.e. different intersections on the log y axis, thus different values of log b.) The difference in the values of log b for this special case (of similar values of α for each taxon) gives the approximate ratio of the values of y (real) for a given value of x (by convention the size related parameter) between any pair of taxa.

In diagram A (p.31-2) two taxa, 1 and 2, of similar range in x are compared using logarithmically transformed variates of x and y. There is a scatter of bivariate points about the best fit line for each taxon. The line is fitted on the assumption of a relationship of simple allometry between the two variates for each taxon. The gradient of each line p/q is the same, α , for both taxa. In this special case the difference between the two lines in the log y axis is the same for any value of log x. This difference, log b_1 - log b_2 is equivalent to log ($^{b_1}/_{b_2}$) and the antilog of the difference is thus the multiple by which the two taxa differ in y (real), for any given value of x (real),

Such cases of parallel allometries are not unusual

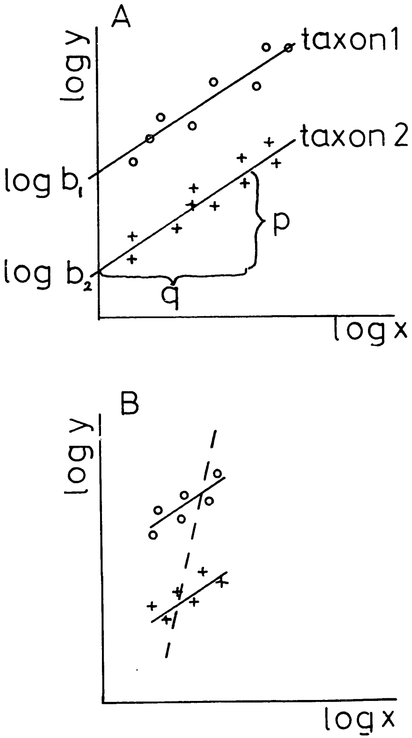
Diagram 1

A. Diagram to show

1) gradient of identical slope for two taxa as p/q, constant α in $y = bx^{\alpha}$

2) value of constant b (in $y = bx^{\alpha}$) for two taxa (1 and 2) as b_1 and b_2.

B. Diagram to show 'choice of group' problem for two closely related taxa (land 2), the only members of a higher taxon. Considered independently the two taxa share similar gradient. The higher slope when the two are taken together is not a consequence of different slope or size range in the two taxa but of differing levels (values of b in $y = bx^{\alpha}$). Note short range of sizes.


A
log y
taxon1
taxon 2
log b_1
log b_2
p
q
log x
B
log y
log x

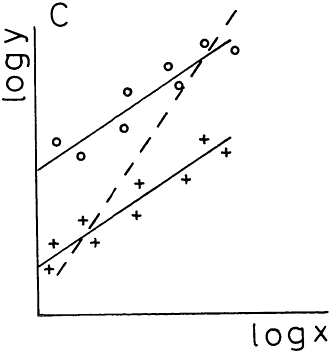
in interspecific studies, and are found for example in the allometry of metabolic rate between the respiratory groups of unicellular organisms, heterothermic animals a and homoiothermic animals (Hemmingsen 1960). Leutenegger (1973) demonstrated that a haplorhine mother gives birth to a litter 2 - 3 times heavier than a strepsirhine mother of a similar weight, for each taxon the allometric slope was the same (see p. 43 for taxonomic description, and p. 40 for further discussion).

These examples of special cases lead to a problematic question, what results would have been obtained if the taxonomic levels had been taken higher, all animals and all primates as single taxa. Statistically it is perfectly possible to fit a line in both these cases for high taxonomic categories, the result would be different values of both α and b for each analysis. This problem is of some importance, since biological significance is often attached to the values of α and b. This problem of 'the choice of groups' is demonstrated diagrammatically in Diagrams B (p. 31-2) and C and D (p. 34-5) with different contingencies affecting the found values of α and b when two taxa are analysed separately and together (see captions). Statistical tests as to the degree of correlation obtained in either case may be informative but such an empirical method as the sole criterion for deciding the level of taxonomic categorization is not advisable. In Interspecific allometry it is probably more instructive to derive categories from considerations of the evolution of the species and employ analysis to test hypotheses based on evolutionary biology rather than empirical criteria. The meaning of particularly well correlated allometries giving different values of α and b at different taxonomic levels will eventually be revealed but

Diagram 2

C. Following Diagram 1, B. Diagram to show 'choice of group' problem, conditions are similar to B except that size ranges in two taxa are greater. The two groups taken together give a lower gradient for the wider size range, dashed line.

D. Following B and C. Diagram to show 'choice of group' problem, conditions are similar to B except that size ranges are exclusive.


C
log y
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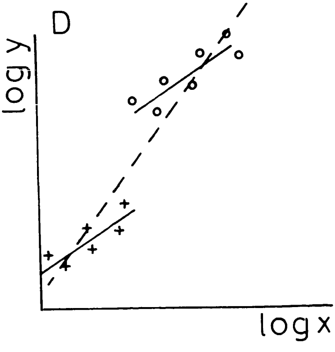
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only through consideration of the interelationships between taxa in their evolution.

This problem is peculiar to static allometries, and is enhanced greatly in multivariate analyses, since levels may or may not exist between any pair of variates for a given taxon. To take a simple example of an interspecific multivariate analysis of all mammalian metabolic rate, brain size and body weight. Levels are found in the relationship between brain and body weight considered alone, (Jerison 1973) and would be expected for metabolic rate and brain size considered alone. However, a single allometry describes the relationship between metabolic rate and body size for mammals (Hemmingsen 1960). The interpretation of multivariate allometric constants under these conditions poses complex problems (see discussion p.345 et sqq).

Whilst this problem is described here, and is an essential one to bear in mind, it has been largely sidestepped in this study. The groups have been selected on criteria supported by the evolutionary development of the taxa and remains the same for each bivariate analysis. When comparing different bivariate distributions the 'choice of group' problem does not arise, except in relation to the whole set of correlations. This is another useful feature of a single taxon study of many variables.

The actual choice of groups for this study is discussed later in this chapter (p. 56 et sqq). The real problem in the choice of groups is the assignation of biological significance to the derived approximations of of α and b, often used to imply functional relationships. This leads us to consider the question of interpretation of allometric constants.

Section c) Interpretation

As mentioned above, the power function might be expected in certain allometric relationships, which Gould (1966) terms 'size required allometry'. It was these relationships that stimulated the early interest in allometry. Spencer (1868) and D'Arcy Thompson (1917) considered the ratio of surface area to volume in organisms of different size. The lower ratio of surface area to volume in geometrically similar forms of larger size is predicted by Archimedes principle. In the simplest model, a sphere, the radius is proportional to the square root of surface area, and the cube root of volume. In organisms of the same geometrical proportions (a necessary criterion for the maintenance of these relationships) a linear measurement (L) will be proportional to the square root of surface area (A) and the cube root of volume (V) for all sizes, yielding the following proportionalities:

$$L \propto V^{1/3}$$
$$A \propto V^{2/3}$$
$$L \propto A^{1/2}$$

It should be mentioned immediately that living organisms of different size are not geometrically similar due to constraints on stationary support (McMahon 1973) and the dynamic stress of movement (Alexander pers. com) imposed by the earth's gravitational field. However, the deviation from the expectation of Archimedian principles is not great and the general consequences of these relationships do aid the interpretation of many features of comparative morphology in living organisms. The most common of the Archimedian proportionalities inferred from interspecific allometric analysis is that of the 'surface law' ($A \propto V^{2/3}$). This law has been ascribed to Interspecific allometries of metabolic rate (or some measure of it (see Benedict 1938, Bertalanffy 1957, Brody 1945, Hemmingsen 1960, Kleiber 1947, 1961, Pearson 1948, Schmidt-Nielsen 1972, 1975, Scholander, Hock Walters and Irving 1950, Zeuthen 1947, 1953), and brain size (see Bauchot et al. 1966, 1969, Brummelkamp 1940, Bonin 1941, Count 1947, Jerison 1961, 1963, 1973, 1976, Sacher 1976).

The 'surface law' is implicated because the static, interspecific mammalian allometries yield the two relationships;

$$\text{Metabolic rate} \propto \text{body weight}^{\cdot 75}$$

$$\text{Brain weight} \propto \text{body weight}^{\cdot 66}$$

which are close enough to $^2\!/_3$ to suggest that both brain weight and metabolic rate are in some way mediated by body or organ surfaces. However, no convincing theory has yet been generated to demonstrate the necessity of these relationships. Despite many years of a generally accepted causal link between metabolism and surface, Kleiber (1969) published a paper refuting a direct causal effect (see p. et sqq), to which no one has yet answered. Despite the long discussion relating body surface to brain size Gould (1966) was able to say of the relationship that it was a 'major unsolved mystery'. From these two examples some of the problems of interpretation may be seen. It is well known to statisticians that a statistical correlation does not necessarily imply a causal relationship between the two correlating variates. An anecdotal example often given is that of the close correlation between the number of clergymen in a given region and the amount of liquor consumed there. This 'correlation' is, as one might guess, not the result of alcoholic priests but rather of the greater density of clergymen in urban centres, where alcohol consumption is greatest.

However, whilst this caution is made the correlation of two variates may be due to a direct causal effect. It is on this account that Gould (1966) is able to point to the value of the metabolic rate allometry 'because it may be further used to suggest explanations of related phenomena'. For example, Leutenegger (1973) discusses the likelihood of the dependency of primate birth weight on either maternal surface area or metabolic rate on the basis of the similarity of the interspecific allometric curve between litter weight and maternal weight with those of metabolic rate and the Archimedean surface. It is a moot point whether such similarities can be considered as 'explanations', since in most cases proposed causal relations are unexplicit and may even be at fault logically (see p. 67 et seq for discussion of an example). In general such interpretations may be accepted only when the necessity of some process linking the two variables is established.

One final point concerning the interpretation of allometric relationships is the danger of extrapolating any correlation beyond the range of the data. In many cases the 'nonsense' of an extrapolation is obvious when the extrapolated curve predicts structurally impossible creatures. However, the actual limits on the real ranges of body size for living species may be explained by two conflicting allometries. Pearson (1948) demonstrated that the surface law and the common mammalian metabolic allometry indicated that mammals below 2.5 grms in weight would lose body heat almost as fast as it could be generated. In fact this is the lower limit for mammalian body size. Similar examples exist in the study of upper limits on body size imposed by mechanical and engineering constraints on support and locomotion of larger bodied animals, (e.g. Schmidt-Nielsen 1972).

Examination of comparable allometries can be instructive, when due caution is taken, and much use of such comparison with certain published relationships is made in this study.

Section d) Found Interspecific bivariate allometries

The most important static interspecific allometry considered in this study is that of adult body weight and metabolic rate. The formalized relationship has already been given (p. 38) and a number of important references also (p. 38). Kleibers (1961) relationship (p. 21) applies to the resting or Basal Metabolic rate (B.M.R.). Under natural conditions the energy flow through individuals is higher than this value. Evans' 1971 study of ad libitum energy intake of zoo animals is the only study in the author's knowledge which has attempted to discover whether the scaling of active metabolic rate is at all similar to the scaling of B.M.R. against body weight. Whilst there are specific deviations, Evans found that the active metabolic rate could be estimated as about twice the B.M.R. for any given body size. This confirmation of the similarity in scaling of both B.M.R. and active metabolic rate with body weight is an important finding. It allows the inference of metabolic scaling factors in wild, and active captive animals, based on the earlier finding of the scaling of B.M.R. Evans formalized the ad libitum energy consumption of active captive mammals as:

$$\text{AMR (Active Metabolic Rate)} = 140W^{3/4}$$

where W = weight in Kilograms
and AMR = energy flow in KCals per day.

Another well-known static, interspecific allometry is that of brain size. Unlike the allometry of metabolic rate for mammals (described above), taxonomic levels are apparent in the allometry of brain size. Whilst within each order of mammals the allometric exponent is about .66, the primates have the highest level of encephalization (relative brain size) (Bauchot and stephan 1969, Jerison 1973). The literature is extensive on this topic, in addition to the authors referred to on p. 38 , the following authors have discussed the cephalization problem; Dubois (1897, 1928), Lapique (1898, 1907), Snell (1892) and Stephan and Andy (1964, 1969).

In 1959, Leitch, Hytten and Billewicz published a paper demonstrating an all mammalian interspecific allometry of total weight of offspring at birth on maternal weight, they suggested a relationship of the form:

$$nW_b = 0.5408\ W_m$$

where n is the number in the litter, W_b the mean birth weight and W_m the maternal weight, weights expressed in grammes. Leutenegger (1973) then demonstrated a difference in level of litter weight to maternal weight allometry in primates. For any given maternal weight a haplorhine mother gives birth to a litter between 2 - 3 times heavier than that of a strepsirhine mother (see next section for basic primate taxonomy). Leutenegger suggests that litter weight is related to maternal surface on the basis of the statistical proximity of the allometric exponent to $\frac{2}{3}$ for each group, and that the distinction in levels is associated with placental morphology (see next section and p. 52 et sqq). Leutenegger further demonstrated (1976) the effect of choice of groups on this allometry (see p. 29 et sqq); for the Eutheria (Infraclass) the slope was .83 (see value of

Leitch et al. above), for Primates (Order) .78, for Strepsirhini (sub-order) .63, for Haplorhini (sub-order) .69 and for the genus Macaca .49.

In a series of papers Payne et al. (1967a, b, 1968) demonstrated the interspecific allometry of foetal litter growth rate to maternal weight on the last day of gestation. Levels may be distinguished in this allometry within mammals, the primates having the lowest values for any given maternal weight. For non-primate species the value of the allometric exponent is .60, for primates, at the lower level the exponent is .56. They further demonstrate interspecific allometric trends between birth weight and protein, and total calorie concentration in milk. The total calorie concentration of milk is lower for heavier neonates and there is a distinction between primate and non primate mammals. Protein concentration is at a lower level in primates however, Payne et al. suggest this is related to the lower relative growth rates of the primates.

This lower relative growth rate (for haplorhine primates at least) has been established by Case (1978) for early postnatal growth. Case further demonstrates that the early postnatal growth rate of many mammalian taxonomic groupings (levels of Class, Order, and Sub-Order) has an interspecific allometry with adult body weight with slopes varying between .35 (Anthropoid primates, see this study p.154 et sqq however) and .87 (Sciumorphs) with the majority scaling to approximately the .67 power of adult weight.

These studies of Payne and Wheeler, and Case are discussed in greater detail in Chapters 4, 5 and 7. Other comparative interspecific allometries will be introduced in later chapters.

The Primates.

Section a) Evolution and Taxonomy.

In this study the Primates are taken as excluding the Tree-shrews. Much discussion has surrounded the inclusion of this group in the order by Napier and Napier (1967), Simpson (1945) and Le Gros Clark (1959). However, the author has followed Martin (1968a, b, 1969) in considering Tree-shrews as evolutionarily and taxonomically distinct from the Lemurs, Lorises, Tarsier, Monkeys, Apes and Man.

The classification of the primates used in this study follows that used by Jolly (1972), adapted from Napier et. al (1967), with some exceptions. Firstly the tarsier is considered to be closer related to the monkeys than to Lemurs and Lorises, and the tarsier is included in the Haplorhini following Hill (1953) and Martin (1973). The major taxonomic division within the primates is considered to lie between the Strepsirhini (lemurs and lorises) and the Haplorhini (tarsier, monkeys, apes and man). Other lesser modifications of Jolly's classification at a lower taxonomic level are as follows: Lemur variegatus is considered as a member of a seperate genus Varecia following Petter, Rumpler and Albignac (1977). Since data is available for quite different subspecies of Galago senegalensis (senegalensis and moholi) and Galago crassicaudatus (crassicaudatus and umbrosus), these subspecies are given the status of species for the inter-specific analyses. This is not done for other species, and is only done for these species on the basis of other morphological evidence supporting a major revision of the old taxonomy of the bushbaby group (Galaginae) and the creation of several new species from old sub-species (Olson pers com, Bearder pers com). With these exceptions the classification of Jolly's (1972) is followed in this study.

In the following description of some of the features of Primate evolution emphasis is placed on those features relevant to this study particularly reproduction and ecology.

Martin (1973) suggests that the common ancestor to living primates lived between 65 - 80 million years ago (MYA). Martin had previously suggested (1969) some of the reproductive mechanisms which may well have distinguished these ancestral primates from other mammals at that time. These include:

a) a 'triplex mode of placentation, with extensive reduction of the role played by the yolk-sac' (The 'triplex' mode would involve foetal nutrition from three main sources, - phagocytosis and digestion of the maternal epithelium at the site of attachment - diffusion of nutrients from the maternal to the foetal blood supply - diffusion of the products of uterine glands through exposed areas of the chorion). Extant primates have in Martin's opinion diverged from this ancestral pattern into two distinct groups following the haplorhine/strepsirhine taxonomic division (Hill, 1953, see also p. 48 et sqq)

b) 'retention of maternal fur carriage of the offspring, associated with retention of the opposable digits and the arboreal habit'

c) 'strengthening of the mother offspring bond, involving maternal toilet behaviour, retrieval behaviour and parental protection of the offspring'

d) 'extension of the true gestation period, associated with the greater development of the central nervous system and the advanced stage of the neonates sense organs at birth. Offspring born with fur'

e) 'development of a long-phase oestrous cycle associated with spontaneous ovulation'.

These suggested distinctions between ancestral primates and other late cretaceous mammals are emphasized in the distinctions between modern primates and other modern mammals (see p. 52). These reproductive features are associated with general morphological criteria by which modern primates are recognised (see Napier et al 1967, Le Gros Clark 1959, and Hill 1953). Furthermore such distinguishing features of primates are often demonstrable in allometric studies (Jerison 1973, Payne et al 1968, this study p. 311).

However, Martin (1973) believes that there was an early and major evolutionary divergence between the lineages leading to extant strepsirhines and haplorhines. Among many associated adaptive distinctions a principal difference was the nocturnality of ancestral strepsirhines and the diurnality of ancestral haplorhines. Considering evolution of these two lineages separately, the strepsirhines are dealt with first.

The evolution of the strepsirhine lineage is best described by Martin (1972, 1973, 1975a), Charles-Dominique and Martin (1970), and Charles-Dominique (1975, 1977), on evidence from fossils, paleogeography,paleoclimatology and by deduction from living forms. It seems that a major division within the strepsirhine lineage occured about 40 MYA when the ancestral Lemuriformes became isolated on

Madagascar, separating from the African continent under the influence of continental drift. There is some indication that in the period of this divergence, and possibly over some millions of years the ancestors of both modern lemurs and probably some lorises were subject to variable and seasonal conditions. This is reflected in some reproductive adaptations of all living Lemoriformes, the family Galagidae (Martin 1972, Charles-Dominique 1970, see chapter 7). The specialized locomotor pattern of the extant Lorisidae, the other branch of the Lorisiformes, a slow quadrupedal grasping locomotion, suggests that their evolutionary history may have been more restricted to forest environments which were possibly more stable than the conditions in which the running and jumping locomotion of extant Galagids has evolved. Certainly no extant lorisid is found in environments as lacking in vegetation and as seasonally variable as those occupied by some extant Galagidae (e.g. Galago senegalensis, Bearder and Doyle 1974). Extant Lorisiformes are all nocturnal, none heavier than about 1 Kg, and are found on the Asian and African landmasses.

The Lemuriformes, isolated on a large island with probably a wide range of habitats, though apparently lacking a diverse mammalian fauna and in particular no haplorhine species (Charles-Dominique 1975, 1977) had a broad radiation. This radiation producing a range of extant and only recently extinct forms covering both diurnal and nocturnal habits, and a body size range from 60g to animals as large as modern apes (e.g. Megaladapis and Palaeopropithecus Simons 1972).

Haplorhine evolution was marked by the early divergence of the Tarsiiforme lineage, and that leading to modern monkeys and apes. It seems that the tarsiiformes were diverse during the Eocene, (Szalay 1975), though they are represented now by only one extant genus Tarsius weighing about 100g found only in forests, in limited regions of the Asian landmass and peculiarly, with nocturnal habits (the only other nocturnal haplorhine being Aotus a new world monkey).

The modern New World Monkeys or Platyrrhini arose later from the haplorhine stock and became isolated on the South American continent. Extant forms are all confined to the forest. It is a matter for dispute as to the size of the early Platyrrhine ancestor, extant species ranging in size from the pygmy marmoset at about 100g, almost as small as the smallest strepsirhines, the lesser mouse lemur (about 60g) and Demidoffs bushbaby (about 60g). Hershkovitz (1977) documents the discussion concerning the small size and habitual twin-bearing of the marmoset and tamarin species. It seems likely that these species have secondarily evolved twin litter size, since other haplorhine species normally deliver singletons, possibly as a consequence of selection pressures which may have operated simultaneously to reduce body size (see Chapter 6 and p. 310 et sqq). The largest extant platyrrhines may reach over 10Kg adult size.

Old World monkeys, apes and man are included in the infra-Order Catarrhini. The distinction between ancestral old world monkeys and ancestral apes appears to be possible in the Oligocene (Simons 1972). Simons believes that on the basis of the fossil record, the present diversity of the old world monkeys is a relatively recent evolutionary phenomenon, since the onset of the Pliocene. The only known fossils suggest that relatively few species of small bodied monkeys charactarised the Catarrhini of the Oligocene, through to the end of the Miocene. Extant old world monkeys range in adult body size from the talapoin at about 1Kg to the baboons in which the female weight averages about 15Kg and the males may attain 30Kg. Modern forms are found in a wide range of habitats from equatorial forest to savannah.

Modern apes range between about 11Kg for the gibbon and up to 70Kg female weight for the gorilla, the male weighing up to twice that weight. Fossil apes of both large and smaller size are known (e.g. Gigantopithecus and Dryopithecus). Extant forms are all forest living. It is generally assumed that the hominid lineage emerged at about the end of the Miocene (Simons, 1972) though the exact course of hominid evolution and in particular the emergence of the hominid lineage from a forest environment is still a matter of debate.

Section b) Ecological overview

Charles-Dominique (1975) has formulated an elegant and largely convincing hypothesis that helps explain the evolutionary development and present ecology of the primates. The basis of his hypothesis are a set of general relationships:

1) Primates have locomotor and other specializations which suggest that the whole order is primarily adapted to an arboreal habitat.

2) The arboreal feeding niche is dominated by diurnal bird species.

3) Smaller bodied homeotherms require a more nutritious food source than larger forms.

4) Birds are limited in maximum body size by constraints

on flight.

In his exposition Charles-Dominique demonstrates that primate species below 1Kg generally feed at night. He suggests that those species above 1Kg, which are almost all diurnal, may escape the direct competition for food resources in the arboreal niche due to the ability of larger bodied species to survive on a coarser food resources. Those primates below this critical size of about 1Kg may avoid some competition with bird species in direct competition for nutritious food sources by restricting their activity to the night. Among strepsirhine species only one does not fit Charles-Dominique's concept, the Aye-Aye, nocturnal at 3Kg. However, it is among the Platyrrhini that the most problematic exceptions occur. Marmoset and tamarin species are all below 1Kg and are all diurnal. However, Charles-Dominique's hypothesis is an attractive generalization in all other respects. Whether it is wholly correct or not, the small bodied platyrrhines do seem somewhat unusual.

In respect of Charles-Dominique's hypothesis some features of primate ecology are noteworthy, if further general principles are considered:

1) the advantage of large body size for stable and efficient thermoregulation in homoiothermic animals and

2) the wider diurnal and seasonal temperature fluctuations in poorly vegetated zones

3) the advantage in heat energy conservation of nocturnal activity and diurnal rest in homoiothermic animals.

4) The likelihood of competitive factors operating between strepsirhine and haplorhine primates within the arboreal niche in regions of sympatric distributions.

In these respects it is significant that diurnality and large body size only arose in the strepsirhine lineage in isolation on Madagascar. All extant lorisiformes are about 1Kg or less in weight and all are nocturnal. It is possible that in the old world, excepting Madagascar, mutual competition between strepsirhines and haplorhines in the forest zones (the primary adaptive niche of primates) has produced the remarkable fact that no lorisiforme exceeds 1Kg or has adopted diurnal activity and no haplorhine (with the exception of the somewhat transitional form Tarsius, see Martin, in press) weighs less than 1Kg (talapoin) or has nocturnal activity.

In Madagascar the lemuriformes lack haplorhine competitors which, enhanced by a general impoverishment of the mammalian fauna, has allowed the evolution of recent species well in excess of 1Kg most of which have, or in the case of the large subfossil species probably had, diurnal activity (Walker 1967).

In the new world it is the haplorhine lineage that has become isolated and a comparable diversification in body weight at least has taken place. With no strepsirhine species it is possible that constraints of competition on lower body size were reduced. The loss of the nocturnal adaptation of the tapetum in haplorhine species (Martin 1978) may have severely reduced their ability to re-enter the nocturnal mode of the ancestral primates. Further suggestion of a general distinction in the adaptability of the strepsirhine and haplorhine groups may be determined from considerations of body size and habitat. Many strepsirhine species occupy quite harsh and often markedly seasonal environments. Despite its small size the lorisiforme Galago senegalensis moholi (200g) is found in acacia thornveldt where winter nightime temperatures may fall below freezing point. During the winter the insect population is severely reduced and during some periods the aminals may be totally dependent on gum-feeding (Bearder, pers com). Recent evidence suggests that the procumbent lower front teeth of many strepsirhine species, the 'tooth comb' is a dietary adaptation to gum-feeding (see Martin 1978). It seems likely that for most species gum-feeding is not very common when other food stuffs are in abundance and that the adaptation is for periods of hardship. (Further support for Martin's hypothesis that many early strepsirhines lived in seasonal conditions of some hardship is given by Walker 1969, 1974 who reports procumbent lower front teeth in Miocene lorisoids, see p. 305 et sqq). Another example of strepsirhine adaptability despite small size is seen in the lemuriforme Lepilemur weighing less than 1Kg in harsh xerophytic forest conditions in southern Madagascar (Hladik and Charles-Dominique 1971). This species lives on a delicate energy balance, and a large proportion of the energy cost of activity is spent in search of food.

It is significant that in contrast, the smallest haplorhines found outside forest weigh at least 6Kg in the female (some macaques and baboon species). In view of these features of the extant primate distribution and ecology it is proposed here (and developed later, see next section and discussion chapter 7) that there may be an adaptive complex basic to the physiology and behaviour of the strepsirhines which allows them to occupy harsh conditions despite the nutritional and thermoregulatory problems of small size. It would thus appear that the haplorhine adaptive form is limited to the less severe forest conditions unless achieving the advantages in nutrition and thermoregulation of a much greater size than those of non forest strepsirhines. The nature and implications of the relative adaptability of strepsirhines to variable and harsh environments as compared to haplorhines are given further generalization in the discussion (Chapter 7).

Section c) General Physiology and Reproductive Anatomy.

In this section some general aspects of physiology and reproductive anatomy of the primates are described for their relevance to the study of energy flow in living systems. Many of these features are established in allometric studies.

The primates are both the most highly encephalized order of mammals and also the longest living for their size. However, different levels of encephalization may be detected between haplorhine and strepsirhine species, the haplorhines being generally more encephalized than the strepsirhines. There are further interesting general differences between these two groups, in thermoregulation and metabolism. It appears that strepsirhine species have a tendency to vary body temperature in relation to ambient temperature, and that body temperatures are often lower than those of haplorhine species and other mammals (Bourliere, Petter and Petter-Rousseaux 1956, Wislocki 1933, Hildwein and Goffart 1975). Low metabolic rates, associated with the low body temperatures, of strepsirhine species have been reported (see Perret 1978). It would seem however that under certain conditions metabolic rate may also be surprisingly high (Perret 1978) as compared to Kleiber's generalized formula (1961, see p. 21). In comparison to the haplorhine species which maintain a more constant body temperature and metabolic rate, it seems that the strepsirhines may be characterized by what is best considered a wide variability in these two important thermodynamic criteria. This variability exists in the diurnal and seasonal rhythms of any given species and appears to exist between different species. In those species studied the lower values for metabolic rate and temperature are associated with the non-breeding season (Russel 1975, Perret 1978, Andriantisiferana and Rahandraha 1973, Chevillard 1976). Reported estimates for B.M.R. are given by Perret (1978) as percentage differences from values predicted from Kleiber's curve (1961). Cheirogaleus spp , - 25%, Microcebus murinus ,- 21 - -5 % Arctocebus calabarensis ,- 30%, Perodicticus potto ,- 45% Galago demidovii ,- 20% - + 17.5%, Euòticus elegantulus ,- 20%. Unpublished evidence of Whittow demonstrates a resting oxygen consumption in Nycticebus coucang of about - 40% below Kleiber's prediction, and heat production of - 65% of the predicted value (Goffart perscom). It is of some interest to note that the same experimenter found an oxygen consumption 2.5 times the predicted value in the Tree shrew Tupaia glis (see p. 43 and p. 272 et sqq). With the single studied exception of the hypometabolic owl monkey (Aotus trivirgatus), interesting in that it is the only nocturnal monkey, (Scholander et al. 1950), the haplorhine species have higher average body temperatures, and apparently a more stable metabolic regime (see Hildwein and Goffart 1975, Sacher 1966, Goffart pers com). Whilst at this stage in the research it would be premature to characterize all strepsirhine species as metabolically and thermoregulatorily 'abnormal', there is growing evididence of a general distinction between the form of strepsirhine and haplorhine physiology in relation to body temperature, heat production and energy flow. An experienced student of metabolism and thermoregulation has said of the two groups in relation to this topic 'Haplorhini apparently raise few problems but there is a puzzling muddle to unravel among strepsirhini' (Goffart pers com). In this study, the flow of energy considered as a fundamental parameter of the living system, this general distinction between the two primate groups is seen as quite significant (see p. 305 et sqq).

Another distinction at the same taxonomic level was revealed by Leutenegger (1973) who demonstrated that haplorhine litters are between two and three times heavier than those of strepsirhine of a similar maternal weight. He has suggested that this may be related to the major differences in placental type between the two groups. All haplorhines have haemochorial placentation and all strepsirhines have epitheliochorial placentation.

Following Luckett (1971, 1974, 1975) Wislocki (1929), Hendrickx and Houston (1971) and Mossman (1937) these differences are described. The classification of Mossman (1967), identifies placental types according to the degree and form of chorionic invasion of maternal uterine tissue. The two types of placentation found in primates are at opposite extremes of this range, the strepsirhines with the least invasive type and the haplorhines having the most invasive.

The chorion develops from the outer layer of the blastocyst endoderm. In the epitheliochorial placenta of strepsirhines the chorion lies up against the intact uterine epithelium. The chorion is densely covered in villi over nearly all of its surface, completely enclosing the foetus in a villous placental sac and aiding adherence to the uterus. Foetal nutrition is maintained through the secretion of uterine milk from specialized glands in the uterine mucosa, and through diffusion and gaseous exchange from the maternal blood through the maternal capillary walls, endometrium and uterine epithelium.

In the haplorhine haemochorial placenta the chorion invades maternal tissue, breaking down the uterine epithelium, endometrium and also the capillary walls in a localized area of the foetal membrane surface and uterine surface, where the chorion is actually bathed in maternal blood. Nutrition, respiration and excretion of the foetal tissue is primarily maintained through the diffusion between the chorion and maternal blood. Though uterine glands secrete uterine milk in haplorhine species as among the strepsirhines, they are not the primary source of nutrition for the haplorhine foetus. The evolution of these two extreme placental types within the order has possibly derived from an intermediate ancestral form, (Martin, 1969). It appears that in the course of strepsirhine evolution the development of epitheliochorial placentation represents a tendency towards poorer foetal nutrition but with reduced risk of maternal and foetal infection. The development of haemochorial placentation in haplorhine species reflects the opposite tendency, towards more efficient foetal nutrition but with the added risk of infection(see p. 305 et sqq).

Section d) Some Implications for this study.

For the purpose of this study it was considered that the differences in energy relations, reproductive physiology and ecology between extant strepsirhines and haplorhines, supported by the fossil evidence suggesting an early divergence of the two lineages soon after the establishment of an ancestral primate stock, warranted the seperate treatment of the two groups in the allometric analysis. Since it was believed that energy flow might affect many of the developmental parameters, the separation of the interspecifically variable energy consumers the strepsirhines, from the comparatively predictable interspecific energy consumers, the haplorhines,was expected to distinguish some of the variance of an all primate analysis between that due to the strepsirhine members and that due to haplorhine members (see p. 305 et sqq).

For this reason values for statistical analysis are given for ; all primates , strepsirhines and haplorhines in most cases. Further analysis of reproductive variables at a lower taxonomic level not given in this study, will be presented elsewhere (Clutton-Brock, Harvey and Rudder, in prep.)

Another feature of the study is that in all analyses involving adult weight, female body weight has been used. In many interspecific allometric analyses an average adult size for males and females has been employed. However, in common with other orders, sexual dimorphism in weight in primates is greater and more common in species with a larger average body size (Clutton-Brock, Harvey and Rudder, 1977). Since it is female energy relations and developmental cycles that are most directly concerned with the whole growth period from conception to weaning, and with the overall reproductive potential of placental mammals, it was decided that female body weights rather than average intersex weights would be more appropriate, and would introduce few interpretational problems. Whilst this decision has certain advantages from the point of view of early growth and reproductive potential, the significance, in energetic and ecological terms, of sexual dimorphism is necessarily ignored.

The presentation of figures will be in the text, in relevant chapters. Unfortunately some reference back and forward is necessary due to the discussion of the interrelationships of variables. Allometric distributions of species are given by numbered points referring to the key (Table 1 pp 350-1), the taxonomic affinity of species is given to a sub family level in Table 2 (pp 352-9). In the results sections, species referred to in the text will be followed by the key number. Preceeding each diagram will be a page of explanation and statistical information. In general best fit lines for logarithmic distribution are only given when the distribution is reasonably correlated (see p. 122).

In the text it was often difficult to delineate spatially those findings derived originally in this study from others in the literature without severely disrupting the line of argument. For this reason correlations given first in this study are indicated by (this study) behind the reference and in the explanatory notes to the figure. Every diagram of results given in the study is calculated from the authors compilation of data, in all cases where the relationship between variables has been presented elsewhere, the presentation in this study has an increased sample size. All such previously demonstrated relationships will be referred to in the text and in the explanatory notes to figures.

The following chapters are arranged so as to introduce some general topics of a theoretical nature (Chapter 2), and also the types and sources of data and statistical method (Chapter 3). Three results chapters follow, dealing in turn with aspects of foetal growth, postnatal growth and the reproductive potential of populations. The discussion (Chapter 7) will attempt to tie together the previous chapters and develop some hypotheses concerning the evolution and maintenance of energetic relations in the primates and other species.

Summary of Chapter 1

This chapter serves as a general introduction to the study. An earlier report submitted in progress is re-examined. The lack of general theory to match the comparative and generalizing method of interspecific allometric studies is mentioned. The concept of allometry is described following Gould (1966), and the method of approximation to allometry, usually the power function, is discussed. Some problems of interpretation are described, particularly the 'choice of group' problem. The significance of the Archimedean principle to the interpretation of allometry is described. Certain found allometries are introduced; those of metabolic rate, brain size, litter weight, milk protein concentration and growth, which will be examined in detail later.

The Order Primates, and the two major taxonomic groups the Strepsirhini and Haplorhini are introduced. The evolution of these groups and lower taxa is discussed with reference to extant distributions and ecologies,(following in particular Charles-Dominique 1977 and Martin 1972). Some physiological characters relevant to energy flow and reproduction are also discussed providing a basis for treating the two major taxa within the Primates separately for analysis. An important feature of this study is that a series of allometries may be compared within the same group. Whilst the 'average' mammalian form may not be characterized by the primates for any given bivariate allometry, comparison between the different bivariate distributions of a single group allows an understanding of the interconnection of the different processes involved.

CHAPTER 2 - THEORY

Section a) Introduction

As explained earlier, it was decided that a short Chapter on some theoretical questions was necessary for this study, in view of the broad generalizations of living systems that are permitted by the examination of interspecific allometry. In this chapter the author will first discuss the early considerations of D'Arcy Thompson (1917) on life as a form of the movement of matter. Thompson's generalizations are then discussed in the light of subsequent discoveries in the biological sciences, with special reference to allometric analyses. On the basis of Thompson's work the theoretical method of interpretation of allometric relationships is discussed with particular reference to the scaling of metabolic rate and the interpretation of the ¾ slope of this scaling.

Finally in respect of the problems posed by aspects of Thompson's method and the 'empirical utility' of interspecific allometries (see p. 29 et sqq, p. 109 et sqq) the concepts of entropy and negentropy are introduced. Both qualitatively and quantitatively, as demonstrated by Sacher 1966, 1967, 1976, Hershey 1963, these concepts of life as a special form of matter in motion are a major development on Thompson's conception. The application of cybernetic theory and its thermodynamic analogue, entropy theory to biological systems is still an issue of some dispute (Bertalanffy 1968). However, no alternative concept has been generated which facilitates so well the understanding of living systems. The confirmation of the qualitative application of the concept to living systems through the use of allometric analyses by Sacher (1976) has important implications for the study of reproduction in the advanced order of primate species. The Discussion chapter (p327 et sqq) will discuss the development of this generalized conceptual outlook with reference to the findings in this study. (p 311 et sqq).

Section b) The Historical approach to living systems as a particular form of matter in motion.

The mathematical consideration of 'size and its consequences' (Gould 1966, p.587) in living systems, the definition of allometry (see p. 25 et sqq), is the examination of the physical nature of whole organisms. In the same sense that modern molecular biology has revealed the general physical form, and its limitation and potential of the most minute components of living tissue (Monod, 1972), so have allometric studies made a start on the examination of the general form, limitations and potentialities of whole organisms.

The history of the concepts of comparative allometry in living objects are intimately related to the development of materialism in biological science and in the physical sciences. As Gould (1966) points out the earliest recorded considerations of the biological consequences of Archimedes' principle (see p. 37) are those of Galileo in 1638. This, almost premature, treatment of the physical properties of living matter was in conflict with the religious notion of the supernatural creation of life. Whilst the development of technique allowed the examination of the physical properties of living things, the continuity and development of metaphysical interpretation of living forms in the eighteenth and nineteenth centuries hampered the development of

Galileo's considerations. In particular the German school of "Naturphilosophie" expressed an essentially metaphysical concept of living forms,and closely associated with the concept of Vitalism or the '<u>elan vital</u>' of Bergson, (Gould 1977). In some respects the "Naturphilosophie" was an empirical rationalization of the religious dogma of supernatural creation. One of the most important concepts held by the followers of Vitalism and "Naturphilosophie" was that of the necessary progression of living forms from less complex to more complex (under the influence of the internal 'vital force'), and of the reflection of this process in ontogeny (Gould 1977, Milne-Edwards 1844).

Opposition to this metaphysical view was provided by the 'mechanistic' school, which in many ways superceded vitalism due to the developments in experimental technique and theory, in particular the Darwinian theory of natural selection (Darwin, 1859). In many ways, in the modern study of whole organisms, the concepts of 'mechanism' remain the unwritten experimental and philosophical approach. Most modern biologists do not believe in the 'elan vital' and would defend the notion of the essentially material nature of living processes. This was the outlook of D'Arcy Thompson in his important synthetic work 'On Growth and Form'(1917), which applies well to modern empirical, and somewhat mechanistic notions in biology. In short, the vitalist school believed in the inner force of living objects as determining their activity and form, whilst the mechanistic school attempted to demonstrate the effect of external forces on the activity and form of living objects. During the decline of the metaphysical domination of biological studies, the use of mathematical models and the elaboration of the physical properties of living systems increased. In the field of interspecific allometry the surface to volume ratios of living organisms acquired much interest, and in particular relation to brain size (Ryder 1893, Spencer 1868, Lapique 1898, 1907, Dubois 1897). The 'surface law' described earlier is believed to determine the form of living organisms, essentially a mechanistic rather than a vitalistic concept, and for the general theoretical framework upon which this law is based, we should turn to Thompson.

In the opening chapters of his book Thompson asserts the requirement of biological scientists to establish a philosophical and methodological framework for their study. Thompson is quite clear on this point 'Physical Science and Philosophy stand side by side and the one upholds the other'. This statement is followed by an affirmation of the materiality of living organisms and a rejection of the belief held by natural philosophers such as Goethe and Pascal (associated with the Naturphilosophie school) that mathematical and physical determinations were inappropriate to biology. These beliefs and the tendencies of vitalism to mystify the form of living organisms are criticized by Thompson on the basis of Newtonian physics. It is in Newtonian terms that Thompson elaborates his opposition to the 'elan vital' asserting the determination of living form largely by external rather than internal forces. One particular section is worth quoting in full since, as a theoretical perspective of the experimental and mechanistic method, it remains to this day the most succinct formulation available.

'In the Newtonian language of elementary physics force is recognized by its action in producing or changing motion or in maintaining rest. When we deal with matter in the concrete, force does not, strictly speaking, enter into the question for force, unlike matter, has no independent objective existence. It is energy in its various forms, known or unknown, that acts upon matter. But when we abstract our thoughts from the material to its form, or from the thing moved to its motions, when we deal with the subjective conceptions of form, or movement, or the movements that change of form implies, then Force is the appropriate term for our conception of the causes by which these forms and changes of form are brought about'.

Thompson's theoretical position is biased in favour of the action of external 'forces'. However, despite the theoretical advance over vitalism that these physical notions allowed, the theory of abstract forces, without their cause, or opposite, like action separated from reaction does not resolve the problems concerning the <u>interaction</u> between living organisms and their environment. It should be remembered that at the time of Thompson's elicitation of Newtonian theory in support of the application of physical and materialist concepts to the study of life, Newtonian physics was undergoing a major transformation at the hands of Relativity Theory (Bondi 1965, Cohen 1961). This particular issue will be returned to later (p. 315 et sqq). In general, however, Thompson's work signified a development over the vitalist school in three principal assertions, all of which have been verified and re-affirmed since his time.

1) Biological systems are a particular form of matter in motion, and, as such, exhibit relationships common to all forms of matter in motion.

2) The determination of the physical properties of

living systems and their mathematical approximation enhances the understanding and subsequent use of living systems.

3) The diversity in living systems is explicable only in terms of both the unity and struggle of the separate parts. (Thompson had spoken of the impact of Darwin's notion of the struggle between organisms or species on the older, religious concept of perfect harmony between the parts of nature. It was as if the picture had been suddenly turned upside down, and Thompson felt that the search for unifying principles in the study of living systems had become overshadowed by the 'contrasts' which 'are apt to loom too large'.)

In support of these three assertions modern research provides many examples, some in the field of allometry. The first two require little substantiation for modern biologists; the determination of the fine molecular structure of DNA (Watson and Crick, 1953), or the effects upon metabolic rate of varying gravitational field (Kelly and Smith 1966, see p. 67 et sqq) are confirmation of the response of living tissue to physical phenomena. As an example of the second of Thompson's assertions an allometric study may be cited, the scaling of brain size and the concept of encephalization. In this case the application of the mathematical approximation of simple allometry to the quantitative measurements of body size and brain size revealed a generalized set of relationships between species that was remarkably similar to, and thus a theoretical deepening of, the morphological and anatomical differences used for the Linnean classification of species. For example, reptiles were found to have relatively smaller brains than mammals for any given body size (Jerison 1973).

The third assertion is not often stated explicitly in modern studies, but is often implied in the concepts familiar to all modern biologists. An example is seen in the notion of the ecosystem, in which the unified and separate nature of living systems is seen in the interdependency of species in the ecosystem and yet the competition between species and individuals for resources and mates. The carbon cycle, and the flow of energy through food webs and chains are examples of the former, whilst the development of ecological succession to climax may be seen as a consequence of competition between species within a developing ecosystem (Roberts 1976).

It is possible that in the evolution of species further unifying principles may operate, an example may be taken from allometric studies. In the interspecific allometry of brain size, the relative size of the brain has increased over evolutionary time within each evolving lineage of the mammals and reptiles. The significance of relative brain size in the development and thermodynamic relations of extant species (Sacher 1976, Sacher et al 1974) strongly suggests that this apparent convergence in the evolution of relative brain size, is an evolutionary trend of both types in the increase of complexity of material arrangement and activity (see p. 73 et sqq, p. 322 et sqq). This effect, if it may be demonstrated with further reference to fossil evidence, will only be properly understood if <u>all</u> life systems are considered in relation to the energy derived from the sun, a necessarily unified feature of life, as is the gravitational field.

Before developing the theoretical discussion of the treatment of biological findings **later** (p. 67 et sqq), a section is introduced to discuss the status of the methods of analysis of allometry with respect to D'Arcy Thompson's (1917) outline. As an example the scaling of metabolic rate, and its interpretation are considered in view of Kleiber's (1969) recent denunciation of the function of heat loss as implied in the 'surface law' as an explanation of the found relationship.

Section c) In relation to allometry; theory and method.

As was described earlier (p. 29 et sqq), the mathematical approximation of the equation of simple allometry to natural phenomena is believed to be based not on a natural 'axiom' but on the criterion of empirical utility only. However, the approximation is often empirically good, and has led to the functional interpretation of the relationship on the basis of the mathematical approximation. The most direct relationships of this sort are those derived from Archimedes' principle (p. 37 et sqq), and in particular the 'surface law' which has been used to identify and propose the mediation of some processes determined by volume by others determined by surface (e.g. interspecific allometry of metabolic rate (Kleiber 1969), brain size (Gould 1975) and litter size (Leutenegger 1973) among others).

It is perhaps in these particular examples that the study of allometry has attempted to demonstrate the material, quantitative and unified nature of living organisms most clearly. However, in many ways the profundity of the found relationships is masked and held back by the one sided notion of external forces which Thompson advocates (see p. 62). The analogy of the equation of simple allometry to Archimedian relationships between length, surface and volume is the most attractive of 'explanations' for many found allometries. However, there is a particular feature of living organisms that often renders the analogy imperfect, unlike geometric solids, living organisms interact with their environment in a continual process. The examination of causal relationships derived from allometric analysis requires the examination of this process of interaction, which may reveal new interpretation of well established relationships.

This is the approach Kleiber (1969) has adopted to the well established 'surface law' of the interspecific allometry of metabolic rate to adult body size in mammals. Kleiber's paper comes after many years personal research into this topic (e.g. 1947) and is interesting in that it is the first in all the years of such studies (see p for references) to examine the process supposedly underlying the 'surface law'. This has always been believed to be a consequence of heat loss across the body surface. Bearing in mind that there is some dispute over the expected interspecific scaling of body surface area to body weight, some assuming geometrical similarity between species (i.e. Surface $\propto$ Weight$^{2/3}$) and others proposing on grounds of stationary structural, and dynamic structural requirements a higher exponent (surface $\propto$ Weight$^{3/4}$) (McMahon 1973, Alexander pers com), we may look at Kleiber's argument in detail. This serves as an example in method, and has important consequences for the interpretation of a basic interspecific allometry relevant to this study.

Kleiber's argument runs as follows: we are hesitant to give up the 'surface law' explanation of metabolic rate because of its attractive simplicity and its empirical utility. However, does the 'explanation' of heat loss stand up to the test, and can we consider 'surface dependency' to exist for metabolic rate? In physics the rate of flow of thermal energy is characterized in Fourier's Law, heat flow being proportional to the flux area (i.e. surface area),

$$Q/_t = \lambda \frac{S}{l} (T_i - T_s)$$

where: $Q/_t$ = rate of heat flow

(i.e. Q = thermal energy, t = time)

S = flux area

l = thickness of isolating surface layer

T_i = internal temperature

T_s = surface temperature

λ = heat conductivity of the surface area.

For the case of homioithermic animals $S \propto W^{2/3}$ where W = weight, (or $W^{3/4}$ following McMahon and Alexander above p. 68). Most mammals have similar body temperatures ($\sim 37.5^\circ C$) and in the experimental cases providing data for the scaling of Basal Metabolic Rate, surface temperature (at the surface of the isolating layer) is usually $-20 - +30^\circ C$. If then the temperature criteria do not vary with body weight, the 'surface dependency' of $Q/_t$ requires that the ratio $\lambda/_l$ is independent of size, (i.e. that the heat conductivity per unit surface area is the same for all mammals).

However, if we assume that the heat conductivity of the surface layer does not differ between species (Kleiber's assumption) then the size independence of the $\lambda/_l$ term should require that all species have skin and fur of the same thickness. As Kleiber demonstrates this is not the case and skin thickness increases relative to the .19 power of body weight (.33 expected from Archimedian principles). (As regard fur thickness, some indication of an approximate isometry of body length and hair length is given for strepsirhine species by Martin 1979, though the correlation is not very good.) Kleiber then predicts the scaling of the rate of heat flow on the assumption that λ does not vary between species, that $l \propto W^{.19}$ and that $S \propto W^{2/3}$, thus: $Q/t \propto \frac{W^{2/3}}{W^{.19}} \quad W^{.49}$, well below the found scaling.

Kleiber uses this as a disproof of the surface law and states '.....we must search for influences on metabolic rate which are related to higher functions of body weight than Fourier's law of heat flow would predict.' In the authors opinion Kleibers argument does not disprove the surface law since it is possible that λ does vary between species, one can imagine that a very dense fur has a lower heat conductivity than sparse fur which traps air less effectively. However, even if this is the case the effect would have to be allometrically quite marked, and allowing for McMahon's and Martin's values to be incorporated as well as Kleiber's, λ would need to be proportional to between the .19 - .42 powers of body weight (from $\frac{S}{l} = \frac{W^{3/4}}{W^{.19}}$, using McMahon's surface area and Kleiber's surface thickness, and $S/l = \frac{W^{2/3}}{W^{.33}}$ using Kleiber's surface area and Martin's surface thickness).

Whilst it may still be possible that allometry in λ will be found to balance the equation in favour of the 'surface law' the course of Kleibers argument has turned the 'surface dependency' and 'size required allometry' (Gould, 1966) upside down. Instead of the surface area determining the basic rate of energy flow, we are now considering the allometry of apparently adaptable features (skin thickness, density of fur, etc.) to explain why the heat flow argument appears unsound. In fact if two of the factors which determine heat flow in this example, l and λ (fur skin thickness and density of fur) are adaptable in mammals then clearly surface dependency of heat flow need not operate. Why is it then that Kleiber's earlier (1947, 1961) correlation of B.M.R. and body weight for homoiothermic species is so good, with little deviation? Here, having briefly disagreed with Kleiber (1969) we may return to his analysis, and agree that if surface dependency is unlikely on heat flow arguments because of the adaptability of the components of insulation, then'higher functions of body weight' must be sought to explain the scaling of energy flow.

In support of this notion Kleiber cites the findings of Kelly and Smith (1966), researching into the effects of gravity on animal physiology as part of N.A.S.A.'s space programme. They found that the experimental increase in the accelerative field (by centrifuge) experienced by growing chicks produced both retarded growth and increased metabolic rate while all other variables were held constant with the control group experiencing the accelerative field of normal terrestrial gravitation. In Kelly and Smith's analysis they calculate that for all homoiothermic species earth gravity is responsible for about 7 KCal per day per Kilogram body weight of energy intake. Thus smaller species expend a smaller proportion of total energy intake as a direct consequence of gravity. Kleiber concludes that the'higher functions of body weight' sought for the explanation of the scaling of metabolic rate may be found in this gravitational effect which 'must increase in direct proportion to body weight.' This factor, combined with other conditions 'such as optimal heat exchange and most effective circulation' are proposed by Kleiber to be at the root of the ¾ scaling of metabolic rate.

This example of the analysis of an allometric relation is extremely interesting, since the examination of the process of interaction between an organism and the environment has permitted a major development in theory, supported by experimental evidence. (It should be remembered that the surface dependency of metabolic rate has been generally accepted for over half a century). Instead of considering the static Archimedian relationships, Kleiber examines the flow of heat. The introduction of the concept of flow between the organism and its environment is a development on Thompson's concept of external forces acting upon the organism. However, in no way do the results of Kleiber's analysis contravene the tenets that had allowed Thompson to develop a concept of living systems in opposition and in development of the Naturphilosophie school. These were the materiality of life, the quantitative and qualitative nature of living systems and the existence of unifying principles in nature as well as the particular and unique features of living organisms. The identification of the relation between accelerative field strength and the rate of energy flow in living systems is a confirmation of the three. In particular, as Kleiber points out, the rate of energy flow is seen to be related to an accelerative field common to all terrestrial life, an important unifying principle.

However, it is perhaps the consequences of Kleiber's analysis that allow him to suggest that metabolic rate may be determined by 'an optimal rate of mechanical work for survival' that are most significant. The implication of essential thermodynamic factors in the activity of living organisms is a highly generalized concept which serves, for the purposes of this study, as an introduction to the thermodynamic generalities of entropy and negentropy first introduced to biology in 1945 by Schrodinger.

Section d) Modern theory of life, its relation to allometry.

The most advanced theory of the essence of life is based on the first and second laws of thermodynamics, principles which apply to all material movement. The first law is a statement of the principle of the conservation of energy. It may be formulated as follows, relating thermal energy to mechanical energy; if an amount of thermal energy dQ is added to a system, this system experiences an increase in internal energy dU and also does work on the environment dW,

$$dQ = dU + dW.$$

Internal energy may be stored also in the form of heat, chemical bonds or in the interaction between molecules in any given phase, solid, liquid or gas. Other forms may be magnetic or electrical storage.

The second law breaks with this ideal conception of the reversibility of energy flow in real systems, which exchange energy in time. The second law states that (in our realm of the universe at least) the flow of energy is necessarily accompanied by an increase in the random movement of matter, known as an increase in thermodynamic disorder or entropy (Schrodinger 1945, Wesley 1974). This universal increase in entropy over time is also the decrease of its opposite negentropy or the specificity of material arrangement and movement.

Living systems exchanging energy, matter and information with this universal environment have, however, the ability to create and maintain molecular structures of highly specific, non-random, arrangement, which engage in highly specific reactive processes. This appears to be a contradiction of the second law, given above, stating the general environmental tendency towards increasing randomness and disorder, or entropy. Engelgardt (1978) has the most succinct view of this effect, quoting him (p.298) 'This tendency towards ordering, however, has a special status. Ths living object in this respect is antagonistic, as it were, to the laws governing all nature, although it conforms to them. We may say that, instead of passively submitting to the law of nature, life ensures the possibility of actively counteracting this law, just as in lifting a heavy object we do not violate, the law of gravitation but counteract it'.

'The tendency towards ordering, towards creating order out of chaos, is simply contradictory to the principle of entropy increase, i.e. the second principle of thermodynamics, ... The ability of living objects to counteract the second principle entails a consequence of the utmost importance. Living objects must represent open systems, i.e. they must be able to interact with the surrounding medium and exchange energy with it. Because of this the contradiction arising from the seeming violation of the second principle is eliminated: local decrease of entropy arising in an isolate living object is accompanied by its increase in the real "living object - environment" system so that in actual fact no violation of the second principle takes place'.

What is actually occurring in a living object is the ultimate production of entropy in excess of the thermodynamic specificity or negentropy through which this entropy flows. The most thermodynamically ordered of living objects must still be generating disorder to an even greater extent. This factor has further consequences for the living object, entropy production itself causes disordering, the activity of living objects both requires and creates disorder. The death of a living object represents the crisis in the relationship between the disorder generated by activity and the order required for its maintenance. It is this process that Sacher (1976) has examined, his results will be described following a brief generalization of the relationship between energy, temperature and the flow of entropy as it is understood in physics.

Following Engelgardt (1978, above), we may state that for living systems of thermodynamic order $-dS$, a greater amount of entropy must be created in the environment as a whole;

$$-dS\,(\text{internal to organism}) < dS\,(\text{environment external to organism}) \quad (\text{Eq I})$$

(Wesley 1974 p.48). Quoting Wesley further, 'Ordering, processes including life, must take place in time, so that life can be supported only in environments that are increasing the entropy of the universe with time, i.e. have an entropy production. The environment that has a greater entropy production, dS/dt will provide a greater potential ϕ for ordering processes such as life to occur, thus

$$\phi = {dS}/_{dt} \qquad \text{(Eq. 2)}$$

Again quoting Wesley (1974 pp 52,53) 'Since a change in entropy may be defined in terms of heat transferred divided by the absolute temperature',

$$(dS = {dQ}/_{dT}) \qquad \text{(Eq. 3)}$$

(where Q = thermal heat energy, T = absolute temperature) 'entropy production implies energy flow in which the character of the energy changes.'

$$(dS = {dQ}/_{dT} = (dU + dW)/_{T}) \qquad \text{(Eq. 4)}$$

(where U = stored energy, W = mechanical work) 'Since energy is conserved, the entropy production associated with a fixed energy flow is given by

$${dS}/_{dt} = {dQ}/_{dt} \left(\frac{1}{T_2} - \frac{1}{T_1}\right) \qquad \text{(Eq. 5)}$$

where T_2 is the absolute temperature to be associated with the final energy state, and T_1 is the temperature to be associated with the initial energy state. It is thus apparent that a supply of energy is required for entropy production and is therefore required to sustain life.....For a given fixed supply of energy per unit time the maximum amount of thermodynamic order (or entropy reduction) that can be sustained will depend upon the optimum utilization of the energy source..... In particular the utilization of an energy source depends upon its conversion from a state of high utility to a state of low utility....' This issue of the utilization of energy refers to a consequence of the second law of thermodynamics which states that thermodynamic order is most efficiently created from energy in the form of mechanical work thus 'the amount of order that can be created by the amount of work W becomes

$$(-\Delta Snet) = {W}/_{T} \qquad \text{(Eq. 6)}$$

where T may be regarded as the ambient temperature of the environment, (p. 10 in Wesley 1974). Another statement concerning the utility of energy important for the consideration of living processes refers to the utility of thermal energy Q at a temperature T_1, where T_2 is the ambient temperature, the ideal utility in this case is

$$(1 - {}^{T_2}/_{T_1}) \qquad \text{(Eq. 7)}$$

As regards living systems, and especially the mammals studied by Sacher (1976) these basic thermodynamic statements (1 - 7) have some important consequences. We would expect that a higher body temperature in a given ambient temperature (especially in mammals) would be associated with an improved utility of thermal energy (eq. 7) and the potential for greater thermodynamic order (eqs 2&5. The general statement concerning the tendency for general environmental increase in entropy is also maintained (eq. 4) so that higher body temperature may result in an internal reduction in entropy production but is absolutely creating an increase in the entropy of the universe in any given ambient temperature, (note notations of T_1 and T_2 in Eqs. 4, 6, 7).

However, as has been mentioned earlier (p 58), in the release of energy some irreversible disordering takes place <u>within</u> the system. The entropy production within a mammal, for example, expresses the relationship between energy flow and the temperature T_b, of bodily reactions,

$$M/T_b \quad \text{(following Eq. 2)} \qquad \text{(Eq. 8)}$$

where M is energy flow as estimated in metabolic rate. Thus for a fixed matabolic rate an increase in temperature can be expected 1) to produce an increased rate of total production of entropy to the universe and 2) to produce a decrease in irreversible disordering associated with the metabolic processes. It is this relationship that Sacher (1976) has studied using the most sophisticated and carefully researched techniques in allometric analysis, for the mammals. Sacher's application of method has yielded important results, confirming in analysis of natural data the conceptual hypotheses of Schrodinger (1945).

His method involves consideration of the interspecific allometry of, in particular, the following variables; Body Weight S, Brain Weight E, Resting Metabolic Rate M, Core Body Temperature T_b, and potential longevity as Lifespan L, for a large number of mammalian species. Following his earlier interest in aging (e.g. 1959) Sacher has examined the relationship between potential longevity and these other variables to test statistically the hypotheses, based on thermodynamic considerations of the life process, that the rate of aging is determined by the irreversible disordering that occurs as a part of metabolism. The results are of significance for all fields of biology, and especially for this study, concerning both interspecific allometry and energy relations of living tissue. For these reasons Sacher's results are described and discussed in some detail. It was found that little summary could be made of the report, and the findings are best explained by the original author, excepting the requirement for brevity here.

In his analysis Sacher reveals two components statistically highly associated with the aging of mammals. He calls them the 'metabolic factor' and the 'cephalization factor'. As we shall see, the metabolic factor is a measure of the rate of entropy production as a consequence of the rate of metabolism. The cephalization factor appears to be a measure of the negentropy or 'information' of the organism associated more with the structure or more exactly the configuration of the chemical reactions that maintain the entropy production of the system. Statistically at least these two factors appear to bear independent relations to the potential longevity of the organism. The deductive method of Sacher is actually as follows, based on the analysis of the multivariate approximation of simple allometry for the variables given on p 61 .

In the multivariate analysis it was found that when body weight was held constant, Metabolic rate was significantly associated only with body temperature. The relationship between M and T_b, can be written

$$\log M.s = 0.05T_b \qquad \text{(Eq. 9)}$$

where M.s is the metabolic rate for constant body weight. The metabolic factor can be defined as

$$Km = M.s10^{-.05T_b} = M.se^{-.115T_b} \qquad \text{(Eq. 10)}$$

The multiple regression of logL (L = Lifespan) on the four constitutional variables is

$$\log L = .62\log E - .41 \log S - .52 \log M + .026T_b + .90 \qquad \text{(Eq. 11)}$$

$$\text{where, } K_c = E.S^{-2/3} \qquad \text{(Eq. 12)}$$

when K_c is the measure of encephalization (following e.g. Jerison 1973), Equation 12 may be written in terms of K_c and K_m (see Eq. 10), to one significant figure, as

$$\log L = 0.6 \log K_c - 0.5 \log K_m + 0.9 \qquad \text{(Eq. 13)}$$

$$\text{or} \quad L = 8K_c^{0.6} K_m^{-0.5} \qquad \text{(Eq. 14)}$$

This description has closely followed Sacher, we may now quote him (1976, p.75): 'It can be seen that Lifespan varies inversely as the square root of K_m , and this inverse relation means that an increase of metabolic rate at constant temperature, or a decrease of body temperature at constant metabolic rate is associated with shorter life, and an increase of body temperature for constant metabolic rate is associated with longer life.'........ 'Equation 6 (Eq. 9 here p 79)' can be rewritten in terms of the theory of absolute reaction rates (Johnson et al 1954)

$$M.s = x\frac{kT}{h} e^{S^*/R - E^*/RT} \quad . \quad \text{(Eq. 15)}$$

The two parameters x and S* are, respectively, the configuration entropy and the activation entropy per mol for the relation of metabolic rate to temperature, and for the metabolism-dependent reactions that govern the rate of aging in mammals.' (T taken as T_b, and E* is activation energy, other symbols are chemical constants)

Sacher's argument develops to demonstrate that the metabolic factor may be considered as closely associated with the activation entropy, S*, in the relation above, Eq. 15. Further, he shows that the cephalization factor is best considered as being more closely associated with the configuration entropy term, x. On the basis of the found relationship between metabolic rate and temperature Eq. 9 and the identity of this relationship with Eq. 15 Sacher shows that if the entropy increase from S^*_1, to $S^*_1 + \Delta S^* = S^*_2$, the metabolic rate at constant temperature increases, associated with more rapid aging. The ratio between the longevities L_1 (for S^*_1) and L_2 (for S^*_2) takes the form ($L_1 > L_2$)

$$({}^{L_2}/L_1)^2 \quad = \quad e^{-S^*/R} \qquad\qquad (\text{Eq. } 16)$$

(c.f. Eq. 14 with reference to K_m). Quoting Sacher again (p.77), 'In terms of the reciprocal life span, or mean mortality rate, ρ , a parameter that is closely related to the rate of aging,

$$(\rho_1/\rho_2)^2 \quad = \quad e^{S^*/R} \qquad\qquad (\text{Eq. } 17)$$

'.....equation (17) is a relation of the rate of aging to the rate of entropy production. This has the corollary that the irreversible entropy production that constitutes molecular aging has a constant proportionality to the total entropy production associated with the dissipative processes of metabolism. It will be interesting to determine whether the same proportionality holds for invertebrate taxa, which presumably have lower levels of organization, i.e. higher values of x and/or S*' (see Eq. 15).

'The fact that the K_c term is related to the size of the brain, which is one of the major information processing systems of the organism, leads to the conjecture that log K_c is a measure of the information content, or <u>negentropy</u> of the organism, and more specicically that it is part of the configurational entropy term, x, in equation..' (15)

'The entropy change resulting from a change, ΔK_c, in the index of cephalization can be evaluated by equating the change in longevity due to ΔK_c to an equal one arising from a change in the metabolic entropy, ΔS^*

$$0 = 1.2 \Delta \log K_c - \Delta S^*/_R \qquad \text{(Eq. 18)}$$

An increase of log K_c by 0,833 is equal to a decrease of the dimensionless quantity $\Delta S^*/_R$ by one unit. The effect of increased K_c can be regarded as an increase of the <u>negentropy</u>, or <u>information</u>, of the system by $1.2 \log_2 e = 1.73$ bits per exponential unit increase of $\log K_c$, so that when K_c increases by a factor of 2, i.e. $\log_2 K_c$ increases by unity, the information increases by 1.20 bits or as the 1.2- power of K_c. This result deserves to be examined carefully, because the number of neurons in the brain, n, increases at about the 0.7 power of brain weight (Tower, 1954), leading to the inference that the information content of the central nervous system varies approximately as $\log_2 n^{1.7}$!

Sacher also refers to the suggestion made by Hershey

(1973) that the correct measure of longevity is the lifetime entropy production, $Q/_K$, where K is the absolute temperature and Q the lifetime energy dissipation. As Sacher says: 'The present paper takes the further step of showing that, when body weight is constant, mammalian life span is inversely related to the rate of entropy production, independent of the level of encephalization.' On p.79 Sacher refers to the importance of the finding that when M is held constant, longevity is a function of K_c Equation 13 p.79)

'The form of K_c (Equation 12 p.79) indicates that it is a measure of a property of the organism as a whole, not of the brain alone. On the basis of its form, and of its additive relation to the metabolic entropy term, the encephalization factor can be assigned the dimensions of <u>information density per unit area</u>. The area in question is not the body surface area, but rather the total area of all epithelial surfaces and tissue interfaces across which interchange of matter, energy, and information takes place between parts of the organism and between the organism and its environment. This generalized area has the same - power dependence on body weight that skin surface area has.' (c.f. McMahon 1973).

Sacher then describes the century of theoretical and empirical study of the 'index of cephalization', as Sacher says 'but this great intellectual effort came to nought because of the inability to establish any independently verifiable relation of the index of cephalization to a measurable neurobehavioural performance. An objective relationship has now been established '(Eq. 11 p 79)' between the index of cephalization and a performance of the organism that has as its measure the duration of life. We do not yet know the nature of that performance, but everything we know about the neurobiological concomitants of mammalian longevity - sensory, intellectual, and motor - supports the intuition that the length of life of a species is closely related to its intelligence and, indeed, that longevity is a major teleonomic purpose and manifestation of animal intelligence.'

In conclusion Sacher points out that the relationships given in his study contradict some current theories of the mechanisms of aging, 'and should, therefore, lead to the abandonment of some unprofitable research. s the interdependence among the molar parameters becomes progressively better known, the constraints on admissable mechanistic theories will increase (c.f. Sacher and Staffeldt, 1974), and the goal of a unified molecular-molar theory of longevity and aging will be brought nearer.'

However, before leaving this paper it is worthwhile consolidating and expanding on the results of Sacher's analysis. Sacher has obtained these results from, necessarily, extant species, and the found relationship of Eq. 9 (p.79) demonstrates that the distribution of values of M.s and T_b indicates that extant species conform to thermodynamic considerations of Eq. 1 - 7 (pp 75-7). It appears that the obtained values of M and T_b are constrained by the fact that in general an increase in body temperature requires an increase in M when S is held constant or more accurately an increase in the density of energy flow per gram body tissue for a given body size. In terms of the energy expenditure of an organism in aquiring food and reproducing successfully, this factor (the density of energy flow.....) is closely associated with the utility of the energy liberated in metabolism, or more exactly the efficiency of the processes transforming metabolic energy into the mechanical work which subsequently creates thermodynamic order. It may be in this sense that in the evolution of animals high levels of encephalization are generally associated with homoiothermy.

However the separate operation of the cephalization factor and the metabolic factor is also of great interest, especially considering the thermodynamic form of the two as information in configuration and entropy generated in the activation of the metabolic processes respectively. That the metabolic factor operates in a similar fashion for all mammalian species suggests that it may be associated with a fundamental property of the respiratory reactions common to all mammals. As Sacher points out, it would be of interest to discover if this metabolic factor is the same for invertebrate species, it may perhaps be associated with the fundamental and ubiquitous role of ATP (adenosine triphosphate) in respiration. If however the metabolic factor is responsible for irreversible damage in relation to aging, perhaps the configurational term, the cephalization factor is associated with reversible 'mistakes' in the reproductive, homeostatic, and anabolic and catabolic processes. Some suggestion of this may be obtained from work done by Hopfield described by Holloway and Kirkwood (in press) which deals with energy relations in reversible reactions of enzymes and their substrates. It has been demonstrated that the chemical activity of many enzymes involves the binding of the enzyme to the substrate with the energy released in the conversion of ATP to ADP (adenosine diphosphate, lacking the energy rich bond to the third phosphate group of ATP). This unstable and energetic conjunction may break down to produce either the original enzyme and the original substrate, or the original enzyme and a product. However, 'incorrect' substrates may bind to the enzyme; whereas the correct binding is most efficiently followed by the production of the correct product, an incorrect binding is most efficiently followed by a dissociation of the bond to the original form, although energy is 'wasted' in this second process. Hopfield refers to the process of 'kinetic proofreading', a dynamic relationship which is essentially the supply of information, or the maintainance of negentropy through the 'discrimination' between correct and incorrect enzyme reactions. A high proportion of 'incorrect' bonding for any given enzyme results in either incorrect products or 'wasted' energy. A similar relationship exists in the construction of polypeptides in animal cells, the binding of amino acids requires the conversion of ATP to ADP. An incorrect binding may only be freed by the further conversion of ATP to ADP. The'information' required to maximise the efficiency of energy use in doing homeostatic (i.e. 'correct') work, is at this molecular level is a measure of the specificity of the conditions of reaction. These conditions may include the temperature, concentration and phases of the component molecules, as well as the electrolytic, hydrolytic and magnetic features of these molecules, for a particular reaction. It would appear from consideration of Sacher (1976) that the 'negentropy' or specificity of these conditions is reflected largely in the cephalization factor of mammals, though in some lesser way associated with the metabolic factor. The maintenance of stable temperatures, and some stability in the concentrations etc of reagents must to some extent involve the metabolic factor, but may be considered as essentially associated with the cephalization factor. As Sacher makes clear, the cephalization factor is a measure of a property of the organism as a whole (p. 82), and thus the cephalization factor is truly seen as a reflection of the pattern of activity of the whole organism, and in particular, that part not directly attributable to the rate of activity - the metabolic factor.

This theoretical extension of the thermodynamic nature of individuals of different species to the pattern and pace of their whole activity was expressed by Sacher in an earlier paper dealing with aging (1966 p.13) 'The differences in longevity and therefore in rate of aging, between mammalian species are due for the most part to differences at the higher levels of co-ordinated behaviour' (my emphasis). Lifespan may reflect the 'ability of the homeostatic systems to maintain the constancy of the milieu interieure'. This concept encapsulates very well the nature of the living, negentropic tendency in the 'open system' forinteraction with the environment (see quote from Engelgardt 1974, this study p. 74). The maintainance of constancy is, then, a quality expressed in a wide variety of forms from chemical activity to behaviour and population dynamics, this is however a subject for later discussion (see p 327 et sqq).

One further issue arising from this general outlook is the thermodynamic basis of the concepts of 'advanced' and 'primitive' characters. It is generally assumed that the evolution of life has resulted in a general increase in the specificity of material arrangement in most lineages. (In fact the very earliest reactions in the evolution of structural specificity of proteins can no longer regenerate the process of our own evolution, since the protein products would be immediately oxidised in bacterial metabolism or by atmospheric oxygen - not present in large concentrations at the origin of life. Dawkins 1976). As Jerison has shown (1973) the evolution of increasing encephalization has occurred in both birds and mammals, which, on the evidence of Sacher's study (1976), suggests the convergent evolution of increased information density and probably lifespan in these two groups. Thus the distribution in encephalization in living organisms does in some ways give a static picture of a process that has occurred in time (earlier forms - lower cephalization, later forms - higher cephalization), remembering that this process has occurred within each lineage that has provided extant organisms. In terms of Sacher's general criteria (p. 87), the 'primitive' nature of extant organisms is expressed in the relatively poorer capacity of their 'homeostatic systems to maintain the constancy of their milieu interieure, and vice versa for the 'advanced' organisms.

The final consideration at this point is the necessary unity of the three flows mentioned by Sacher (see p. 83), those of energy, matter, and information, all three arising from the movement of matter. (in this fashion is Thompson sustained 1917, see p. 60 et sq). But they interact as an open system with the environment. (In this fashion is Thompson superceded - i.e.

the conception of external forces acting on an isolated system can not wholly describe the living object, see p 62).

This chapter serves as an introduction to some of the sophisticated uses of allometric analysis and also to a general theory of the living state. In this study techniques are much simpler, but Sacher's work is an essential basis for some of the more general considerations arising from the results. Whilst the following four chapters deal with more specific topics, the general framework is kept in mind, and developed in the last chapter with much reference to the topics discussed in this chapter.

Summary of Chapter 2

The materialist outlook of D'Arcy Thompson (1917) at the turn of this century is described as an advance in theory over that of the 'Naturphilosophie' school. Thompson had called attention to three aspects required for successful biological theory - an understanding of
1) The materiality of living objects and processes
2) The quantitative as well as the qualitative nature of life and 3) the unified features of life.

However, Thompson considered that movement and change of form in organic matter was best understood as largely the consequence of external forces. This one sided outlook may be traced in many 'deterministic' theories in the study of allometry, where the process of <u>interaction</u> between the organic, material system and its environment are ignored. Kleiber's (1969) paper examines the theory that heat loss from the body surface determines metabolic rate by considering the <u>process</u> involved. He concludes that the work done against gravity must be taken into account and suggests a factor such as ..'optimal heat exchange..' may be involved. This outlook is in agreement with the thermodynamic account of life given first by Schrodinger (1945). Life is considered in this recent but generally accepted theory as being an open system tending to lower entropy. Sacher 1976 has found experimental corroboration of this outlook in determining statistically a high association between encephalization and the thermodynamic entropy of metabolism and length of life. Lifespan may be considered as a fundamental measure of the stability of the organic matter and may be enhanced by a higher index of encephalization, but declines with an increase in the rate of flow of energy through the organism unless this is compensated by a higher body temperature.

The measure of brain size appears to be a measure of the negentropy of configuration of the reactions which generate energy. These issues will be re-examined later.

CHAPTER 3 - MATERIALS AND METHODS

Section a) Introduction

As a taxonomic group the primates are particularly suited for a study of interspecific scaling in reproductive functions. They have been relatively well researched in both field and captive conditions, and the bulk of research has been carried out in the last decade and a half, when scientific methods of data collection and recording have been well established in animal studies.

Whilst for many aspects of interspecific study information is scarce, for example metabolism or behavioural development, this is not the case for reproductive data. Knowledge of reproductive function of a species is a basic requirement for descriptive and analytic academic studies, medical research and commercial breeding, though the quality and form of information from these sources may be varied. If resources are available for a detailed field observation or captive breeding programme, reproductive data are not difficult to obtain and little further capital equipment is required.

It is evidence to the expected, and in part obtained, value of primate studies that despite the relatively slow growth and reproductive turnover of the order as a whole the primates are one of the best and most thoroughly researched of mammalian orders. The long term nature of the research and difficulties faced in studying a primarily forest living order, often difficult to rear in captivity only emphasises the collossal effort that has been mounted in recent years to obtain primate data. The practical use deriving from this endeavour in medical research and resulting from the clarification of general biological principles as well as man's unique position within the order is still to be largely realized.

Another feature of reproductive functions which suits them well at this time for comparative allometric analysis is their relative invariability within species. Whereas ecological or social quantitative data are subject to great variation under local conditions (see Clutton-Brock and Harvey 1977), this is not the case for either the physiologically or developmentally determined parameters of reproductive function.

The major part of this study is based on the mathematical analysis of numerical date. It has also been necessary to compile a large body of non-statistical information to substantiate the quantitative values. Such information is indispensible for the interpretation of the results of statistical analysis. Most of the numerical data used in the analysis is taken direct from the original sources. Some quantities of interest have been derived from these basic values, for example the calculation of aw - the specific foetal growth rate from the values of gestation period and birth weight (see Chapter 4), and r_m maximum reproductive rate (Chapter 6).

The availability of information on primate reproduction has been the main factor in the choice of parameters for analysis. However the limitations on time and the author's attempt to concentrate on interspecific allometry has led to the exclusion of available information on population and ecological variables. This type of data often has a wide variance due to intraspecific variation in environmental conditions. At present the limited information on these variables, often from single field studies reflecting particular local conditions, is difficult to compensate for in an interspecific study where the general or 'average' population and ecological adaptations of a species are required.

The selection of particular parameters for bivariate analysis is also important, in order to extract from the distribution the closest approximation to functional relationships, these questions are dealt with in the Methods section. Whilst the available information on primate reproduction is sufficient to permit an attempt at outlining the basic physiological interdependencies which underly the inter species differences in reproductive turnover, this may be the limit on such types of research at present. The problem is that systematic research on species to obtain a full set of data has been hampered by the rarity of some animals, the many different intentions of the research projects on species, and by the short history of intense scientific work on such subjects. The problems of analysis and interpretation are discussed later (p. 109 et sqq) but they are not a limiting factor on the degree of sophistication of such comparative studies. It is important to remember, despite the many problems in the use of the technique that the basic features of relative scaling are indisputable. That a female Tarsier produces an infant one quarter of her own body weight whilst a human mother's infant weighs about one twentieth of her body weight is a fact that only allometric analysis can come anywhere near explaining.

Section b) Materials:

Some general features of the information employed in the analysis will be discussed prior to sections on each particular parameter. These include, the sources of data, their heterogenous form and the checking of each data source against errors and unsuitability.

The limitations of time and the search for quantitative data have meant that the references consulted are by no means a complete bibliography of primate reproduction. However, the author considers that the information derived from the sources and used in the analyses is a reliable basis for this and any further interspecific study on primate reproduction at the present level of scientific enquiry (Rudder, in prep).

Sub-section 1) Information sources

Literature: Most of the information used in the analysis has come from published sources. The purposes of each published project are extremely varied, some are reports on breeding programmes, others detailed analysis of medical research problems, or academic field observations. From all of these types of study the author has taken information. The most useful published material comes from the last decade or so, when quantitative data has become an integral part of nearly all animal studies. Earlier work, prepared with poorer resources and facilities and often purely descriptive, often does not have numerical information and is generally less comprehensive and prone to inaccuracy as compared to recent studies. For example, Crile and Quiring's (1940) massive pathological report on zoological specimens contains information on a large number of obviously emaciated animals whose body and organ weights have been employed in previous allometric studies. Wild shot and healthily reared specimens of the same species are often twice the body weight of these pathological specimens.

Early studies also contain many old taxonomic names and it is often doubtful which species were actually studied. Certain texts, quoted to this day in authoritative reviews, are, in the light of recent research, quite obviously mistaken. Jennison, (1927), gives Howler monkey gestation period as 139 days (amongst other simians mysteriously, and certainly mistakenly with the same value) which is employed by Sacher and Staffeldt (1974), as well as Indri gestation as 60 days. In recent literature there is no supporting evidence for these figures and they are not used in this analysis. These, and other, examples confirm the need for a detailed literature search by those wishing to use comparative data. At this point in time comparative studies attempting to generalise and extract important relationships in living systems are considerably hampered by this time consuming requirement. In future computer retrieval systems and improved methods of vetting and collating data may overcome this problem. However, it is most important that those dealing with the comparative and theoretical study of living systems inform those undertaking the basic source studies which parameters are of greatest interest and what hypotheses may be tested out in the field on the basis of comparative research.

Zoo records. The value of records taken in zoological garden management is often underestimated. Not only are basic details of lifespans, births, and ages at first delivery generally derivable from records taken for accountancy and general management, but many zoos in recent years have taken more sophisticated details of the growth and breeding of species in captivity. The commercial necessity of maintaining the health of often rare and expensive animals requires the keeping of veterinary records.

Animal keepers, usually keenly interested and dedicated to the animals in their care, often keep very reliable information on the daily changes of the condition of their charges. The author has been fortunate in being able to use such records for checking against existing studies, and often providing new information for the analyses. Records were consulted at the Zoological Society of London, and the Jersey Wildlife Preservation Trust.

Personal communications. The author has been permitted to use unpublished data communicated to him by colleagues engaged in research work. These sources will be credited in any published data tables and reference lists (Rudder in prep) and are acknowledged in the Acknowledgments section (p. 12 et sqq).

Personal observations. Accidental deaths of primates kept at the Zoological Society of London, Twycross Zoo, Jersey Wildlife Preservation Trust, Chester Zoo, and the collections at the Dept. Ecologie, Musee d'Histoire Naturelle, Brunoy, France, have made specimens available for dissection and measurement. These specimens with pathology reports were checked for any obvious abnormalities likely to affect body weight, brain weight or organ weights and only apparently normal specimens were used for data. Those specimens without pathology reports, and some obtained from the wild used by kind permission of Dr. P. Charles-Dominique and Dr. R. D. Martin, were examined by the author for signs of abnormality.

Some information was obtained for museum collections at the Natural History Museum, Kensington, and the Cotton-Powell Museum in Kent. In particular well preserved skins were examined for the presence of teats, usually easily detected.

Museum Records. Some specimens in the Natural History Museum still have the collector's data on body weights. These have also been employed in the numerical data for analysis, with collectors name and reference to the Museum.

Sub-section 2) Heterogeneity of Information

Aside from the variation in methods and designs of projects in the published literature, and the particular features of zoo recorded material, there are other sources of heterogeneity in the compiled data. In particular is the necessity of using data from both wild and captive studies in the same analyses. Also important are the great differences in the amount of research effort expended on different species.

Captive and Wild sources. Much of the information on reproductive parameters can only be accurately obtained under captive conditions. It might be expected that captive diets and conditions would alter the physiology and breeding of wild animals. This appears to be the case for some reproductive variables in the primates which often have specialized diets and generally complex social organization.

Most captive primate projects use artificial pellet diets with some supplements; in general no attempt is made to match the proportions of proteins, carbohydrates and minerals to wild diets except indirectly by the fitness of the animal. (Rivers pers. com.) This artificial diet is usually fed regularly and without any seasonal variation, unlike most wild feeding habits. Also captive animals may not get as much exercise as they might in the wild. All these dietary differences from the wild condition almost certainly affect the physiology of captive primates as compared with the wild specimens. Nutrition is known experimentally to affect gestation length in macaques (Riopelle and Hale 1975) though the effect is not prounounced. Payne et al (1968), also presented evidence demonstrating the effect of human maternal malnutrition on the weight of newborn babies. Long term captive programs for marmosets and cercopithecines report a tendency for a shortening of the prereproductive period and decreasing adult body weight in successive generations (Van Wagenen 1972, Hadidian pers. com., and Hiddleston 1976). Apes in captivity have a tendency to become obese however. Kolata (1974) reports for human !Kung nomadic hunter-gatherer females a drop of 30% in the interbirth period and age at menarche when they shift to an agricultural cereal based diet and sedentary existence.
May (1978) reports that the accumulation of body fat to a certain level may act as the trigger for menarche, by

stimulating the production of female hormones and bringing on sexual maturation. There is some controversy as to the nature of this relationship. There is not space here to present the discussion but references are given in May (1978) and Frisch (1978).

Other apparent effects of captivity may be associated with the effects of the imposed captive conditions of social structure, spatial distribution, and often stress, due to manipulation and human contact. In the wild social restrictions on mating are known to delay breeding in adolescent males and probably females long after physiological capacity. In higher primates (Van Lawick Goodall 1969, Koford 1965) captive records for the apes show for both males and females younger successful conception than are quoted in wild studies.

Caging conditions and access to males are reported to affect oestrous cyclicity in Saimiri (Rosenblum, 1972), Lemur (Boskoff pers. com.,1977) and Homo (McClintock, 1971). Hiddleston (1977) reports a tendency in second generation captive marmosets to produce triplets in relatively high numbers, one of the infants is usually lost since it seems the parents can only rear successfully the normal twins.

Maternal and infant behaviour associated with the development of locomotor and feeding activities may be affected by caging conditions and differs from that seen in the wild for two cercopithecine species studied by Rowell (1970) is almost certain, then, that captive conditions of breeding will give different values from the wild condition. At the present time there are insufficient studies to distinguish between captive and wild data in the analyses. The necessity of compiling the data from both captive and wild studies places limitations on the type of questions and conclusions that may be demanded from or provided by the analyses. In general the data can be considered as a reflection of the physiological or energetic potential of the species derived in a variety of situations of which the common feature is the successful reproduction of the species. While statements as to the physiological functions of reproduction may be adequately substantiated, those dealing with demographic effects of reproductive adaptations of species can be only very general. These limitations on the data mean that the author's intentions to extract the general features of the physiological basis of reproductive scaling are in fact necessitated by the present form of the problem. As is discussed in the Methods section there is a further confirmation of necessity of this generalistic approach arising from the features of the statistical analysis.

Features arising from Historical study. In researching the literature on primate reproduction it is immediately apparent that certain genera are extraordinarily well represented and others completely absent. Whilst ecological studies are well scattered through the whole range of species, reproductive studies have tended to concentrate on species which can be easily raised in captivity or closely followed in the wild. It is in fact the exceptions in the primate order which have received most attention. In an order which is primarily adapted to forest living, with a small average size and often specialized diets, it has been generally large bodied, savannah or ground living omnivores that have been best researched. For the genera Macaca and Papio there is detailed information, arising from medical interests, on hormone levels, ovulation, placental function, and even assessments of foetal metabolism.

Some genera are poorly represented though not particularly rare; the Colobine genera with highly specialized leaf-eating diets are extremely difficult to rear in captivity, and in general the South American monkeys in territory inhospitable to field workers are notable.

Genera such as *Allocebus* from Madagascar and *Brachyteles* from South America are extremely rare and this is reflected in the almost complete absence of any study in the literature.

These inconsistencies in the available data will give the analysis a particular bias for which it is difficult to compensate. Rather than reduce the sample size by limiting the representation of genera like *Macaca* the author has decided to include all available information in the analyses to retain their interspecific character, and approach closer in sample size to the finite number of species, which will in any case have a particular distribution (see next section).

Sub-section 3) Parameters employed

Adult body weight. Adult status, determined usually by pelage or dentition, has been given for all sources used. In this study adult female body weight is of principal interest and only data referring to the sex of the individual is taken. Captive animal reports are used only when fitness is confirmed, no obese or emaciated animals are included.

Neonatal body weight. Figures in the literature often do not state sex, and for the purpose of this study male and female weights are combined. All neonatal weights used are from captive births. Still births are not included, and are often below the normal birth weight, but living newborn dying soon after birth due to parental neglect or accident are included.

Full term placental weight and umbilical length. Most primate mothers like most mammals eat all the afterbirth, presumably high in digestible nutrients. Most cases where placental weights have been obtained are in this respect possible abnormal, either as a result of miscarriage or disrupted maternal behaviour. In captivity it seems however, that higher apes frequently leave the afterbirth, without apparent patholcgy, and it is not known whether this occurs in the wild.

Adult and Neonatal brain weight. Adult brain weights come entirely from the literature based principally on Bauchot and Stephan's (1966, 1969) massive survey. However, certain figures quoted in these studies are clearly abnormal, brain weights are taken from those specimens that fall within the range of fit adult body weights. The sexes while combined in Bauchot and Stephan's study have been seperated for this study.

Neonatal brain weights, with the exception of those quoted by Sacher and Stafeldt (1974), are derived from the author's own dissections of zoological specimens Unless very fresh the brain is difficult to remove unpreserved. Most of the quoted data are measurements of formal saline fixed material, as are the author's. Formal saline fixation causes an initial increase in brain weight up to a peak of + 10 - 15% at about one month after fixation. The weight subsequently declines over a further 3 - 5 months stabilising at about - 5% of the fresh weight (Frontera, 1958, author's obs.) Unfortunately most sources do not state the period of fixation prior to weighing. The data used for preserved material, brain weights and ovary and testis weights, suffer from an error within the range + 15 - - 5%. As with neonatal body weight, small sample sizes and probable lack of significant sexual dimorphism in neonatal size generally, have lead to the use of combined data from both sexes for neonatal brain weight.

Age at weaning and first solid food. Weaning of infants is rarely a traumatic event, and usually spans a considerable period between the infant's first experiments with solid food and the birth of the following infant. Data are from both captive and wild observations. Both sources have their particular drawbacks: Captive diets and conditions may affect both maternal and infant behaviour (Rowell 1970, 1972) and reports from the wild are hampered by the difficulty in determining the age of the weaning infant without a long-term, continuous study.

The age at consumption of first solid food is mainly from captive studies. Once again it is a transition from milk diet to completely solid food, and median values of a range are usually given in the literature.

Age at menarche. Most primates exhibit a visually detectable sign of menarche, though it may require careful observation to record. The strepsirhines have either vaginal opening or some small swelling of the genital region. Some of the Old World Monkeys and apes have some genital swelling, the exceptions being among the Colobines and the genus <u>Cercopithecus</u> where menstrual flow may be seen or blood detected in the urine. For the New World Monkeys and those of the other groups for whom detection is difficult, the age of menarche may have to be determined entirely be behavioural observation of oestrus, though recent studies using endocrinological methods may detect hormonal changes associated with incipient sexual maturity (Dixon pers. com. in reference to <u>Aotus</u>). As discussed earlier in the chapter, there is some evidence that captive conditions may lead to a younger age at first oestrus than the natural condition. Data are largely from captive studies, and this effect may reduce age at menarche by 7% in large bodied forms, such as <u>Pan</u> (c.f. Hunt 1976, Keeling and Roberts 1972) and is although a small effect one that is considered in later discussion.

Oestrus is defined by mature female sexual behaviour. Menarche however, marks the first physiological sign of mature female sexual activity. For larger species it appears that first behavioural oestrus may precede 1st menstruation (e.g. <u>Pan</u> Hunt 1975, <u>Macaca</u> Hadidian, pers. com.) by much longer than half the menstrual cycle. In any case early menstrual cycles in young animals are often erratic and may be anovulatory. The period elapsing between first oestrus and first conception for larger species may be due to either a failure to cycle, anovulatory cycles or foetal incompatibility with an immature maternal physiology (see Doring, 1969).

<u>Age at first delivery</u>. Data are from captive animals in most cases. As another point in growth it also appears

to be reduced in captive studies, where high protein diets may have the effect of advancing physiological development. For the few cases where both wild and captive measurements are known (e.g. Teleki 1976 c.f. Bourne 1972, Pan and Koford 1965 c.f. Pickering 1968, Macaca) this difference may be up to 20% in larger species, an effect discussed later (p. 243 et sqq). In small primates, especially strepsirhines, first oestrus often results in successful birth. In the chimpanzee (Pan) however, a period of 1 - 4 years may elapse between menarche and first delivery. This is discussed later (p. 243 et sqq).

Maximum Captive Lifespan. Figures taken are the maximum lifespans in captivity, from the literature and zoo record sources. Average ages of death in the wild are almost impossible to obtain and their use depends on a knowledge of the age structure of the population very rarely obtained. Sacher (1975) has discussed the use of this parameter as being more useful than average wild figures for determining the physiological potential of the organism, see discussion (p. 77 et sqq).

It is most likely that captive diet and conditions alter the physiological potential of life for the organism, but this effect has not been studied.

Gestation period. Figures from the wild are often very unreliable and are usually only given to the nearest month. These are not used. In captivity various methods have been used to determine gestation length:
1) The period from the last observed copulation to birth. This value is often unreliable due to the chance nature of sightings of copulation unless the animals are

under constant observation. For some species mating is reported to occur during pregnancy (e.g. Orang-utan - Coffey 1975, Chimpanzee - Van Lawick Goodall 1969, Macaque - Mahoney 1970). These two factors may lead to both under and overestimation of gestation by this method.

2) The period from last oestrus to birth. If oestrus is known not to continue into pregnancy, this value may be quite accurate. It assumes that ovulation coincides with behavioural oestrus and any associated visual signals (a condition known for the Chimpanzee - Bourne 1972, Crab-eating macaque - Nawar and Hafez 1972, Man - Roberts 1976, and Baboons - Saayman 1972). However, the possibility of intrapregnant oestrus may have led to underestimation in the early studies when hormonal and palpational evidence was not used to confirm evidence as it is nowadays.

3) The period between a single timed mating and birth. This value is the only exact measure of gestation. Usually, however, the requirement in captive breeding for animals to reproduce makes continuous paired or group caging the normal condition. Single timed matings have been recorded for very few species (Gorilla - Martin pers. com., Owl Monkey - Hunter et al in press, Stump-tailed macaque - Trollope and Blurton-Jones 1975, Thick-tailed bushbaby - Valerio and Dalgard 1975).

Most of the recorded data is of the second type. It is also true that food intake may alter gestation experimentally in macaques (Riopelle et al 1975), and that parity of the mother affects the gestation period, again in macaques (Broadhurst and Jinks, 1965). These effects are not great in relation to the differences between species average gestation lengths. They are effects probably occurring in the wild and are impossible to remove from the data.

Interbirth period. All data apply to normal birth spacing with healthily reared infants. Although captivity may well produce altered maternal and infant behaviour either extending or reducing normal wild birth spacing the limited data from both captive and wild studies have been compiled together. Whilst the resulting distribution of values is expected to correlate poorly with other more exactly determined variables the underlying trends in the allometry of this parameter may still be discernable.

Oestrous cycle length. Although data on oestrous cycle length was collected, no analysis is reported in the results section. Some tests were performed on the average mean and modal values to assess the possible lunar periodicity of oestrous cycle length and the possibility that cycle length may be a subunit of the timing of gestation. Whilst most species of primates have oestrous cycles of about 28 days, most have slightly longer cycle lengths and some appear to have cycles considerably less than 28 days (e.g. Squirrel monkey - Rosenblum 1972, Owl monkey - Dixon pers. com.).

No statistical evidence supports the second hypothesis and it was concluded that individual animals must be followed in order to determine the possible relationship between cycle length and gestation period.

Postnatal Growth. Growth curves are available for individuals of about twenty species. Most only cover the period to weaning. For the purpose of this analysis the initial period of growth to weaning is characterized as linear, a characterization also adopted by Case (1978) in his recent study of mammalian growth rate. For smaller bodied species of primate this assumption does not differ greatly from the empirical evidence. In larger bodied species the growth rate declines over the period from birth to weaning, allowance for this feature is made in the analyses. Some of the weights at age of consumption of first solid food, and weaning age are derived in most cases from growth curves, often combining data from different sources.

Foetal Growth. The rate of growth of the foetus has been approximated from timed abortions in some species, (e.g. Rhesus monkeys - Van Wagenen 1972). The curves of growth in weight are well approximated by the cubic growth curve of Huggett and Widdas (1951) which is also demonstrated in a wide range of mammal species (Payne et al 1967a). Whilst empirical data are absent for most species an approximation of foetal growth rate is used in this study following the authors above, and Frazer and Huggett (1974). (See discussion on characterization of foetal growth pp.126 - 131).

Section c) Methods - Statistical technique and approximation of allometry.

On the basis of published studies of interspecific allometry, approximately linear distributions of bivariate plots were expected for previously unresearched parameters, (see p. 22 et sqq) for reference to some earlier studies). The equation of simple allometry was adopted on the strength of its empirical utility (see p. 29 et sqq) and following visual inspection of the bivariate, logarithmic distributions derived from compiled data. This method of discerning underlying allometric trends is well established in the literature as discussed in the first chapter. However, the method usually requires the statistical characterization of an imperfectly correlated distribution of logged values as a straight line (see p. 37 et sqq). As described earlier, the equation of simple allometry, $y = bx^{\alpha}$, has been employed as a powerful generalization of allometric tendencies. The estimations of the descriptive values b and α are determined from the intersection and gradient of this straight line characterization of the relationship between log y and log x.

For this purpose the two statistical techniques of Regression and Correlation have been used in the past for a wide variety of allometric studies. However, statistical methods are devised for data of a particular form, and recent studies have considered this point, (Gould 1966, Sacher 1970, 1976). It is generally agreed that Regression analysis is unsuitable for most studies of allometry. Regression analysis is designed to evaluate the <u>dependency</u> of a dependent variable (Y) on an independent variable (X). Certain assumptions are made of the form of the data for Regression, i.e. that the investigator is determining the <u>effects</u> of <u>changes</u> in X on Y. This normally requires experimental conditions, where the variable X is a controlled and continuous variable throughout the experimental range. Regression analysis can then be used to explain the variation in Y in terms of X.

These conditions for Regression analysis are rarely satisfied in allometric studies, espeically those dealing with interspecific allometry, where neither variable in a bivariate distribution may be considered a 'dependent' variable. In the case of interspecific allometry for example, the data points are not the results of changes in body weight, and there is no indication of the one-way dependency of the other variable on body weight. In such studies it is possible only to consider the interdependence of the variables, both of which will also have sampling errors. The interdependence of the two variables may be due to the effects of a common functional association with higher relationships, and as has already been discussed, no direct functional dependency can be assumed from statistical correlation (see p. 38 et sqq and p. 67 et sqq).

The second method, of Correlation analysis, is properly suited to the general form of most allometric studies, since it allows the estimation of the degree to which two variables vary together (Sokal and Rohlf 1969). Despite necessary selection of Correlation analysis for the form of allometric information there are further problems with the use of the statistical technique, for all types of allometry (see p. 27).

In Correlation analysis, both the measure of covariance and the derivation of the underlying linear character of the bivariate distribution are based on the assumption that the sample comes from a normally distributed population. As explained earlier the Correlation analysis is applied to the logarithms of the two variates in a bivariate study, it is the logarithmic values that are assumed to have normal distributions for each variate.

Since this aspect of statistics in allometric analysis is not often discussed, it may be worthwhile briefly running through the main categories of allometry (p.27). in relation to this issue. In intraspecific allometry where real sizes and functions are approximately normally distributed the logarithmic values will produce a skewed distribution of variates. For Ontogenetic allometry, while it is possible to select a normal distribution of logarithmic values, the distribution of values in a random sample will reflect the age structure of the population, (which will be further distorted in logarithmic form). In Phylogenetic allometry where individual data points usually represent adults from different evolutionary periods, any logarithmically normal distribution in the available data from fossil material would be purely accidental, and highly unlikely.

In this study of Interspecific allometry each point in any bivariate distribution represents the logarithm of a mean value for each species. Sample sizes vary between each point and each distribution is different due to the varying availability of data for each species for every parameter. Even if all species provided information to the analysis, it could not be expected that, in the case of the Primates, 70 million years of divergent evolution from a common ancestor would produce a logarithmically normal distribution of species average sizes or reproductive parameters. There are in fact some theoretical and empirical reasons for supposing a distribution of average species sizes following a pattern of distribution about sizes differing by factors of 2 within every Order (see Lovtrup, Rahemtulla and Hoglund, 1974). In the authors opinion this tendency in evolution is not yet adequately demonstrated, and no special account is made of this theory in this study.

As Figures 1, 2, and 3 (pp114 -7) demonstrate the distributions of the logarithms of mean female body weights for 103 of the 182 extant species of primate, are not normal either considered together or in the two major groups, haplorhines and strepsirhines. The distribution of real body weights is even further from a normal distribution, where for all primates in a range for adult female body weights from 60 - 60,000 grammes, the majority of values fall below 8,000 grammes.

Since most of the reproductive parameters studied here are well correlated with body weight it may be assumed that the non normal distribution in adult female body weights is reflected in the other parameters. In its proper sense, Correlation analysis is thus impossible for this study and many others like it. Nevertheless the technique will give more appropriate values for the linear characterization of the logarithmic distribution than Regression analysis for the reasons given above (p 111), associated with the general form of the data. There has been some confusion in the literature over the application of statistical techniques in studies of allometry. Many major works have employed Regression analysis to determine the values in the hypothesized relationship of simple allometry, $y = bx^{\alpha}$ (e.g. Stahl 1965, Kleiber 1947 and Leutenegger 1973). When the covariance between variables is relatively high, the discrepancy between the approximated values of α and b calculated by Regression and Correlation analyses respectively is not great. However as covariance between variates becomes poorer, the discrepancies increase. This can be seen from the values obtained from Regression analysis given, for comparison only, for the correlations in this study.

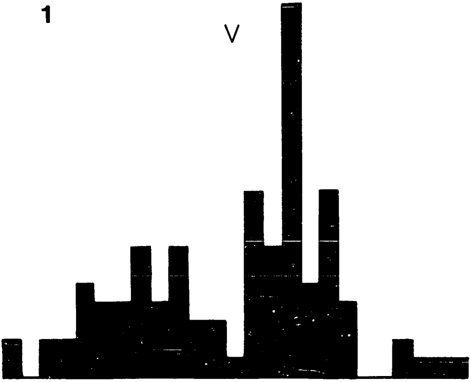
Figures 1, 2 and 3

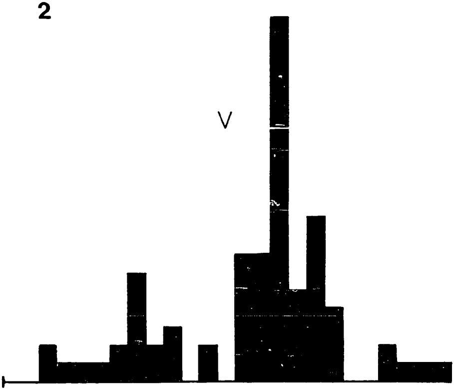
Distributions of logarithms of average adult female body weight for:

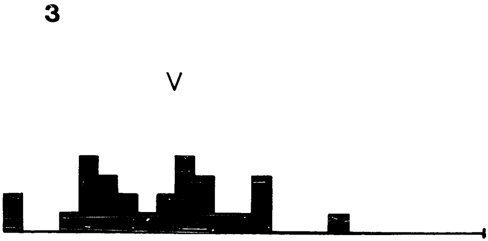
1) Known values for Primates N = 103
   (real range: ~60 - 70,000 grms)
2) Known values for Haplorhine species N = 76
   (real range: ~100- 70,000 grms)
3) Known values for Strepsirhine species N = 27
   (real range: ~60 - 12,500 grms)

V indicates median

(Total extant species of Primate = 182)


1
V


2
V


3
V

Those authors who have attempted to avoid the general inapplicability of Regression analysis in favour of Correlation analysis, have not discussed the problems associated with the usual non-normal distributions of their logarithmic data. All confidence limiting, and linear characterizations are affected by this usual feature of the natural data employed for allometric study. The mathematical procedures for confidence limits and approximation of linear character may, of course, be carried out on the data. However, the values obtained serve only as mathematical indices with qualities determined by the particular nature of the data, and are not properly associated with the statistical definitions normally applied to them. This problem in applying statistical tests to the allometric distribution is usually further enhanced by the heterogenous sources for the data and the usually wide range of sample sized for any particular value. Rather than hold back research into the subject on the basis of 'inadequacies' in the data it is more profitable to proceed in the knowledge that the statistical techniques can, at present, give only general indications of the relationships under examination.

Despite these issues, which are important to clarify, the author has based his interpretations of the interspecific allometric relationships on the values obtained by the Principal Axis (P.A.) of Correlation, supported by consideration of a technique devised by Kermack and Haldane (1950) for conditions where Regression analysis is unsuitable, giving the Reduced Major Axis (R. M. A.) The Principal Axis is derived from Correlation analysis, and is the long axis of the elipsoid bivariate distribution of assumed normal distributions of variables, (not obtained in this study as described above). The Reduced Major Axis is derived from a technique more similar to Regression analysis. The important difference is that unlike Regression analysis, the R. M. A. is based on the assumption of equivalent variance in both variates. The R. M. A. is obtained through the minimization of the perpendicular deviations of points from the characteristic linear relationship, (Regression analysis minimizes the deviations in the Y axis only).

In view of the preliminary nature of this study (p 21) and the difficulties in the application of relatively simple statistical techniques to the particular form of the data used in the study of interspecific allometry, interpretation is based on the Principal Axis. From the results given in this study it may be seen that where the correlation coefficient, r, is high, the Principal Axis and Reduced Major Axis do not differ greatly. Both these axes pass through the point in the distribution marked by the mean of values in the x and y variates.

For the purpose of this study the calculations of these values follows Sokal and Rolhf (1969). Values for the Principal Axis, Reduced Major Axis, and Regression coefficients, 95% confidence limits for the gradient of the Principal Axis, and the correlation coefficient r, and the proportion of variance in one variable explained by variance in the other r^2, are presented for most bivariate analyses. As mentioned earlier these values are, strictly speaking, of use as indices applicable only to each particular analysis, (p. 118). In general, where r^2 is above .5, the indices are considered as meaningful abstractions from the data, (see

Clutton-Brock and Harvey, 1977). However, due to the problems associated with the statistical testing of the method no assertions made by the author are considered as final or unalterable.

For the purposes of this study, this introduction is considered sufficient, though the discussion of statistical techniques is continued in the discussion Chapter (7). As mentioned earlier (p 22) multivariate analysis is not attempted in this study, at this point a practical reason for the absence of such analysis may be given. Multivariate analysis properly requires data for each species for every parameter. In this study the heterogeneity of the data would produce a low sample size (~25), even for the basic parameters of adult and neonatal brain weight, gestation period, and adult and neonatal body weight, for example.

One further point concerning methods of analysis is associated with the need to use variables compatible with the line of enquiry. A simple example will suffice as explanation; if the growth of the individual is under discussion, we may be properly interested in the weight of the single infant at birth. On the other hand if the stress on the mother at the end of pregnancy is being considered, total full term litter weight will be of more interest and use. For certain analyses special indices are calculated from the source data for specific purposes, for example the value a_w, the specific foetal growth rate, which is employed in Chapter 4.

Summary of Chapter 3

The materials and methods employed in the study are considered. Material and data were collected from a wide range of sources including zoos, museums, personal communications and most importantly, the literature. Whilst the Primates are well studied despite long development and often difficulties in maintenance in captivity, the wide variety of sources for the data present problems for an intensive study on the group. The student is constrained to consider only general features of comparative analysis, of size, developmental stage, and age. This approach is further necessitated by the statistical methods available for approximating to the underlying allometric tendencies of any parameter. Of the two methods of analysis, Regression and Correlation, the latter is properly used here (Sokal et al 1969), since covariance, and not dependency of the variates is being examined. However, Correlation analysis assumes a bivariate normal distribution of the population from which the sample is taken. This is not the case for logarithmic transformations of real average female primate body weights. It is thus necessary to state clearly that the values for major axes of the distributions given, and the coefficients of correlation are not properly derived, and may not in the strict statistical view be compared between analyses. This limitation must be acknowledged and interpretation of results not based exclusively on statistical comparisons.

Explanatory note to Figures

The reader is referred to this note for all Figures with statistical information. All data presented follows a similar layout. First comes a definition of the abbreviations for X and Y axes. All Figures with statistical calculations are presented in natural logarithm form. The statistical information is presented as follows:

1) Taxonomic group for inclusion of data; e.g. <u>Haplorhines</u>.
2) Sample size, i.e. no. of species in data set. e.g. N = 13
3) Arithmetic mean of variates, i.e. the natural logarithm of the real average values for both parameters e.g. $\bar{x} = 7.30$, $\bar{y} = 3.46$
4) Principal Axis gradient, with 95% confidence limits e.g. P.A. = 0.34 (0.28, 0.40).
5) Reduced Major Axis gradient e.g. R.M.A. = 0.35
6) Regression coefficient, i.e. minimized deviations in Y-Axis only e.g. (Linear) Regression = 0.32
7) Calculated statistical values of correlation coefficient, r, and r^2 - the fraction of variance in one variate attributable to variance in the other e.g. $r = .97$, $r^2 = .94$

Note that both axes P.A. and R.M.A., and regression line pass through $\bar{x}$, $\bar{y}$. Discussion of these estimates may be found in Chapter 3.

Points with horizontal bar in Figure are not included in statistics.

Note on results chapters.

As has been discussed earlier, particularly in reference to Kleiber's (1969) analysis of metabolic rate and heat flow (pp. 67 et sqq), the examination of the processes underlying allometric correlation is the most fruitful and proper method of analysis. The following three chapters deal with interspecific allometries associated in turn with foetal growth, postnatal growth, and population dynamics. In an attempt to examine some of the processes which underly the correlations studied, the three chapters include discussion of theoretical aspects of the respective subjects. These discussions precede the main part of the results in each chapter. The Introduction to the following chapter serves as a theoretical evaluation of the problem of examining the process of both foetal and postnatal growth in interspecific comparison, and draws on the perspective of chapter 2.

CHAPTER 4 - FOETAL GROWTH

Section a) Introduction

Chapters 4 & 5 are concerned primarily with the growth of the individual. With the exception of the data on early postnatal growth rates, none of the available data describes the course of growth. Rather, they give points in the growth process, points of major qualitative transformation in the form of growth. For example, the weight of the growing infant at birth gives its size at a critical turning point in its mode of existence. Particularly important are the changes from an umbilical source of oxygen and readily available nutrients to lung breathing and alimentary digestion. Thermal conditions also suddenly alter, and the neonate experiences movement in a gaseous medium. These changes are especially important for consideration of energy flow, and are discussed in detail later (p. 150 et sqq). For the moment however, it is simply worth noting that despite the fixed, categorical, nature of the data used in this study, the process of growth and development underlies the values obtained.

To exploit these data fully, it is necessary to examine the nature of growth in mammalian species. Two fundamental points may be made, relating to both 1), the course of development and 2), the form of growth at any period.

1) The individuals development from conception to death involves a transition from complete energetic dependency on the preceding generation to eventual energetic sacrifice to the following generation. This development is not a gradual continuous process, but is marked

distinct and often, as in the case of birth, sudden changes in the mode of individual existence. These changes can be considered as the result of a crisis in the development of the individual in the preceding form of growth. For example, the crisis in development immediately prior to birth, perhaps in nutrient or oxygen supply to the foetus, is resolved by the expulsion of the foetus and continued development under a new form of nutritional and respiratory relations. This new form of relations may be expected to alter the rate and type of development, the growing offspring is in any case moving away from its dependency on the mother.

The periods between these major developmental crises may appear more or less stable in form. At a lower level the process of growth and senescence continues within these stable forms. For example, within the gestational form, the embryo grows from a fertilized egg, the neural crest is formed, the foetal heart starts to beat and the locomotor system develops. For the mammal, the intrauterine period is necessary for these developments, a major transformation occurs at birth when continued development is impossible within the uterus.

2) The second point is that the growth of the individual cannot properly be considered in isolation, or as a closed system (see p. 67 et sqq). The individual does not grow in a vacuum, and both the stable periods and also the sudden changes in the form of growth are only properly considered as interaction of the individual with its 'environment' (for much of growth the mother is a major part of the individual's 'environment') Taking again the example of birth; not only does the infant experience a change from umbilical supply of

metabolites to alimentary digestion and lung breathing, but also the mother no longer supplies oxygen to the infant but must necessarily then supply nutrients in the form of milk, rather than by diffusion through the placenta. In the period of offspring nutritional dependency from conception to weaning we may consider that the pregnant or lactating female has a certain quantity and quality of resources available to her. These are distributed between the offspring and the mother. This relationship between the offspring and mother is one that unites the two, whilst they are simultaneously in conflict over the distribution of resources. This conflict may be covert in time of surplus food but will be more apparent when resources are scarce. In this sense the demands of the foetal metabolism are also the sacrifices of the adult female metabolism. It is implied that the form of growth and its theoretical description must take into account the interaction of the individual with its environment.

Growth Theory. So as to exploit the limited nature of the data, and to demonstrate interspecific allometries associated with growth, it is useful to characterize the quantitative pattern of mammalian growth. It is then possible to integrate the interspecific comparison of points of transformation of growth with the description of the common pattern of mammalian growth. This permits an examination of the nature of the crises in development but also the course of this development as it is revealed in interspecific comparison.

Much research effort has been expended on providing a 'model' of growth. Such a major topic may only be touched upon here, but it is necessary to draw on some theoretical studies to determine a useful and practical approximation to the pattern of mammalian growth. The most significant aspect of growth 'models' described in the literature is their tendency to be one-sided in their theoretical formulation. That is, they treat the increase of body size as determined either by the self-regulation of the individual (in an implied but unstated perfectly 'fertile' environment for uterine, infant or adolescent growth), or by the external (usually nutritional) constraints on what must in opposition be considered a growing individual of infinite potential growth.

Of the first type of growth model the most advanced and empirically tested is that of Laird et al (1965) based on early work by Wright, and Weinbach (1941) amongst others. This model is based on the concept that, 'the growth trajectory of the embryo and the young postnatal organism....(is) dominated by a single process, whose regulatory constants are preprogrammed,.... (Laird et al, 1965) and elsewhere in the same paper that their model regards the growth changes 'to be explained ultimately in terms of the dynamics of cell proliferation'. (see p. 129 et sqq for further discussion).

The general form of the model is a Gompertz equation, based on a mathematical function derived for economists in the early nineteenth century. The theory proposes that, with adaptive variation and sampling error, the specific growth rate decays exponentially with time. The overall form of growth is characterized as

$$W\ (t) = W_o^{\left\{\frac{A}{\alpha} - \frac{A}{\alpha}^{(-\alpha t)}\right\}}$$

where W (t) is the mass of an organism or its part at time t, W_o is the initial mass, and A and α are constants. A is a constant related to the initial specific growth rate and α a constant related to the rate of decay of this specific growth rate.

Laird et al (1965, 1966) claim good experimental fitting of this formula in the growth of many species of mammals and birds. However, they are forced to admit inconsistencies in the application of the formula, especially about the time of birth when growth rates may abruptly change, either increasing or decreasing (see Chapter 5, and p. 150 et sqq).

For the primates and especially for man Laird claims a further exception to Gompertz growth. This takes the form of a period of interruption in the decay of the specific growth rate at approximately the time of onset of sexual maturity. A period of linear growth in weight follows before the continuation of Gompertz growth to the adult weight assymptole. Nelson and Cooper (1975) discuss these inconsistencies in the model from the aspect of empirical evidence. They point out that the Gompertz model is acceptable only if the onset of growth is mathematically adjusted to 'start' at various times later than conception in most species, or even before conception for some species including man, with a 'start' of growth 4 days <u>before</u> conception.

There is not the required data to test adequately any growth model for primates, but data available for five haplorhine species varying in size from the marmoset to the gorilla, shows that the non-primate Gompertz growth model consistently underestimates the attained adult weight (this study). This may be accounted for by the assumption of a pubertal linear growth interruption for haplorhine species, if not all primates. However, these are further 'exceptions' to mammalian growth in Laird's conception.

One further point in relation to the assertion that 'the dynamics of cell proliferation' underlie the changes in growth is discussed by Sacher and Staffeldt (1974). They argue that the found values of in vitro cell proliferation do not account for the wide range in foetal and postnatal growth rates found in living organisms. They suggest that in the case of foetal growth, foetal growth rate is limited by the rate of growth of the brain, (this hypothesis is examined later p. et sqq).

Theoretically however, despite the apparent heuristic attraction of this model, exceptions are to be expected. The model can only account for the changes in the external relations of the growing individual as determined by the operation of forces on the internally 'preprogrammed' expected course of growth. This undynamic, one-sided concept of growth is shared by other models, notably those of Weiss and Kavanau (1957) where growth is understood to be determined by an individuals feed-back regulation of cell proliferation and by the individuals surplus metabolites in the balance between anabolism and catabolism respectively. However the complexity of the heuristic device obtained and the failure to account for the interaction of the individual with its environment render this characterization of growth unhelpful, (see also p. 186 et sqq).

The second main approach considers the external conditions of the growing individual. Thus, the changes in the external conditions of the growing individual in development are seen to divide up the course of growth into distinct phases, and growth theory devised to cover only part of the development of the individual. The foetal period is perhaps best described in this fashion since, in comparison to the adult, mature state, the foetal individual is poorly organized and dominated, osmotically, thermally and nutritionally by its immediate environment, in the uterus. It is in fact for foetal growth that external dependencies are invoked by Huggett and Widdas (1951) and Payne et al (1967a, b). In their view the foetus grows at a rate determined by the rate at which metabolites pass through the vascular surface of the foetus and the surface of the placenta. This hypothesis is supported by empirical evidence from a wide range of mammalian and avian species with a wide range in average adult body size.

Though derived initially from empirical observation there is a sound theoretical basis for what they call the 'cubic law' of foetal growth. The hypothesis is that the rate of increase in foetal weight is determined by the rate at which nutrients pass through the foetal vascular surface or placental surface.

Thus, $\frac{dW}{dt} \propto W^{2/3}$

where weight of the foetus is W and t time since start of growth. The assumption is that all foeti are the same shape, i.e. that the actual surface area of any foetus is isometric with Weight , (c.f. MacMahon 1973)

Integration of this function yields the proportionality between the cube root of attained weight and time since the onset of cubic growth

$$W^{1/3} \propto t.$$

Both groups of authors report and confirm that for a number of species without delayed implantation that cubic growth does not commence until about $1/5$ of total gestation has elapsed (see McDowell and Allen 1927). The generally accepted form of the equation requires a further constant, a_w - the specific foetal growth rate, so that $W^{1/3} = a_w(t-t')$ where t = time since conception, t' = 'lag phase' ($\simeq 1/5\,tg$ where tg = total gestation period). (This is the form used by Huggett et al 1951; Payne et al 1967a use the form, $W = a(t - t')^3$ expressing the same cubic relationship but the constant $\underline{a}$ does not have the same dimension or value as $\underline{a_w}$).

The value a_w is dimensionally equivalent to the rate of weight increase per unit surface area. Payne et al (1967a) have called this 'the rate of supply of nutrients per unit of surface area' however it should be remembered that besides the process of accumulation of organized matter in the somatic tissue of the foetus, there is a constant exchange of matter through the vascular walls and across the placenta, associated with metabolic maintenance.

For the purpose of this chapter the author has chosen to employ the second characterization following Sacher et al (1974). Of the two approaches the second is most clearly along the line of Thompson (1917) as discussed in Chapter 2 (p 60 et sqq) whilst the former is closer to 'vitalism' in its formulation. In the author's opinion neither of the two main formulations of growth rate may be considered as good approximations, though that of Huggett et al has a more materialistic theoretical basis, and has testable theoretical assumptions rather than an inaccessible 'preprogramme'.

Section b) Foetal Growth; interspecific comparison.

It was assumed by Huggett et al (1951) that the variation in the value of a_w between species was associated with taxonomic affinity only, and that, for any order of mammals an average value of a_w would characterize the rate of foetal growth. However, Sacher and Staffeldt (1974), demonstrated that between related species there is no linear proportionality between the cube root of birth weight and total gestation period. Only if this were the case would a_w be constant for a given order. The value a_w is estimated from the formula

$$a_w = \frac{5Wb^{1/3}}{4tg}$$

where Wb = weight at birth and tg = total gestation period (following authors cited above, t', the lag phase is assumed to be $\frac{1}{5}$tg for all species). The value a_w is dimensionally a rate of flow of mass per unit surface area. The surface in question is taken to be that of either or both the vascular surface of foetal tissue and placental surface.

Whilst, in general, the primates have the lowest known values of a_w , within the order there is variation in a_w . In this study the relationship is examined as that between a_w and litter weight at birth. (This formulation demonstrates simultaneous consequences of the scaling in gestation and litter weight at birth as they relate to the <u>process</u> or course of growth characterized by the cubic curve a common pattern for Mammalia). The results are given in Figure 4 (pp134 - 5). As can be seen, the haplorhine species show a fairly clear body size dependence, this is not evident for strepsirhine species. The author believes this difference between the groups to be associated with the differences in metabolic rate and ecology described earlier, (see Chapter 7). The body weight dependency of a_w, for haplorhine primates at least, explains the apparently contradictory findings of Kihlstrom (1972), and Leutenegger (1976), and Leitch et al (1959) described earlier (pp et sqq). These may be written:

Gestation Period $\propto$ (Maternal Body Weight)$^{.17}$

- Kihlstrom, average value of regression for separate mammal orders,

Litter Weight $\propto$ (Maternal Body Weight)$^{.67}$

- Leutenegger, regression value for Order Primates,

Litter Weight $\propto$ (Maternal Body Weight)$^{.83}$

- Leitch et al., regression value for Mammalia.

On Huggett et al's (1951) assumption that a_w is constant within orders, we would expect gestation period to scale to a power of maternal weight lying between

.67/3 and .83/3 , (.22 and .28)

Both extremes of the expected range are above Kihlstroms value (above). This discrepancy, noted by Sacher et al (1974) is apparently accounted for by the interspecific allometry of a_w. Whilst within the primates the strepsirhine species show no significant allometry, the common trend in most mammalian orders is of allometry of a_w (readers may satisfy themselves of this by consulting Frazer et al, 1974). In this

Figure 4

X-Axis, ln:Nbl:g Natural logarithm of litter weight at birth in grams.

Y-Axis, ln:a_w Natural logarithm of specific foetal growth rate (after Huggett and Widdas, 1951).

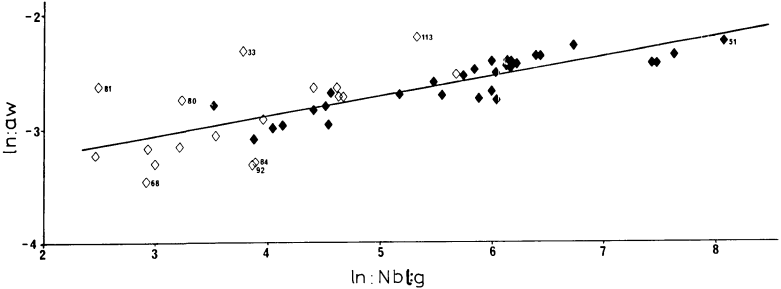
All Primates: N = 49 : $\bar{x}$ = 5.05, $\bar{y}$ = -2.69
P.A. = 0.18 (0.14, 0.22)
R.M.A. = 0.20, (Linear) Regression = 0.18
r = .79, r^2 = .62

Haplorhines: N = 31: $\bar{x}$ = 5.77, $\bar{y}$ = -2.57
P.A. = 0.18 (0.14, 0.21)
R.M.A. = 0.20, (Linear) Regression = 0.18
r = .87, r^2 = .76

Strepsirhines: N = 18: $\bar{x}$ = 3.82, $\bar{y}$ = -2.88
P.A. = 0.28 (0.12,0.44)
R.M.A. = 0.40, (Linear) Regression =0.25
r = .62, r^2 = .39

Solid line: P.A. (Haplorhines)

First presented in this form in this study, with new data, (see also Sacher et al. 1974, Frazer et al 1974).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respect the haplorhine species demonstrate the more common pattern for this relationship, unlike the strepsirhine species. Further discussion of this tendency refers to haplorhine primates, and by extension, to other mammalian orders.

Scaling of a_w : some implications. Large bodied species have, in general, higher rates of mass flow per unit surface area of either the placenta or vascular tissue or both. Two allometries might be expected from this relationship, either in the velocity of mass flow or in some subdivision or corrugation of the Archimedean surface ($\propto$Foetal weight$^{2/3}$). For the purpose of the following argument, the Archimedean surface; proportional to the two-thirds power of Foetal weight will be referred to as the 'gross' surface area, whilst the real surface area including corrugations and folds will be referred to as the 'minute' surface.

An allometry in the velocity of mass flow (per unit minute surface) implies an allometry of chemical diffusion rates and active transport rates between species. However, an allometry in the ratio of minute/gross surface areas implies only structural folding of the surface, a tendency commonly detected in the structure and function of many living systems (Gould, 1966). The latter tendency is thus expected to account for allometry in a_w.

To return briefly to the assertion made earlier that the surfaces involved are considered to be those of the placenta and foetal vascular tissue. It is necessary to check that some interspecific allometry between the two is not involved in the scaling of a_w. The results of this test are given in Figure 5 (pp137 - 8), and

Figure 5

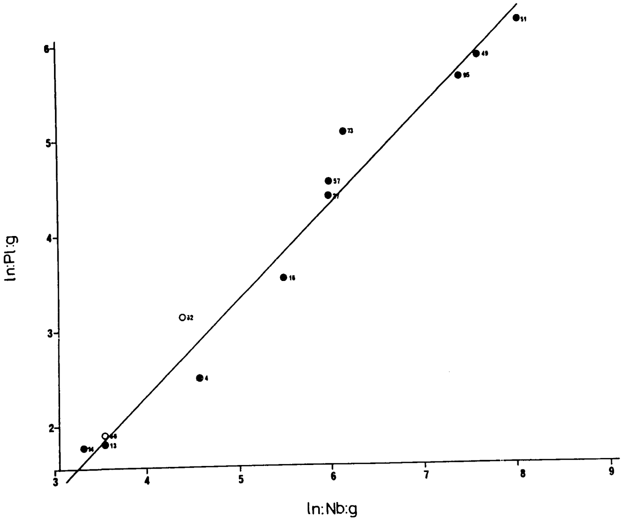
X-Axis, ln:Nb:g Natural logarithm of single neonatal weight.

Y-Axis, ln:Pl:g, Natural logarithm of single, full-term placental weight.

Haplorhines: N=10, $\bar{x}$ = 5.67, $\bar{y}$ = 3.95
P.A. = 1.01 (0.92, 1.11)
R.M.A. = 1.01, (Linear) Regression = 1.00
r = .99, r^2 = .98

Solid line: P.A. (Haplorhines)

This study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in fact full term placental weight and neonatal weight are in interspecific isometry. This relationship does not rule out some size-dependent features of gross placental shape, but further work will be required to determine such effects.

So far as the earlier argument above is concerned, we may expect that corrugation of placental surface suggests a similar corrugation of foetal vascular surface.

It had earlier been expected that any corrugation of surfaces related to the allometry of a_w would involve the ratio of gross to minute surfaces of the placental villi (Rudder 1977). This conjecture had been proposed on the basis of a visual inspection of a series of sectioned strepsirhine epitheliochorial placenta, as compared with the specific estimates of a_w. However, this assessment must be reconsidered in the light of findings by Ludwig and Baur (1971), obtained from study of the haemochorial placenta of five haplorhine species. Ludwig et al reveal that the ratio of gross to minute surface of villi is actually higher in larger species. That is to say that larger species of haplorhine tend to have a less corrugated villous surface of the placenta than smaller species, exactly opposite to the tendency expected from the allometry of a_w. However, Ludwig et al also calculated the surface area of the capillaries in the placenta and found that in this case the placental capillaries present relatively more surface in larger species. The two relationships, based on calculations from Ludwig et al's admittedly limited sample, may be written in terms of the ratio of real or minute surface of the term placenta to neonatal body weight in interspecific allometry;

Minute Villous Surface $\propto$ (Neonatal Weight)$^{.3}$
- Expected 'gross', Archimedean, exponent,

and

Minute capillary surface $\propto$ (Neonatal Weight)$^{.85}$
- Expected 'gross', Archimedean, exponent, $^{2}/_{3}$

It is thus interesting to note that in the latter relationship the discrepancy between the expected and the found relationship is a factor of (Neonatal Weight)$^{.19}$ very similar to the scaling of a_w interspecifically.

For haplorhine species then, the assumption must be that the allometry of a_w, (a rate of mass flow per unit surface area), is associated with the density of placental capillaries, rather than villi. As for strepsirhine species, either the earlier assessment (Rudder 1977) is incorrect, or villi are in fact more densely arranged in larger species suggesting a differing role of placenta villi in the strepsirhine (epitheliochorial) placenta and the haplorhine (haemochorial) placenta (see pp 52 et sqq).

Whilst this feature of foetal growth is of interest in its own right, the processes that regulate the rate of growth still remain unclear. We are already familiar with some arguments dealing with the relationship between metabolic rate, body size and surface area in mammalian species, (pp. 37 et sqq). These lead to the conclusion that the hypothesis of a mechanical determination of metabolic rate by the rate of heat flow across body surface is unsound. On the contrary, it seems rather that surface features of insulation, thickness, and corrugation are adapted to a 'higher' criterion as suggested by Kleiber (1969), possibly some optimum condition for efficient mechanical work. It is in this sense that the author believes that the surface features of the placenta that 'account' for the scaling of a_w are not mechanistically determinant of the value of a_w. Rather, they reflect some underlying relationship, possibly once again associated with optimum conditions for efficient mechanical work, in the interaction and exchange between maternal and foetal tissues.

Before proceeding to the next topic (on Birth p150 et sqq) an hypothesis of Sacher et al must be dealt with since it represents a development in our knowledge of the type of factor that is associated with foetal growth rate, namely the rate of growth of foetal brain tissue. However, as we shall see such considerations still do not clarify the nature of the relationships which regulate the process of growth.

Foetal brain growth: a_w brain. Sacher et al (1974) proposed that the rate of growth of the foetal body is limited by the rate of growth of the foetal brain. This conclusion was based on the results of a multiple regression analysis of 91 mammalian species revealing that gestation period is best correlated with neonatal brain weight (as compared with neonatal body weight, maternal body weight and brain weight). In this cross-mammal analysis they found that gestation period varies as the .334 power of neonatal brain weight. They suggest that this may be due to a fundamental law of mammalian foetal brain growth, limited, possibly, by a constant rate of linear elongation of axons and dendrites in the foetal brain. This, in Sacher et al's view, is in agreement with the found relationship of their analysis, that the size of the neonatal brain is proportional with the cube of gestation (for an all mammal, interspecific analysis).

As will be demonstrated, (see below) this relationship does not hold within the primates when they are considered as a separate group from others mammals as in this study. This presents a theoretical problem familiar in the study of allometry, that of differing levels and gradients with variation in the level of taxonomic group considered (see p. 29 et sqq). This analytical problem is associated with the difficulties described earlier (p. 31 et sqq) of detecting the nature of the processes which underlie the allometries found.

Thus, there are differences in the interspecific allometry between neonatal brain weight and gestation period when considered for primates as compared with all mammals. The latter of which is the basis for a hypothesis law of foetal brain growth.

The proposed interspecific relationship between the cube root of neonatal brain weight and gestation period is analogous to the proposal of Huggett et al. (1951) that there is an interspecific relationship between the cube root of neonatal body weight and gestation period, i.e. that a_w is constant within orders (see p. 137 et sqq). Whilst Huggett et al (1951) had suggested that foetal growth rate was determined by the surface area of the foetal body, Sacher et al hypothesized that foetal body growth is determined by the rate of foetal brain growth, a direct consequence of a constant mammalian rate of foetal dendrite and axon elongation.

The form of the two processes in individual growth are the same however, relating the cube root of weight, (foetal body and foetal brain respectively), to gestation period, or rather a fraction of gestation. Thus whilst the body growth equation is

$$W^{1/3} = a_w (t - t') \qquad \text{(see p.132),}$$

the brain growth equation is

$$W^{1/3} = k \ (t - t') \qquad \text{(after Sacher et al 1974)}$$

the constant k in this equation is referred to here as 'a_w brain' due to its analogous relation to a_w described earlier.

The distribution of primate values of a_w brain in relation to neonatal brain size is given in Figures 6 & 7, (pp144 - 5 ,146 - 7). Figure 6 gives the primate values of the cube root of neonatal brain weight against gestation period, the radiating lines from the origin are values of constant 'a_w brain', (this presentation follows Sacher et al 1974, with additional data). The interspecific allometry of 'a_w brain' is presented more conventionally in Figure 7.

It can be seen that the distribution of primate values is similar in form to that of a_w presented earlier (Figure 4, pp134 - 5). (This result is closely associated with an interspecific isometry between neonatal brain and body weight for all primates to be discussed in its proper context later, p. 170 et sqq). As is the case for a_w (body) the strepsirhine values are poorly correlated whilst haplorhine values show a clear interspecific allometry of a similar magnitude to that of a_w. This result, a least for haplorhine species, necessitates some reconsideration of Sacher et al's hypothesis. In their terms the allometry of a_w brain suggests that the foetal brains of larger species of haplorhines have faster rates of axon and dendrite elongation (By analogy with a_w (body) it may also imply

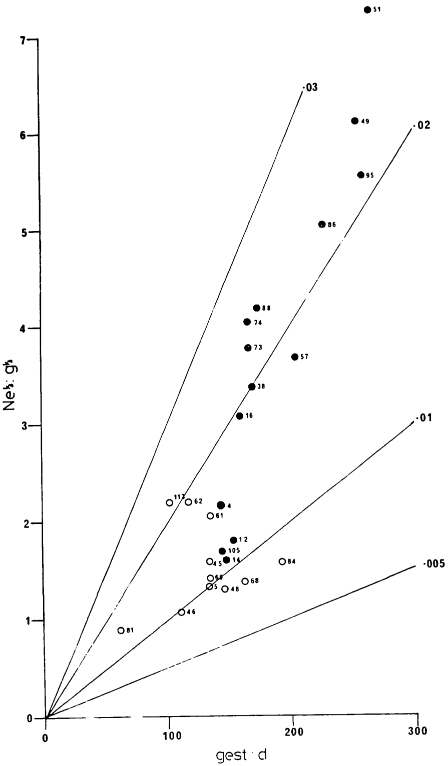
Figure 6

X-Axis, $Ne^{1/3}:g^{1/3}$. Cube root of neonatal brain weight (in grams)

Y-Axis, gest:d. Real gestation period in days.

Figure displays range of primate values for a_w brain, constant along line radiating from origin. Those species with shorter gestation periods (generally with smaller adult body size, Hunter et al, in press) have lower values for a_w brain. See text p 143 et sqq

Following Sacher et al. 1974 with additional data.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81

Figure 7

X-Axis:ln:Ne:g. Natural logarithm of single neonatal brain weight in grams.

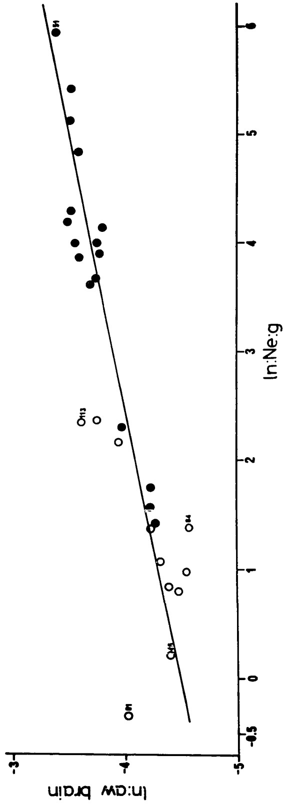
Y-Axis:ln:a_w brain. Natural logarithm of single specific foetal brain growth rate.

All Primates N = 28, $\bar{x}$ = 2.76, $\bar{y}$ = -3.92
P.A. = 0.19 (0.15, 0.24)
R.M.A. = 0.22, (Linear) Regression = 0.19
r = .85, r^2 = .72

Haplorhines N = 17, $\bar{x}$ = 3.76, $\bar{y}$ = -3.75
P.A. = 0.20, (0.16, 0.23)
R.M.A. = 0.21, (Linear) Regression = 0.19
r = .92, r^2 = .85

Strepsirhines N = 11, $\bar{x}$ = 1.21, $\bar{y}$ = -4.21
P.A. = 0.23 (0.03, 0.45)
R.M.A. = 0.38, (Linear) Regression = 0.21
r = .55, r^2 = .31

Solid line· P.A. (Haplorhines)
This study (c.f. Sacher et al, 1974)


ln:gw brain
-3
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the greater rate of flow of neural material per unit 'gross' surface area of the foetal brain of larger species.) It should be pointed out that the results presented here do not contradict the results of Sacher et al but do contradict the determinist hypothesis that they have deduced from their results. Whilst it is clear from Sacher et als evidence that the foetal brain is of great significance during intra uterine growth, we are once again forced to question if not reject an hypothesis of mechanistic determinism compatible with only one form of data presentation (that of an all mammal interspecific comparison). The issue of foetal brain growth will be returned to later (p 169 et sqq, p 178 et sqq, p 181 et sqq) for the moment however it is sufficient to re-assert the comment made earlier that Sacher's hypothesis does not clarify the process of growth.

In the author's opinion the regulatory relationships governing foetal growth rate may require a more direct analytical method than this interpolative approach. In particular, in vivo studies of foetal nutrient uptake, and metabolic rate during the course of growth are essential. Furthermore, data from a range of species for which the entropic and energetic parameters may be estimated, following Sacher (1976, see p. 79 et sqq) would allow both interspecific and intraspecific effects to be examined in great detail.

Before leaving the topic of the course of foetal growth it may be instructive to reconsider the theoretical formulations that, for want of the re-examination of earlier studies, have been employed in this section.

The theoretical formulations of both Huggett et al (1951) and Payne et al (1967a, 1968) are based on the assumption that a_w is a measure of 'the rate of nutrient uptake per unit surface area of placental and vascular tissue.' However difficult it may appear to incorporate theoretically, it must be remembered that both the foetal vascular and the placental surfaces are properly considered as surfaces of exchange of matter, energy and information (see p 83 et sqq). Since a_w is a measure of mass increase it refers most directly to the exchange of matter. The interspecific allometry of both a_w and a_w brain implies, in general, a greater intensity of mass accumulation on the foetal side of these exchange surfaces in larger bodied species. We might speculate that in some sense larger bodied species are better at incorporating organized matter into foetal tissue (be it somatic or brain tissue). It is to be hoped that this more dynamic conception may allow a more fruitful analysis of this subject in the future.

Another line of study suggested by this latter description of foetal growth might involve analysis of the waste products generated by the foetus and the rate of their production. Clearly, the excretion of the foetus may be expected to be of great significance to foetal growth rate.

This section has dealt with the course of foetal growth, inseperable from the rate of growth, i.e. incorporating gestation period. This is properly distinguished from the next section, dealing with the 'moment' of birth, as we shall see this moment seems to be best described without direct reference to the rate of the preceeding growth. It is, rather, as if birth is 'triggered' by some crisis in the relationship between the mother and the foetus, more closely associated with the ratio of their respective weights, than with the overall rate of foetal growth.

Section c) Birth.

Throughout pregnancy and particularly in the period immediately preceding birth, the complete dependency of foetal material on maternal nutrient supply may be considered as serving two major functions. Firstly, the maintenance of foetal tissue already established, and secondly, the anabolic building up of new tissue. The total energetic 'cost' to the mammalian mother is of course greater than the supply of oxidizable nutrients. Other energy costs of pregnancy might include, the supply of oxygen to the foetus to drive the anabolic and catabolic activities of nutrient material, the mechanical work done by the mother in carriage of the foetus, and mechanical work done against the activities of the foetus (especially late in pregnancy), energy cost in lost heat to foetus, and energy cost in preparation of the uterus and maternal homeostatic functions for pregnancy.

For the purpose of examining the nature of the trigger for birth and most direct and costly dependencies may be considered first. These are likely to include the supply of nutrients and oxygen to the foetus through the maternal blood supply to the uterine/ placental surface. As yet no studies have attempted to determine the relative energetic costs of these major dependencies of the foetus.

Some early experiments were carried out in vitro, to measure the metabolic rate of foetal material. Since we shall refer to this work later it is worth quoting Kleiber's (1961) comment on the results of such studies, 'Kleiber et al 1943 measured the metabolic rate of rat embryos in vitro and obtained good evidence that the foetus does not behave metabolically like a small independent homeotherm. The fetal metabolic rate per unit moist weight was of the same order of magnitude as that of normal adults rats and considerably smaller than that of newly born or 12-day-old rats. This observation, like others mentioned, supports the idea that to a considerable degree cellular metabolic rate is adapted to the condition of the animal as a whole. The effect of the metabolic regulators, however, appears to persist in the tissues after removal from the animal and to affect the respiration.'

More recent experiments have succeeded in giving information on the in vivo metabolism of the foetus, estimated from the oxygen deficit between venous and arterial blood in the umbilicus and between maternal and foetal blood as measured by indwelling catheters. The calorific value of oxygen is about 5 Cal for each ml consumed for mammals (Benedict 1938). The oxygen consumption of the foetus gives an indication of the total energy liberated within the foetal tissue for maintenance and growth. This, is of course, only a portion of the total energy cost to the mother (see above). These studies are discussed shortly. The growth rate of the immediately pre-partum foetus may be estimated following Huggett et al (see p. 130 et sqq) as

$$\frac{15Wb}{4tg}$$

where Wb is birth weight and tg the total gestation period.

These three sources provide some evidence for the examination of the energetic contigencies existing in the maternal/foetal relationship at birth.

However, some simple qualitative observations of the birth process may give some idea of the critical factors in the timing of birth, as they are seen in the energy relations of the maternal/foetal system. We may run through some of the maternal costs mentioned above and determine how birth alters them. In general, whilst the infant depends on maternal milk the infant is still entirely dependent on maternal energy sacrifice. However, the alteration in the form of this dependency may give some clues as to developments associated with birth itself.

Nutrient supply for anabolic growth and for respiratory oxidation: must generally increase with foetal size during growth. At birth however it is most likely that this maternal cost is traumatically increased, for two reasons. Firstly, as mentioned above, the infant is entirely dependent energetically on the mother, but several life functions of the infant are more costly after birth, - heat maintenance, and infant movement in particular. Secondly, these functions are maintained by the infant after birth from the liberation of energy internally, from the metabolism of maternally supplied nutrients. It is most likely that the efficiency of nutrient transfer between mother and foetus is greater than that between mother and suckling infant. The cross placental transfer is essentially the transfer of nutrients between similar mediums, maternal blood and foetal blood. After birth the transfer of nutrients passes through from maternal blood to mammary, glandular secretion, to alimentary digestion and finally infant blood. The latter process probably involves a greater requirement for alteration of the chemical formation of the oxidizable nutrients transferred. Any alteration of this sort must inevitably be less than 100% efficient (see p. 73 et sqq). In fact, the efficiency of milk nutrition is known for some mammals, and it ranges between 60 - 64% efficient (Kleiber 1961). This value is the ratio between the digestible (oxidizable) energy of milk nutrients to the metabolic cost of maternal production. Thus, the increase in size during growth suggests a general increase in the supply of nutrients, the increased cost of some infant life functions and the probable reduction in the efficiency of nutrient transfer after birth suggest a further traumatic increase in the maternal energy cost of nutrient supply.

Oxygen supply: as an immediate relationship between mother and offspring, terminates at birth, traumatically. The energy cost of this supply is, finally, a maternal deficit but its form is traumatically altered at birth.

Carriage of foetus: in most mammals terminates at birth, though not generally speaking in primates. In species where nest living is common this 'burden' on maternal energy may be considerably reduced after birth. However, for most primates and many non-nest-living species carriage either continues after birth or must be supported by maternally originated energy supplied to the infant.

Mechanical work against activities of infant: probably increases after birth when maternal maintenance of hygiene, play, protection and retrieval of the infant commence.

Maintenance of heat: may cease as an immediate relationship between mother and infant, though huddling with parent after birth may often occur in nest living species or primates. Once again the final maternal energy cost of this process increases with infant size generally, and probably traumatically at birth.

Energy cost of maternal homeostasis associated with infant-bearing: in general this may decrease after birth when the hormonal balance of the female alters towards a more 'normal' state and, for example, when the rich nutrient and oxygen supply to the uterus ceases. However, maternal homeostatic systems still give important support to infant systems after birth in particular the immune system of the infant, (Brambell 1972).

Of the relationships above, the most important difference in the form of the maternal/offspring relationships at birth is that associated with oxygen supply, with some important changes in the maintenance of heat and carriage of the offspring. We might expect that the event of birth may represent, in particular, the resolution of crises in the maternal/foetal relationship for these factors.

Weight and growth rate at birth. The meaning and implications of the interspecific scaling of attained size and rate of growth at birth are not clear. The author has already described the findings of Leutenegger (1973, 1976) and Leitch et al (1959) concerning the interspecific allometry of litter weight to maternal weight (p. 40 et sqq). Primates, as an order, are not markedly delineated from the other mammals in general in respect of this allometric covariance. Western (1977) remarks that generally, for any given maternal weight, primate litters are slightly lighter than those of carnivores and artiodactyls. Certainly, the peculiarly of primates is not remarkable in respect of litter/ maternal weight ratios. This is not the case when the rate of growth of the foetal material is taken into consideration, the time taken for primate foetal material to reach its maximum size being markedly longer for primates than any other mammals for a given maternal weight (excepting those with delayed implantation). This feature of primate pregnancy was noticed by Payne et al (1967b). They proposed that this signified a lower 'maternal stress' during pregnancy (and the suckling period, but see later discussion p. 219 et sqq) for primate mothers of any given size as compared with other mammals.

It may be deduced from Payne et al's analysis that they consider that the accumulation of foetal material places a greater demand on the maternal system than the maintenance of already accumulated foetal tissue. Whilst further analysis may confirm this hypothesis, the indications from the interspecific comparison of primate data are that the event of birth reflects more exactly the ratio of foetal to maternal weight, than any parameter associated with the rate of foetal growth. That is to say that birth is marked more exactly by an attained weight, than by any measure of the rate of accumulation of weight. Interestingly it is the strepsirhine species which provide the most persuasive evidence of this phenomenon.

Figure 8 (pp 157 - 8) shows the covariance of primate, single neonatal weight and maternal weight, the calculations (without figures) for values for both average litter weight and twin weights for species habitually producing twins are given in the Tables (4a and 4b , pp 361 - 2). These results may be compared with those which are associated with the rate of foetal growth, for gestation period (Table 3 , p 360), a_w (Figure 4, pp 134 - 5), and those given in Figure 9 (pp 159 - 160) which gives the covariance of litter growth rate at the end of pregnancy with maternal body weight.

It can be seen that in general for either major group of primates, the constraints on attained weight at birth are greater than for any measure of the rate of growth required to achieve that size. This is particularly true for the Strepsirhini where, for example, for some species the growth rate of the litter at birth is as high as the most rapidly growing haplorhine litters for any given maternal weight, Microcebus murinus (81), Cheirogaleus major (33), and Varecia variegatus (113). The wide, poorly correlated distribution of strepsirhine values of a_w, gestation period and the growth rate near term against some measure of size, as compared with that for litter weight against maternal weight, suggests some peculiarities as to the event of birth. The author has already alluded to his belief that the variation in, for example, a_w in strepsirhine species may be related to apparent variations

Figure 8

X-Axis, ln:Ab:g. Natural logarithm of adult female weight in grams

Y-Axis, ln:Nb:g. Natural logarithm of single neonatal weight in grams.

<u>All Primates</u> N = 64:$\bar{x}$ = 7.62, $\bar{y}$ = 4.98
P.A. = 0.87 (0.81, 0.93)
R.M.A. = 0.87, (Linear) Regression = 0.84
$r = .97$, $r^2 = .93$

<u>Haplorhines</u> N = 45 : $\bar{x}$ = 8.14, $\bar{y}$ = 5.60
P.A. = 0.78 (0.73, 0.83)
R.M.A. = 0.79, (Linear) Regression = 0.77
$r = .98$, $r^2 = .96$

<u>Strepsirhines</u> N = 19 : $\bar{x}$ = 6.37, $\bar{y}$ = 3.53
P.A. = 0.72 (0.64, 0.81)
R.M.A. = 0.73, (Linear) Regression = 0.71
$r = .97$, $r^2 = .96$

Upper solid line: P.A. (Haplorhines)
Lower solid line: P.A. (Strepsirhines)

After Leutenegger (1973) and Martin (1975a), with additional data

see also tables 4a, 4b.

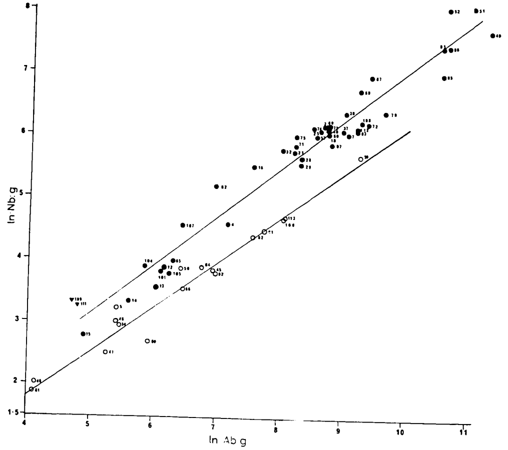
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Figure 9

X-Axis, ln:Ab:g. Natural logarithm of adult female body weight in grams

Y-Axis, ln:Ftgr:gd^{-1}. Natural logarithm of litter growth rate on the last day of gestation in grams per day.

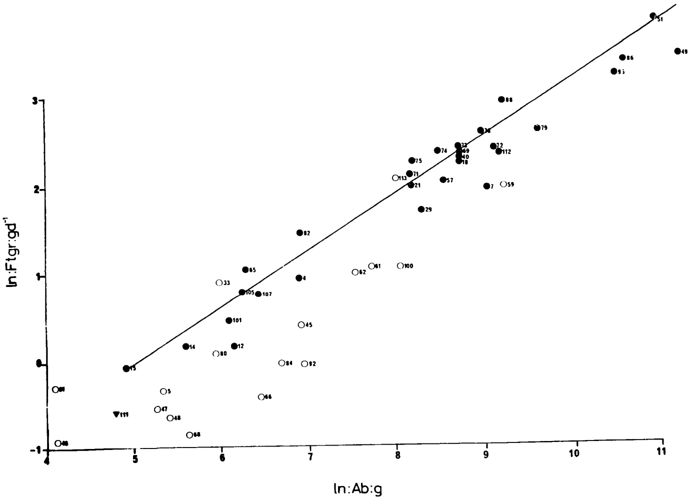
All Primates: N = 46, $\bar{x}$ = 7.62, $\bar{y}$ = 1.34
P.A. = 0.70 (0.63, 0.77)
R.M.A. = 0.71, (Linear) Regression = 0.68
r = .95, r^2 = .89

Haplorhines N = 30, $\bar{x}$ = 8.23, $\bar{y}$ = 1.92
P.A. = 0.61 (0.56, 0.66)
R.M.A. = 0.62, (Linear) Regression = 0.60
r = .97 r^2 = .95

Strepsirhines N = 16, $\bar{x}$ = 6.48, $\bar{y}$ = 0.24
P.A. = 0.61 (0.46, 0.77)
R.M.A. = 0.64, (Linear) Regression = 0.51
r = .89, r^2 = .79

Solid line: P.A. (Haplorhines)

After Payne et al (1968), additional data in this study.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111

(inter specific) in metabolic rate and body temperature. In this respect it is odd that of all the parameters at present available for the foetal period it should be the weight of the litter that is most clearly associated with maternal weight. When, presumably, the rate of supply of nutrients and oxygen to the foetus is closely related to the size of the foetus, we might have expected that the distribution of litter weight to maternal weight might reflect the distribution of metabolic rate to maternal weight. In fact, maternal metabolic rate has been proposed as a determinant of size at birth by Martin (1975a), in some respects an attractive hypothesis (see next section). If, despite the contradiction with the author's description of the general metabolic features of the strepsirhines (p.56 et sqq), we follow this hypothesis briefly we might expect that the metabolic rate of the foetus would be largely determined by the demand for maintenance rather than that for growth.

Of the few studies of in vivo foetal metabolic rate two are of Macaca mulatta, a haplorhine species (Behrman et al 1970, and Comline and Silver 1975). The total oxygen requirement of placental and foetal tissues amounts to an energy liberation of 30KCal per day. The increase in foetal weight on the last day of pregnancy is about 8 grms, of which roughly 80% or more is water (Behrman et al, 1964). The solid component of this weight increase may be assumed to be largely composed of protein with some fat and inorganic salts. The energy required to construct the complex foetal tissue is unknown but it may probably be compared to the energy liberated in the normal mammalian catabolic reduction of these types of compound. Whilst the building up of complex proteins by organic tissue is likely to require more energy than the catabolic process, (since the former requires the flow of information, see p. 83 et sqq), the nutrients provided by the maternal system are in a higher energetic state than the normal simple compounds produced in mammalian catabolism.

If, despite the approximate nature of this method, the energetic cost of construction of the solid component of foetal weight increase is taken as 4KCal per grm (the catabolic value for protein), then the energy expenditure in accumulation of weight for the near term macaque foetal material is 6.5 KCal per day. That is, approximately 1/5 of the total calorific consumption of the foetal material. Similar approximations, admittedly crude, from Comline et al (1975) suggest that the near term cow and horse foetal material require respectively about 1/5 and 1/7 of their calorific uptake for weight accumulation. These values are some weak support for the hypothesis that it is a factor of maintenance that breaks down at birth rather than that of growth. The issue of the determinant nature of metabolic rate in the size of the litter relative to the mother at birth is still unresolved. However, it is clear that as far as the event of birth is concerned, litter/maternal weight ratio gives the most exact description, of all the other known parameters. For this reason it has attracted the greatest interest, and given rise to two hypotheses of its determinance, these are considered prior to some further discussion of the still unclear nature of foetal growth and birth.

Scaling of neonatal weight. Leutenegger (1973) and Martin (1975a) have both considered the interspecific allometry of neonatal size in primates. In brief, Leutenegger found that whilst for strepsirhine and haplorhine groups considered separately the interspecific exponent of maternal weight was similar, the strepsirhine mother gives birth to a litter approximately one third the weight of the litter of a haplorhine mother of the same size. Using linear regression analysis, he concludes that within each group, litter weight varies as, $(\text{Maternal Weight})^{.67}$

Leutenegger had doubled the single neonatal weight for those species habitually bearing twins, and using this method but with a larger sample of species and a correlation rather than regression analysis his results are confirmed (Table 4 , see p. 360 for discussion of techniques). It can be seen that for both groups the value .67 lies within the confidence limits of the Principal Axes.

Martin however considered the interspecific allometry of single neonatal weight to maternal weight and concluded that this value fell close to the metabolic size of the mother, i.e. close to the .75 power of maternal body weight. Using Martin's method but with an enlarged sample size his results are confirmed here (Figure 8, p. 157 - 8). In this case the value .75 can be seen to lie within the confidence limits of the Principal Axes.

In a statistical sense the higher slopes for the computations using single neonatal weight are due to the greater incidence of twin births in the smaller bodied forms of both groups. The computed values for correlation coefficient are not greatly different for either of the analyses, and cannot help in determining which of the two approaches yields the most significant result.

In the author's opinion, the variance attributable to specific adaptation and error do not allow an empirical test of the conflicting assertions of Leutenegger and Martin. That, respectively, neonatal size is determined by maternal surfaces and that neonatal size is determined by maternal metabolism. On theoretical grounds Leutenegger's hypothesis looks the weaker of the two due to internal inconsistencies in his argument, however, as mentioned above, if metabolic rate is poorly correlated between strepsirhine species how may it determine a relatively well correlated distribution of neonatal body weight?

Taking Leutenegger's hypothesis first, that maternal surfaces determine litter weight. It is clear that of all 'determinant' factors surface area is least reliable, since corrugation and folding commonly occur in nature, apparently in compensation for size constraints of the simple Archimedean ratios, (Gould 1966, Harman 1947, see also this study pp 136 et sqq). Further aspects of Leutenegger's hypothesis bear examination. He suggests that the size of the placenta will vary isometrically with maternal body size interspecifically, as do the majority of maternal organs (Stahl 1965), so that the surface area of the placenta will be proportional to maternal mass to the $^2/_3$ power interspecifically.

This is theoretically questionable particularly for the strepsirhine species, for which the epitheliochorial placenta covers most of the internal lining of the uterine surface. Although nothing is known of the relative volume of foetal fluids in these species it seems unlikely that the uterus expands much beyond the foetal material it contains. In the few strepsirhine, whole specimens with near term foetal tissue examined by the author, the embryo was tightly enclosed in the placenta, and the placenta was immediately apposed to the uterine wall.

Thus, near the time of birth the interspecific scaling of uterine volume is almost certainly similar to the scaling of litter weight against maternal weight, i.e. not isometric but to approximately .7 power of maternal weight. The interspecific scaling of the uterine surface, equivalent to the placental surface for strepsirhine species, against maternal weight will be to the $(.7 \times \frac{2}{3}) = .47$ power of maternal weight, well below the $\frac{2}{3}$ expected by Leutenegger.

Applying Leutenegger's hypothesis to haplorhine species, where the haemochorial placenta covers only part of the uterine wall, we would expect the placenta of larger bodied species to occupy a greater proportion of the uterine surface than for smaller species. This is not reported in the literature on placentation (see Luckett 1974, 1975 and Young 1972)., and not observed by the author in comparison of marmoset, celebes ape and orangutan specimens.

Furthermore, the placenta cannot properly be considered a maternal organ, it is in part of foetal origin. These theoretical objections to Leutenegger's hypothesis of the functional relationship of the 'gross' maternal surface dependency of neonatal weight at birth are further supported by the findings reported earlier in this study on the interspecific isometry of placental weight with neonatal weight (Figure 5 p.137 - 8). However, it should be recalled (from p. 140 et sqq) that the 'effective' placenta surface may be expected to scale to the $\frac{2}{3}$ + .18 power of neonatal weight (= .85). This would be equivalent to an exponent of maternal weight of $\sim$ (.85 x .7) = $\sim$ .6 which is certainly comparable to Leuteneggers expected value of .67. Despite the possible concurrence of real surface area of the placenta and (maternal weight) this does not represent a confirmation of Leuteneggers' hypothesis since his was based on the unfounded assumptions given earlier.

The general principle deserves further consideration, in respect of the primate data at least, since, as mentioned earlier, the hypothesis of Martin (1975a) asserting metabolic rate determinance of litter weight ratio. The author has earlier favoured the hypothesis that birth size is a threshold criterion in the maintenance of foetal tissue (see p. 156 et sqq). If this maintenance factor is not metabolic rate dependent then it is possible that it is determined by a factor equivalent to a rate of diffusion, independent of metabolic rate. Two such factors are immediately apparent, firstly the diffusion of gases across the placental surface (remembering the expected role of oxygen supply in the event of birth, p. 153 et sqq) and secondly the movement of long-chain essential fatty acids in the development of the foetal brain (the foetal brain having been already identified as a key factor in foetal growth, see p. 141 et sqq). The second topic will be considered later (p. 169 et sqq), following some analysis of the limited data on oxygen uptake in the near-term foetus.

Foetal metabolic rate and oxygen uptake. The metabolic rate is often estimated from the oxygen consumption of an organism, the two processes are not identical but may, in general, be equated. The oxygen uptake of the adult female is scaled to the .75 power of body weight (see p. 21 et sqq). That is to say that the uptake per unit weight of maternal tissue, or the 'intensity' of uptake, is lower in larger species, scaled to the -.25 power of body weight.

We may consider two hypotheses. Either the intensity of maternal oxygen and nutrient supply will not satisfy foetal demand beyond an attained size, or the absolute demand on maternal resources passes a generally critical point at such a size.

The first alternative is unlikely, since the intensity of foetal growth, (perhaps a rough indication of the intensity of metabolite demand), declines during the growth of the foetus. This decline is in proportion to $W^{-1/3}$ where W = foetal weight, following Huggett et al 1951 (see p. 132 et sqq).

In the postnatal growth of the individual, just as in the interspecific relationship, the intensity of metabolic activity per unit weight of body tissue declines with increase in body size. In the growth of the foetus it would seem unlikely that the intensity of nutrient demand <u>increases</u>, which would have to be the case if metabolic intensity were the source of the incompatability of mother and foetus at the time of birth.

The alternative is that in general a certain fixed portion of the normal metabolic turnover of the mother can be sacrificed to support the intra uterine foetal material for all species. A similar effect has been described by Brody (1945) and Payne et al (1968) in the calorific value of maximum milk production, which is proportional to the metabolic size of the mother, (see discussion of this effect however, p. 219 et sqq). If this were the case then the scaling of neonatal litter weight to maternal metabolic size would be explained if there was an isometric (interspecific) relationship between foetal size and foetal oxygen consumption and metabolism. That is to say that regardless of size the intensity of foetal oxygen consumption (per unit weight) is similar between species for the near term foetus (or possibly throughout pregnancy). If this were the case it would contradict the interspecific tendency for adult metabolic rate.

Despite this peculiar contradiction, the hypothesis might account for the results of *in vivo* experiments measuring the oxygen consumption per Kilogram for five species ranging in near term, foetal size from 450g to 25Kg, from macaque foetus to horse foetus (Comline et al 1975). In free living adults differing in size by a similar factor we would expect that the smallest would have an intensity of oxygen consumption about 3 times greater than the largest, on the basis of Kleiber's curve (1961, see p. 21 et sqq). In fact Comline's team discovered that the values are all remarkably similar, close to 7 mlO_2 /Kg min.

These results are hard to explain on the basis of the adult tendency but until they are repeated and extended, the hypothesis of interspecific isometry of near-term foetal oxygen consumption deserves consideration. Kleiber's (1961) concept of metabolic regulators (see quote p. 151) may be applicable in this respect. The phenomenon of the higher oxygen affinity of foetal haemoglobin in comparison to maternal haemoglobin could also be usefully studied on a comparative basis in regard to this hypothesis.

The final part of this chapter is devoted to the relative size of the foetal brain at birth and its oxygen consumption, as well as the role of essential fatty acids in the development of the foetal brain.

The brain at birth. In the section dealing with the growth of the brain (see p. 141 et sqq) the isometric growth of the brain and body of the foetus was described (from the work of Holt et al, 1975, and Van Wagenen, 1972). From their work, and the values in Sacher et al (1974), it may be confirmed that the isometry of individual foetal growth of brain and body is approximated by an interspecific isometry (within orders) of the ratio of neonatal brain weight to neonatal body weight. That is to say that the characteristic ratio of foetal brain to body weight ratio of an order appears early in growth and is maintained throughout foetal growth to birth. However, as Sacher et al (1974) demonstrated that, in general, this ratio is inversely related to the specific foetal growth rate between orders. The primates have the highest birth (and during growth) ratios of brain to body weight but the lowest values of a_w (see p. 40 et sqq). This relationship is not apparently direct or mechanical judging by the comparison of the strepsirhine correlations for a_w and neonatal brain weight in their interspecific allometry and isometry (respectively) with neonatal weight (compare Figure 4 p. 134 - 5 with Figure 10 p. 171 - 2).

It is of some interest to note that the two major groups of primates have similar characteristic foetal and neonatal brain to body weight ratios (Figure 10, p. 171 - 2), the highest ratios found in Mammalia. The principal feature that distinguishes the two groups at birth is the smaller relative size of the whole neonate at birth to its mother's weight, Figure 8 p. 157 - 8 Although the adult females of haplorhine species have a higher level of encephalization then strepsirhine species (Figure 11, p. 173 - 4) this factor is unlikely to 'explain' the lower birth weight of strepsirhines relatively. If that were the case generally for mammals we would expect that species with low levels of encephalization would have relatively lighter litters, this is not the case (from Sacher et al 1974, Western 1977, see p. 40). Even within the primates this factor is unlikely to explain the difference in relative birth weight (or relative brain weight at birth) since despite the difference in levels of adult encephalization the relative size of the neonatal brain to the adult female is distinguishable between haplorhine and strepshrhine species, (Figure 12, p. 175 - 6). This latter relation between the size of the brain at birth and the size of the adult brain is in fact quite variable between mammals, and is believed by Sacher et al to be a measure of the Vermehrungsfaktor for brain development at birth defined by Portmann (1962) and Mangold-Wirz (1966), except that their parameter is the reciprocal, i.e. Adult brain weight divided by Neonatal brain weight. This factor is closely associated with the altriciality

Figure 10

X-Axis, ln:Nb;g. Natural logarithm of single neonatal body weight in grams.

Y-Axis, ln:Ne:g. Natural logarithm of single neonatal brain weight in grams

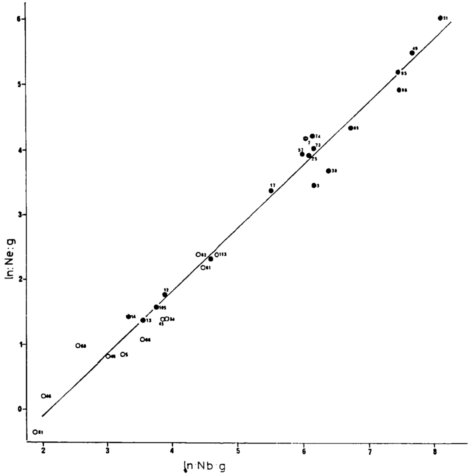
<u>All Primates</u> N = 29: $\bar{x} = 4.92$, $\bar{y} = 2.69$
P.A. = 0.96 (0.91, 1.01)
R.M.A. = 0.96, (Linear) Regression = 0.95
$r = .99$, $r^2 = .98$

<u>Haplorhines</u> N = 18: $\bar{x} = 5.84$, $\bar{y} = 2.69$
P.A. = 0.95 (0.88, 1.03)
R.M.A. = 0.95, (Linear) Regression = 0.94
$r = .99$, $r^2 = .97$

<u>Strepsirhines</u> N = 11: $\bar{x} = 3.41$, $\bar{y} = 1.21$
P.A. = 0.88 (0.73, 1.06)
R.M.A. = 0.89, (Linear) Regression = 0.85
$r = .95$, $r^2 = .91$

Solid line: P.A. (All Primates)

First presented in this form in this study, with new data, (see also Sacher et al 1974).



ln:Ne:g
ln·Nb·g
6
5
4
3
2
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0
2
3
4
5
6
7
8
51
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95
86
81
74
7
73
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25
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3
17
62
113
61
12
105
14
13
45
84
66
68
48
5
46
81

Figure 11

X-Axis, ln:Ab:g. Natural logarithm of adult female body weight in grams.

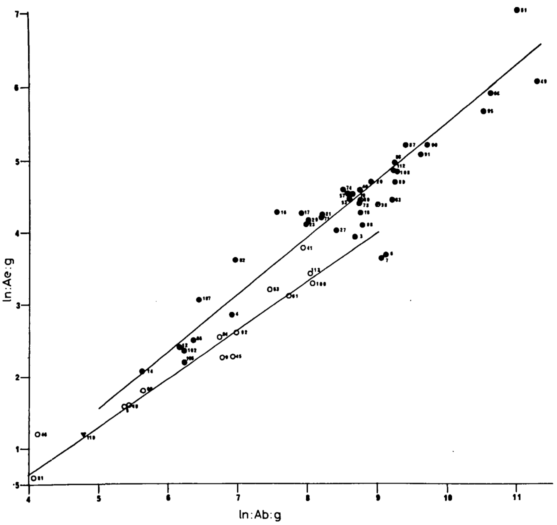
Y-Axis, ln:Ae:g. Natural logarithm of adult female brain weight in grams.

<u>All Primates</u> $N = 65$, $\bar{x} = 7.98$, $\bar{y} = 3.81$
P.A. = 0.85 (0.80, 0.91)
R.M.A. = 0.85, (Linear) Regression = 0.83
$r = .97$, $r^2 = .93$

<u>Haplorhines</u> $N = 49$, $\bar{x} = 8.44$, $\bar{y} = 4.28$
P.A. = 0.80 (0.74, 0.86)
R.M.A. = 0.80, (Linear) Regression = 0.77
$r = .97$, $r^2 = .93$

<u>Strepsirhines</u> $N = 16$, $\bar{x} = 6.59$, $\bar{y} = 2.37$
P.A. = 0.67 (0.58, 0.78)
R.M.A. = 0.69, (Linear) Regression = 0.66
$r = .96$, $r^2 = .92$

Upper line: P.A. (Haplorhines)
Lower line: P.A. (Strepsirhines)
First presented in this form (separated sexes) in this study, following amongst others Bauchot and Stephan (1969) and Jerison (1973).


ln:Ae:g
7
6
5
4
3
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1
.5
ln:Ab:g
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20
112
87
91
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107
4
14
102
110

Figure 12

X-Axis, ln:Ae:g. Natural logarithm of adult female brain weight in grams.

Y-Axis, ln:Ne:g. Natural logarithm of single neonatal brain weight in grams.

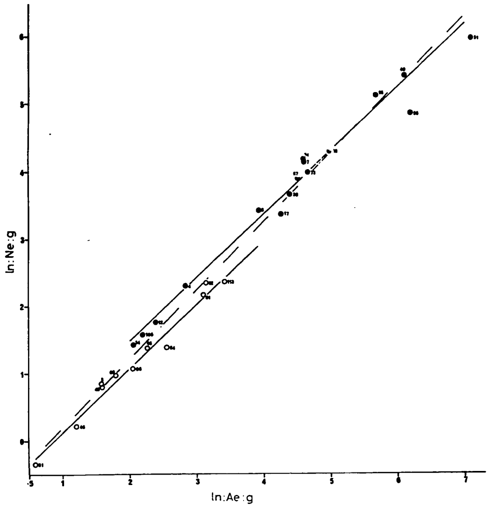
All Primates N = 25, $\bar{x}$ = 3.54, $\bar{y}$ = 2.77
P.A. = 1.02 (0.97, 1.07)
R.M.A. = 1.02, (Linear) Regression = 1.01
$r = .99$, $r^2 = .98$

Haplorhines N = 16, $\bar{x}$ = 4.39, $\bar{y}$ = 3.72
P.A. = 0.94 (0.87, 1.00)
R.M.A. = 0.94, (Linear) Regression = 0.93
$r = .99$, $r^2 = .98$

Strepsirhines N = 9, $\bar{x}$ = 2.02, $\bar{y}$ = 1.09
P.A. = 0.94 (0.86, 1.03)
R.M.A. = 0.94, (Linear) Regression = 0.93
$r = .99$, $r^2 = .98$

Upper Solid line : P.A. (Haplorhines)
Lower Solid line: P.A. (Strepsirhines)
Dashed line : P.A. (All Primates)

This study (c.f. Sacher et al, 1974)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ln:Ae:g
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or precociality of the offspring at birth. Gould (1977, p.369) summarizes Portman's arguments, and defines his concepts,
"Portman (1941, 1945,) in a series of widely neglected but fascinating essays, argues that the general trend in mammalian evolution leads from large litters of rapidly growing, highly undeveloped (altricial) young to small, slowly developing litters of advanced (precocial) young."

The primates are generally of the precocial type at birth with a relatively high proportion of their final adult brain laid down at birth. In the authors opinion however, this trend must also be associated with a more distinct inter Order series of differences in the ratio of foetal brain to foetal body weight, the primates as explained sharing the highest values for this ratio. It may be proposed that these two factors serve slightly different functions. The relative altriciality/ precociality at birth may be particularly associated with the requirements of the infant at birth in locomotion and defence for example: The characteristic ratio of brain/body weights at birth and during foetal growth may be generally associated with the level of adult encephalization, the principal feature of the foetal period being that isometric growth may occur between brain and body. It may be that a high brain/body ratio at birth allows greater subsequent growth of the brain relative to the adult body, since brain growth after birth is not isometric but negatively allometric (with one notable exception - Homo sapiens, see p. 336 et sqq).

Both these factors, altricial/precocial development at birth and low/high ratios of brain to body weight in growth and at birth are generally phenomena which may further be related to the population dynamics of r/K selection in species respectively (see Gould 1977, and p. 267 et sqq).

It is significant that the high ratio of brain/body weight in foetal growth of the primates is related to, or perhaps only maintained by relatively low foetal growth rates. This might suggest that the greater 'cost' of a relatively larger brain in the foetus is not unimportant. For this reason future research of comparative metabolism of the foetal brain may yield some more conclusive hypotheses than those discussed here, (see also discussion p. 182 et sqq). However for a few species there is some information on <u>in vivo</u> metabolic rates of foetal brain tissue that do suggest a high maintenance 'cost' of brain tissue.

Behrman et al (1970) report that in the near term macaque foetus the intensity of foetal metabolism is about twice that of somatic tissue, at about 13 ml O_2/Kg min. This value is comparable with values of newborn brain intensity of oxygen uptake in both man and baboon (Cross et al 1974, Levitsky et al 1977).

For these three haplorhine species, differing by a factor of up to 7 in neonatal weight, we might expect from Kleiber's rule (1961) to find differences in the intensity of oxygen consumption of a factor of 2. In fact for all three, brain oxygen uptake is about 13-14 ml O_2/Kg min, whilst somatic O_2 uptake averages at between 5.5 - 7 ml O_2/Kg min. Not only does this phenomenon deserve further examination, apparently reconfirming some form of interspecific isometry in foetal oxygen uptake (see p. 141) but indicating the form of an extra 'cost' to the maternal system in maintaining a foetus of a high characteristic brain/body weight ratio.

It is also important to note that in the adult the difference in the intensity of brain and body oxygen uptake increases. In the human adult 18% of body heat is generated in the brain. This is equivalent to an oxygen uptake in the brain of about 33 ml O_2/Kg min whereas the somatic tissue declines slightly during growth from the newborn figure of about 5.5 ml O_2Kg min to a value closer to 3.5 ml O_2/Kg min. The increase in the intensity of brain oxygen uptake after birth may well be associated with the decline in the relative growth of the brain (in relation to the whole body) after birth.

It may be that the 'cost' of the brain of the foetus in growth is further emphasized by an isometric factor. Placental weight is roughly isometric, interspecifically, with neonatal brain size (between 1.2 and 2.8 times the size of the brain independently of total body size for 9 haplorhine species). It has been found in three non-primate species that placental oxygen uptake is roughly twice that of somatic foetal tissue, (but similar to primate brain oxygen consumption), (Comline et al 1975). A close, 'regulatory' relationship between the placenta and the prenatal brain has been proposed by Zamehof et al (1972) on the basis of both the isometric growth of placenta and brain in the rabbit (noted also for the macaque, Van Wagenen 1972,) and in particular the constant relationship during growth between placental size and the number of cells and amount of DNA in the developing foetal brain.

Although the evidence is lacking for placental, somatic, and brain metabolism and foetal temperature, it may be assumed that the method of Sacher (1976), described at length earlier (p. 79 et sqq) might be usefully applied to the whole generative cycle and foetal growth in particular. Whereas Sacher's (1976) method was applied to the relatively static adult form of the thermodynamics of the mammalian living state, many new features may be expected to arise when the thermodynamic relations of the growing infant are considered. One particular aspect of Sacher's (1976) discussion of the level of encephalization is already suggested by the results given here in relation to foetal growth. Sacher has suggested, (see p. 83) that the encephalization of the adult ..'is a measure of a property of the organism as a whole, not of the brain alone, (1976, p.79). The fact that a high characteristic foetal brain/body weight ratio is associated with low foetal growth rates of both brain and somatic tissue suggests that the laying down of complex organized tissues in the foetal brain is matched by a similarly complex process in somatic tissue. This may at first seem obvious but as Gould points out, (1977, p.396) there has been in the past, concentration on the brain, seen in isolation from its living function. That the brain is not simply an 'arithmetical' addition to somatic tissue, would appear to apply to the foetus, in support of the contentions of both Sacher and Gould mentioned above.

The adaptive significance of a particular growth rate of the foetus may be expected to rest on some overall measure of the 'efficiency' of the reproductive function of the whole organism. It is to be expected that the optimum conditions for the expression of, at one extreme for example, the slow intrauterine development of a complex and elaborate foetal structure will reflect the relatively high probability of survival of the foetus through infancy to reproductive maturity. This is not a new concept, and the qualitative basis for the interconnection of specific physiological development to the population dynamics of the species has been laid by the generalizations of Portmann (1962), and excellently developed by Gould (1977, chapter 9). This issue is examined in greater detail in this study in Chapters 6 & 7.

In the author's opinion the quantitative evaluation of this aspect of interconnection between growth and population ecology must rely heavily on the conceptual framework developed by Sacher and Gould. These authors have, respectively, provided both an understanding of the thermodynamic essence of the living state and a theoretical framework for evaluating the nature of discontinuity in the evolution and differentiation of living systems. It is with regret that the author at this point must refer such an analysis to future research. Many of the principal contradictions in the interpretation of the allometry of the growth periods (in this and the next chapter) remain unresolved in this study. However, in leaving the topic of foetal growth it is worth remarking on two aspects of the foetal period which have emerged in the course of this chapter. Firstly the hypothesis of an important role in the determination of discontinuity through 'passive' diffusion rates (of oxygen especially) and secondly, the recurrent emphasis on the pace of development of the foetal brain as a measure of the organization of the whole foetus. However, throughout this chapter there has been a dominating concentration on energy flow. In studying the development of the life cycle we are in reality considering not simply the flow of energy but the inter connected flows of both information and matter (see p. 83 et sqq).

In respect of the latter, the work of Crawford et al (1977) expresses an element of development entirely compatible with the general theoretical position given in Chapter 2. They introduce to the subject of foetal growth important data on the flow of matter, in particular the complex, necessary and metabolically 'expensive' Essential Fatty Acids (E.F.A.'s)

Quoting from their study,
'The developing brain accumulates long-chain (C20 and C22) polyenoic fatty acids, particularly during cell division.... De novo synthesis of these acids does not occur in higher animals and they are derived either directly from food or by metabolism from the parent essential fatty acids, linoleate and - linolenate. ....Reduction of brain EFAs in young animals has been successfully achieved by feeding EFA - deficient diets to the mother during pregnancy. Reduction of brain EFAs using this technique was associated with retardation of brain development......'

The intensive breeding of rat mothers without the normal interbirth period results in lowered concentrations of EFAs in the neonatal brain. Since EFAs may be synthesized by the mother only in small quantities after a series of slow reactions, it seems that EFAs are 'leached' out of storage in the maternal reserves (in the brain especially) faster than they may be synthesized under these abnormal breeding conditions. The result is both maternal and neonatal debility. The authors propose that this process of diffusion (and some subsequent secondary metabolism) of EFAs may be an important determinant of brain growth. Quoting again; 'As it is the large mammals which have the smallest brains relative to their body mass, and have the smallest proportions of long-chain polyeonates in their tissue pools, these findings suggested to us that the long-chain polyenoates might have been important determinants of brain growth. It seemed that the degree of brain and nervous system development was somehow related to the availability of long-chain polyenoates to the developing brain.'

It may be seen that the proposed operation of such a factor in the development of the foetal brain mirrors the general outlook stated earlier (p. 169 et sqq) that high characteristic brain/body weight ratios in the foetus is associated with high adult encephalization. Furthermore the maintenance of the foetal growth isometry (both interspecific within orders, and for the individual) places a greater burden on larger bodied species (within orders) requiring longer gestation periods. Finally, the slow synthesis and apparent 'leaching out' of EFAs suggests a factor perhaps not immediately influenced by metabolic rate, a conclusion reached earlier on different grounds (p. 167 et sqq).

Future evaluation of the complex nature of foetal growth will require the incorporation of this evidence as an element in the flow of matter. As stated earlier

(p. 180) the assessment of the information (or entropy) flow and the energy flow (foetal metabolic rate in particular) in foetal growth assume a major priority in the study of comparative reproduction.

Summary of Chapter 4

Two types of growth model are introduced, one assuming a preprogramme for growth, the other assuming dependency on external conditions. The latter is preferred for the foetal period, for its simplicity and recognition of the possible interaction between the developing foetus and its 'environment'. Employing the cubic growth curve of Huggett et al 1951 it is found that a_w scales interspecifically higher for larger bodied species. The poor correlation of the strepsirhine species is attributed to their interspecific flexibility of metabolic rate in relation to body size. Evidence is presented to suggest that the scaling of a_w in haplorhine species is associated with a greater density of exchange surfaces in the vascular tissue and placenta of the foetus in larger bodied species. Sacher et al's (1974) identification of the importance of foetal brain growth is supported, but the mechanism is rejected on the basis of an intra Order analysis of a_w brain which is not constant for all members of the primate order.

The moment of birth seems to be related to the attained size of the foetus relative to the maternal weight. It is suggested that this is associated with a largely passive rate of diffusion of oxygen and possibly E.F.A.s across exchange surfaces. The apparent interspecific isometry of foetal metabolic rate per gram may also be involved.

CHAPTER 5 - POSTNATAL GROWTH

Section a) Introduction

As discussed in the introduction to the last chapter, the individual growth of mammals, whilst obviously continuous, is marked by relatively sudden changes in the form of the individual's relation to the external environment. This is reflected in the overall growth curve of the developing individual. Brody (1945) compares mammalian growth to insect growth, suggesting that the different periods in the course of mammalian growth are separated by abrupt transformations similar to the metamorphoses of insect development. It is for this reason as Brody explains, that it is both empirically and theoretically impossible to arrive at a mathematical model for mammalian growth which can describe the whole course of growth. Brody himself considers growth in parts, the method adopted here. However, before describing the allometry of postnatal growth it is necessary to examine the differences in the biology of foetal and postnatal growth, and the consequent differences in the methods of data use between this chapter and the last.

For any living organism, at any specific time in the course of growth and throughout the growth process itself we see the interaction of the genetic content of the original zygote with the phenotypic manifestation of this information as it comes into contact and relation with the mass movement of its external environment. Throughout growth these interactions and developments are associated with the real transformation of the zygote into the reproductive adult. In this sense the overall similarity of all mammalian embryos and the common cubic growth curve for mammalian foetal growth reflects the dominance of the foetus' external dependency on its form. As the individual develops, its genetic characteristics become more obvious and the immediate dependency on specific conditions for development decline. In this way the genetic content is tested out on the world through the development of the adult phenotype capable of changing the environment on a wide scale, and relatively free from the immediate constraints of successful early development.

As mentioned in the last chapter (p. 131) the principal theoretical reason for using Huggett and Widdas' (1951) cubic growth curve as a basis for interspecific comparison of foetal growth is the great dependency of the foetus on the environment created in the maternal uterus. This is in agreement with the conception that the rate of growth is determined by the surface area of the foetus at any point.

At birth however, this immediate dependency on maternal conditions is suddenly changed and reduced. As will be discussed, there is no common mammalian post natal curve, which makes the Interspecific comparison of the course of postnatal growth a little less easy than for the foetal period. Also, as we shall see, the postnatal growth from birth to adulthood covers a period when the stages of development become less associated with energetic dependency on the parent and increasingly associated with the unfolding of inherited and wide ranging features of the successful growth to adulthood. This transition between zygote and adult can thus be seen in its connection with the previous adult generation and with its own future adult stage. For example, the age and weight of the weaning infant reflects both the end of maternal supply of nutrients (the mother entering into a new pregnancy) and a step towards the final adult size. Thus the interspecific comparison of weight at weaning and adult female weight is both associated with the dependency of the infant on the mother, and the proportion of adult size attained at weaning.

Mammalian Postnatal Growth and the primates. Laird (1967, 1966) and Payne and Wheeler (1968) have described the relatively slow postnatal growth of the primates, (Case 1978 applies term 'slow' to anthropoid primates and marsupials), as distinct from other studied mammals. Sacher (1970) suggests that this is a reflection of the high level of encephalization of the primates, the highest of all species.

Generally for mammals birth marks approximately the point of inflection in the overall sigmoid shape of mammalian growth in weight from conception to adulthood. Following birth for all mammals except the primates a reasonable fit is obtained by Brody (1945) with a regular decay of the specific growth rate $\frac{dW}{dt} \times \frac{1}{W}$ with time. Laird's (1966) model of exponential decay of the specific growth rate has been discussed earlier (Chapter 4). One of the inadequacies of her model is associated with the period about birth, Laird is compelled to admit that birth requires a 'resetting' of the constants of her growth equation. This sudden alteration in growth rate at the time of birth is particularly exemplified by the strepsirhines (see next section).

Neither Brody's nor Laird's models for the generalized mammal can accomodate primate growth which is slower, and may include a pubertal growth spurt. The existence of a pubertal growth spurt is a moot point since empirical testing of growth models is inconclusive. The delayed growth in larger primate species does reveal some slight alteration in growth rate at puberty but the factors of body size and the accuracy of data make the detection of such a change in smaller species impossible (see Gould 1977 Chapter 10). The effect of the generally slow growth and pubertal phase is that early growth in weight and a section of later growth, for all purposes is linear, that is growth in weight is a constant regular increase for relatively long periods of time. The constancy of this daily increment can be quite surprising, infants of two small strepsirhine species, Microcebus murinus and Galago demidovii reared in captivity predictably put on ¾ grm in weight per day up to weaning age, (Glatston pers. com., Brand pers. com.).

Whilst this early, apparently linear phase is seen in all primate species for which growth curves are available, it does not last up to weaning age in the larger bodied forms. In man and the chimpanzee for example growth is roughly linear up to the end of the first year after which it declines. Weaning in these species is about 3 years.

With this complex picture of primate growth curves, and with no single pattern applying to all species, the interspecific comparison of the course of postnatal growth is not possible in the way foetal growth was considered in the last chapter. However, more information on the developmental stages of the individual is available for the postnatal period. The interspecific comparison of postnatal growth considers the timing of these stages in the context of the developing independence of the infant from its mother.

Section b) The transition from foetal to postnatal growth.

The components of the sudden alteration at birth in the mode of existence of the neonate have been described earlier (p. 152 et sqq). These alterations might be expected to have a drastic effect on the growth rate of the individual. Immediately after birth there is usually some drop in weight of the newborn. The maternal milk supply does not usually start immediately the infant is born. Colostrum, a pre milk secretion, important for the early protection of the newborn against infection, does not contain all the nutrients required by the infant. For this very early period the infant metabolism and heat is maintained through the burning up of glycogen (animal starch) and fat stored in the foetal tissues towards the end of pregnancy (Dawes 1971). As soon as milk production starts, growth in weight will commence.

For many species the rate of growth postnatally will differ from the growth velocity attained by the last days of pregnancy. This is the 'resetting' of growth at birth which causes problems for the model used by Laird (see p. 126 et sqq). For the primates this 'resetting' can be seen in Figure 13 (p. 190 - 1). The solid line is the line of identity of both early postnatal linear growth and growth velocity at the end of gestation as calculated from the Huggett and Widdas equation. As can be seen from the diagram the haplorhine species generally scatter about this line of unity, there is a tendency for the smaller bodied forms to increase their growth rates after birth whereas the large bodied forms either maintain or decrease their

Figure 13

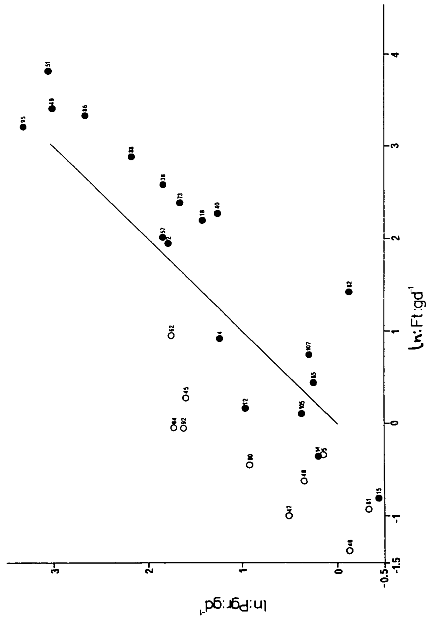
X-Axis, $\ln{:}Ft{:}gd^{-1}$. Natural logarithm of single foetus growth rate on the last day of gestation in grams per day.

Y-Axis, $\ln{:}Pgr{:}gd^{-1}$. Natural logarithm of single infant growth rate immediately after birth in grams per day.

Solid line indicates identity.

This study.

see also Figs 14 (p 193 - 4), and 15 (p 195 - 6).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growth rate. Whilst this allometric effect may be partly responsible for the acceleration of growth at birth in smaller bodied forms there is also a clear taxonomic difference between haplorhine and strepsirhine species. All the strepsirhine species accelerate in growth at birth, even Microcebus murinus (81), a species with a final uterine growth rate similar to haplorhine species (see Figure 9 p 159 - 160).

This postnatal acceleration of growth of the strepsirhines is a reflection of firstly, the relatively low intra uterine growth velocity at birth. (In fact the lowest of all living mammals, a feature which has been associated with the evolutionary 'advancement' of the order Primates (Payne et al 1968), though as this study reveals within the primates, the strepsirhines have the lowest relative growth rates at birth (Figure 9 p 159 - 160). And secondly, of the high rate of growth after birth relative both to infant weight and to maternal weight, (Figures 14 p 193 - 4 , and 15 p 195 - 6).

It is at the time of birth that the differences in the patterns of growth of strepsirhine and haplorhine species are most clearly shown. However there are differences throughout growth, during the foetal period and after birth that distinguish the general pattern of growth of the strepsirhine from the haplorhine.

We shall concentrate for a while on the physiological aspects of strepsirhine growth as compared with the haplorhine pattern and with the general mammalian pattern and then proceed to discuss these strepsirhine features in relation to the ecology of the group.

Figure 14

X-Axis, ln:Nb:g. Natural logarithm of single neonatal body weight in grams.

Y-Axis, ln:Pgr:gd^{-1}. Natural logarithm of single infant growth rate immediately after birth in grams per day.

All Primates N = 36: $\bar{x}$ = 4.72, $\bar{y}$ = 1.10
P.A. = 0.51 (0.41, 0.63)
R.M.A. = 0.57, (Linear) Regression = 0.47
r = .83, r^2 = .69

Haplorhines N = 25: $\bar{x}$ = 5.43, $\bar{y}$ = 1.24
P.A. = 0.66 (0.56, 0.77)
R.M.A. = 0.68, (Linear) Regression = 0.63
r = .93, r^2 = .86

Strepsirhines N = 11: $\bar{x}$ = 3.10, $\bar{y}$ = 0.78
P.A. = 0.94 (0.66, 1.33)
R.M.A. = 0.95, (Linear) Regression = 0.82
r = .87, r^2 = .75

Upper Solid line: P.A. (Strepsirhines)
Lower Solid line: P.A. (Haplorhines)

First presented in this form in this study, with additional data to Case (1978).

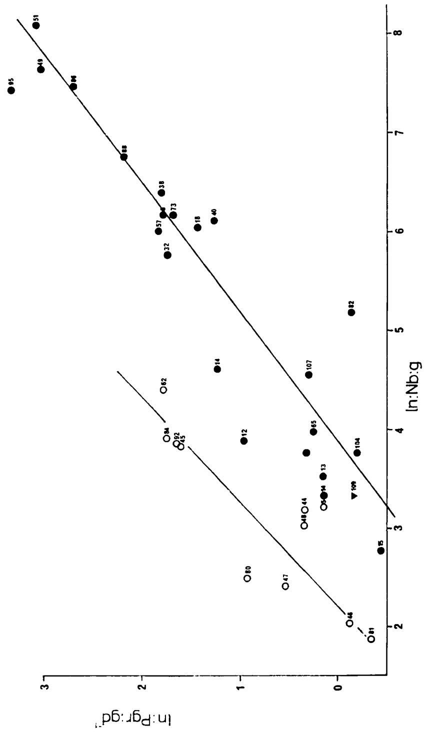
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Figure 15

X-Axis, ln:Ab:g. Natural Logarithm of Adult female body weight in grams.

Y-Axis, ln:Pgr:gd^{-1}. Natural logarithm of mean single infant growth rate to weaning in grams per day.

<u>All Primates</u> N = 37, $\bar{x}$ = 7.27, $\bar{y}$= 1.08
P.A. = 0.45 (0.38, 0.53)
R.M.A. = 0.49, (Linear) Regression = 0.43
r = .89, r^2 = .78

<u>Haplorhines</u> N = 26, $\bar{x}$ = 7.89, $\bar{y}$ = 1.20
P.A. = 0.51 (0.43, 0.59)
R.M.A. = 0.53, (Linear) Regression = 0.49
r = .93, r^2 = .86

<u>Strepsirhines</u> N = 11, $\bar{x}$ = 5.82, $\bar{y}$ = 0.78
P.A. = 0.69 (0.58, 0.80)
R.M.A. = 0.69, (Linear) Regression = 0.67
r = .96, r^2 = .93

c.f. Case 1978, additional data in this study.

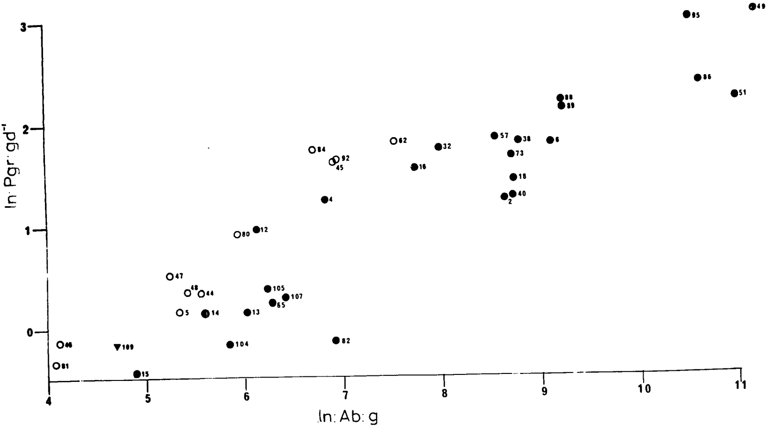
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Figure 16

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:Wt 1st Sol:g. Natural logarithm of single infant weight at age of first consumption of solid food in grams.

<u>All Primates</u> N = 21, $\bar{x}$ = 6.81, $\bar{y}$ = 5.24
P.A. = 0.76 (0.70, 0.83)
R.M.A. = 0.77, (Linear) Regression = 0.75
r = .98, r^2 = .96

<u>Haplorhines</u> N = 12, $\bar{x}$ = 7.50, $\bar{y}$ = 5.71
P.A. = 0.78 (0.73, 0.84)
R.M.A. = 0.79, (Linear) Regression = 0.78
r = .99, r^2 = .99

<u>Strepsirhines</u> N = 9, $\bar{x}$ = 5.89, $\bar{y}$ = 4.62
P.A. = 0.79 (0.61, 1.00)
R.M.A. = 0.80, (Linear) Regression = 0.75
r = .94, r^2 = .88

Solid line: P.A. (Haplorhines)
Dashed line: line of identity.
(calculations exclude value for man, 51)

This study

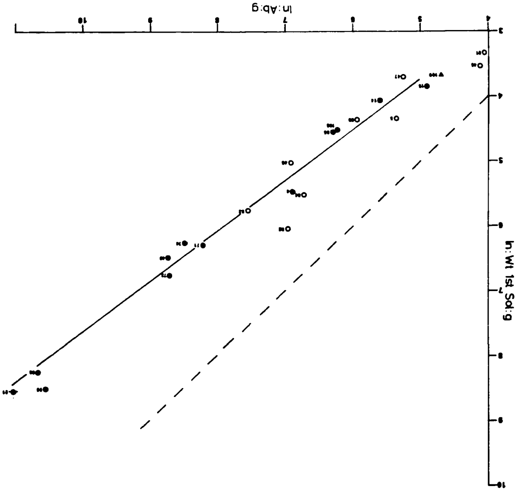
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Figure 17

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:Wt wean:g. Natural logarithm of single infant weight at age of weaning in grams.

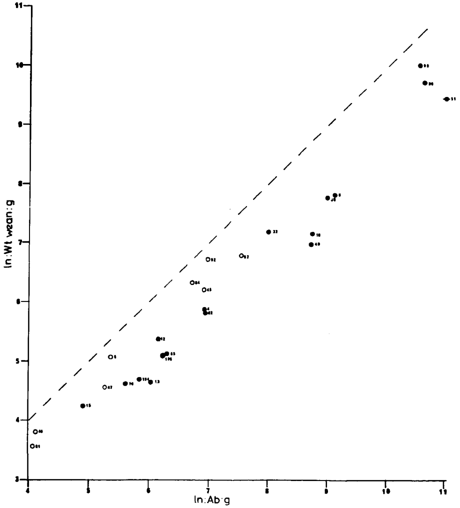
<u>All Primates</u> N = 24: $\bar{x} = 6.97$, $\bar{y} = 6.03$
P.A. = 0.89 (0.82, 0.97)
R.M.A. = 0.89, (Linear) Regression = 0.87
$r = .98$, $r^2 = .96$

<u>Haplorhines</u> N = 16: $\bar{x} = 7.63$, $\bar{y} = 5.28$
P.A. = 0.94 (0.87, 1.02)
R.M.A. = 0.94, (Linear) Regression = 0.93
$r = .99$, $r^2 = .97$

<u>Strepsirhines</u> N = 8 : $\bar{x} = 5.88$, $\bar{y} = 5.38$
P.A. = 0.97 (0.87, 1.07)
R.M.A. = 0.97, (Linear) Regression = 1.02
$r = .99$, $r^2 = .98$

Dashed line indicates identity

This study.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Strepsirhine growth and energetics. The strepsirhine infant at birth is relatively lighter than the haplorhine in relation to the mother at birth, (see Figure 8, p 157 - 8). The long gestation periods of all but a few strepsirhines suggests a relatively reduced stress of pregnancy, in comparison to the haplorhines. After birth the strepsirhine infant grows much faster than the haplorhine of the same size. During the very early post natal growth of the infant it might be that (in comparison with the haplorhini) the relatively lower cost of metabolic maintenance of the smaller infant to the strepsirhine mother frees relatively more nutrients for growth. However, this period passes rapidly and by the age that the infant first takes solid food both strepsirhine and haplorhine infants are at equivalent weights in relation to maternal weight (Figure 16 p 197 - 8). At this size though the strepsirhine infant is still growing faster than the haplorhine infant so that by the time of weaning strepsirhine infants are relatively heavier in relation to the mother (Figure 17, p ,199- 200). This suggests that whilst during pregnancy the strepsirhine mother endures less energetic stress than the haplorhine, this position is reversed after the birth of the infant.

This feature of strepsirhine growth pattern suggests some adaptation to seasonal environments. As discussed earlier the birth of strepsirhine infants is usually associated with the onset of seasonal food abundance. Gestation is often during harsh conditions whilst the period from birth to weaning occurs in aleviated environmental conditions.

Martin has suggested (1972) that at some period in their evolutionary history, the strepsirhine ancestors lived in strictly seasonal environments.

This is supported by the Interspecific comparisons of the growth of primates presented here. The maximum energetic stress placed on the mother is during lactation at the point of maximum milk consumption of the free living infant. The most critical period for the survival of the mother and infant in terms of energy supply is during the lactation period. Brody (1945) has estimated for the rat, goat, and cow the efficiency of maternal conversion of nutrients to milk is 60%. This must then be converted to useful energy by the infant, for maintenance of tissue and temperature and growth of the body at its greatest weight since conception whilst still totally dependent for nutrients on the mother. This method of maintenance is almost certainly markedly less efficient than foetal energy exchange from mother to offspring.

In conditions of strict seasonal changes in food availability the optimum use of the prevailing conditions requires the maximum stress on the energetic relations of mother and infant to be coincident with the maximum availability of energy from the environment. In the strepsirhines the extension of gestation and the relatively low stress during pregnancy in the season of poor food availability followed by rapid postnatal growth to weaning in the period of maximum food availability, fully support Martin's contention. These patterns must have been well established in strepshrhine evolutionary history since they persist in captive conditions of regular food availability and only photoperiodic indications of seasonal change, and in relatively constant conditions in Madagascar rain forest, and African and Indian forest (Martin 1972, Charles-Dominique 1977). The three species identified earlier with relatively high foetal growth rates at birth, Microcebus murinus (81), Cheirogaleus major (33) and Varecia variegatus (113) deserve special consideration in respect of this hypothesis.

For the purpose of estimating maternal stress during pregnancy Payne et al (1968) extrapolated from growth rate of the gestating foetus at birth to estimate post natal growth (see Figure 13 p 190 - 1). From it can be seen that this estimate is roughly correct for the haplorhines though not for the strepsirhines. There is a slight tendency for the smaller bodied haplorhines to accelerate their growth rate after birth whilst the larger bodied forms maintain or slightly decrease the rate of growth after birth.

In opposition to the evolutionary conditions of strepsirhine ancestors it would seem that relatively stable environmental conditions allow gestational growth and post natal growth to run into each other without sudden changes in the haplorhinii. The smallest bodied haplorhines the tarsier and the marmosets, live in tropical rain forest areas with relatively constant food supply. Larger bodied forms may live in seasonal environments but the slower growth rates and low stress of pregnancy and lactation (see last Chapter p. 155 et sqq and this Chapter next section) may allow the larger species to overcome the 'problems' of fitting in the changing stresses of the reproductive process into the patterns of seasonal availability of food.

Another aspect of the less traumatic growth process in the haplorhine species is associated with the more stable metabolic regime of these species mentioned earlier (p. 52 et sqq). In this connection the relatively larger brain size attained by the adult haplorhines is an important feature of their adaptation and requirement of relatively stable conditions for successful reproduction. These features of the divergence of haplorhine and strepsirhine reproductive processes will be discussed in the following chapter which will consider more fully the species adaptations and evolution of the whole of the reproductive pattern.

One particular species which stands out among the haplorhines is the talapoin monkey Miopithecus talapoin (82). The exceptionally slow growth of this species is probably associated with its relatively large adult brain size (Bauchot and Stephan 1969) which these authors suggest is a product of evolutionary 'miniituarization'.

Section c) Postnatal development of the brain.

A section on the postnatal growth of the brain is included, not because of the discovery of any profound relationships in the available data, but to briefly discuss some expected relationships which with present information are inconclusively tested. In the previous chapter the relationships between brain growth and body growth *in utero* were considered. The crude picture of development given by the growth in weight of the foetal brain and body, and their interspecific allometry suggest a close parallel in the development of the two. In post natal development the changing relationship between mother and infant in both the qualitative and quantitative sense are certainly correlated with brain development. Analysis of the very crude and limited information available for this period in brain development do not, in the author's opinion, yield much clarification on this expected correlation but the exercise may at least expose the limitations of present knowledge.

Little is known of the comparative development of the brain post natally, most research has been concentrated on the rat and on man. With two species so different in size and evolutionary history it is not known whether the differences in brain development are associated principally with allometric factors (size dependent) or on the taxonomic distinction between rodents and primates.

The qualitative development of the brain follows a roughly similar pattern for all mammalian species but the timing of the stages in development in relation to the course of foetal and postnatal growth may differ markedly between species. Marshall (1968) has divided the common pattern of brain development into four stages:

I Cell division dominant
II Division almost complete, but growth of cells, axons and dendrites
III Continued growth of neurons now associated with myelination
IV Myelination dominant

For man period I occupies about the first two thirds of foetal growth, period II being complete by the time of birth; period III lasts about four months after birth and period IV then continues for several years (the adult brain size is achieved by about ten years though important chemical changes associated with puberty and physiological maturity continue into adulthood). Man may be a poor model for primate post natal brain development since an important and unique feature of the human primate post natal brain growth is that foetal isometry of brain/body ratio is maintained for about 1 year of post natal growth (Gould 1977, see p. 336 et sqq).

For the rat however, period I lasts to birth, period II to the first 10 days after birth, period III for another 10 days and period IV up to adulthood (Marshall 1968, Sinclair et al 1972).

These stages in development are associated with a complex pattern in the growth in weight of the different parts of the brain. For instance the cerebral cortex with unmyelinated fibres achieves a greater proportion of adult size by birth than the lower parts of the brain, which do not approach adult size until the myelination of fibres gets under way. The absolute size of the brain in development is therefore not a very informative measure of the development of its parts and their integration.

There is no allometric trend in the proportion of adult brain size at birth for either of the two main groups of primates. For the haplorhines the variation lies between 31.3 - 62.2% (n = 16 $\bar{x}$ = 51.7%) and for the strepsirhines between 31.3 - 47.4% (n =9 $\bar{x}$ = 39.7%). The difference in mean values between the two major primate groups is associated with the relatively smaller brain weight of the strepsirhines. As we have seen, the size of the brain at birth is linearly proportional to body size for all primates, (Figure 10 p 171 - 2). Whilst the size of the adult brain is slightly smaller for a given body weight for the strepsirhines (Figure 11 p 173 - 4), the size of the newborn is relatively smaller still in the strepsirhines for a given maternal body weight (Figure 8 p 157 - 8).

The lack of allometric trend in the proportion of adult brain size at birth can be seen as the interrelation of the similar scaling of maternal brain size and litter size against maternal weight, and the linear proportion of neonatal brain size as a proportion of total neonate weight regardless of absolute size (Figure 10, p 171 - 2 , see p. 141 et sqq). It would seem from the limited data available for haplorhines that the principal source of the variation in the proportion of adult brain size attained at birth arises from the post natal growth of the brain. The size of the neonatal brain appears to be well correlated with the neonatal body size (Figure 10, p 171 - 2) and neonatal body size well correlated with maternal body size (Figure 8, p 157 - 8). Certain species with a low proportion of adult brain size at birth are seen to have relatively large brains in adulthood for example Cebus capucinus (17) Miopithecus talapoin (82), Homo sapiens (51). Ateles geoffroyi (7) on the other hand with the highest value for neonatal proportion of adult brain size has a relatively small adult brain.

Whilst the suggestion here that within the haplorhines relative brain size in the adult is largely a result of postnatal growth is based only on a few exceptional species, (there is not enough evidence to support a systematic testing of the hypothesis), these same species show a corroboration of this suggestion in the timing of their postnatal development. The relatively slow growth to weaning of species such as Saimiri scuireus (107), Miopithecus talapoin (82) Homo sapiens (51/52) is matched by their relative late development to weaning, menarchy, age of first delivery. (Figures 18, p 209 - 210 , 19, p 211 - 2 , 20, p 213 - 4). So it would seem that within the haplorhines, postnatal growth of the brain to a relatively large adult size is associated with relatively delayed behavioural and physiological development, and slow rates of somatic growth in weight.

However, whilst this may seem to reflect an extension of the general features of the primates (i.e. relatively large brains, slow growth rates and long development), it is important to see that the comparison of the haplorhines with the strepsirhines yields the opposite conclusions in relation to the generally smaller proportion of adult brain size at birth in the strepsirhines. Whilst within the haplorhines as a group, those species with a small proportion of adult brain size at birth appear to have slow growth and late development, the strepsirhines, with a generically lower proportion of adult brain size at birth develop more rapidly postnatally than the haplorhines.

In fact, this apparent contradiction is an example of the dangers of extrapolation from one level of allometric variation to another, (see p. 34 et sqq, p. 345 et sqq), and of the problems in model building

Figure 18

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:wean:d. Natural logarithm of age at weaning in days.

All Primates N = 33 : $\bar{x} = 7.50$, $\bar{y} = 5.19$
P.A. = 0.51 (0.44, 0.59)
R.M.A. = 0.54, (Linear) Regression = 0.49
$r = .91$, $r^2 = .83$

Haplorhines N = 22, : $\bar{x} = 8.03$, $\bar{y} = 5.50$
P.A. = 0.56 (0.46, 0.66)
R.M.A. = 0.58, (Linear) Regression = 0.54
$r = .93$, $r^2 = .86$

Strepsirhines N = 11 : $\bar{x} = 6.44$, $\bar{y} = 4.56$
P.A. = 0.33 (0.21, 0.46)
R.M.A. = 0.37, (Linear) Regression = 0.32
$r = .85$, $r^2 = .71$

Solid line : P.A. (Haplorhines)
Dashed line: P.A. (Strepsirhines)

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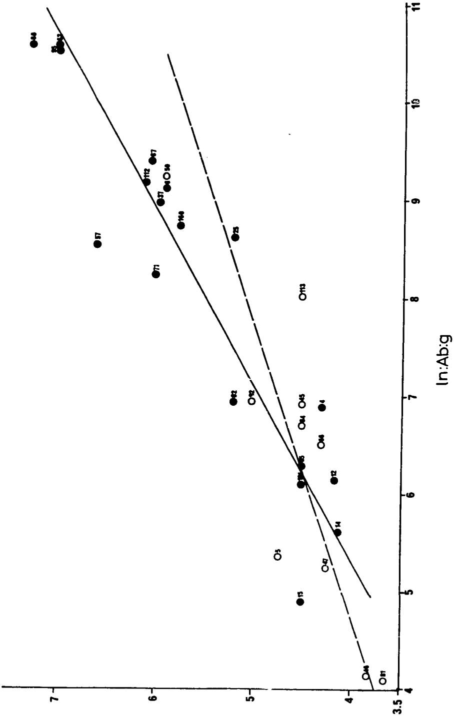
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Figure 19

X-Axis, ln:Ab:g. Natural logarithm of adult female body weight in grams

Y-Axis, ln:Men:mo. Natural logarithm of age at menarche in months.

<u>All Primates</u> N = 37, $\bar{x}$ = 7.95, $\bar{y}$ = 3.48
P.A. = 0.42 (0.34, 0.51)
R.M.A. = 0.47, (Linear) Regression = 0.40
$r = .85$, $r^2 = .72$

<u>Haplorhines</u> N = 27, $\bar{x}$ = 8.66, $\bar{y}$ = 3.86
P.A. = 0.36 (0.24, 0.48)
R.M.A. = 0.44, (Linear) Regression = 0.33
$r = .75$, $r^2 = .56$

<u>Strepsirhines</u> N = 10, $\bar{x}$ = 6.03, $\bar{y}$ = 2.47
P.A. = 0.26 (0.08, 0.44)
R.M.A. = 0.35, (Linear) Regression = 0.25
$r = .69$, $r^2 = .48$

Solid line: P.A. (Haplorhines)

This study.

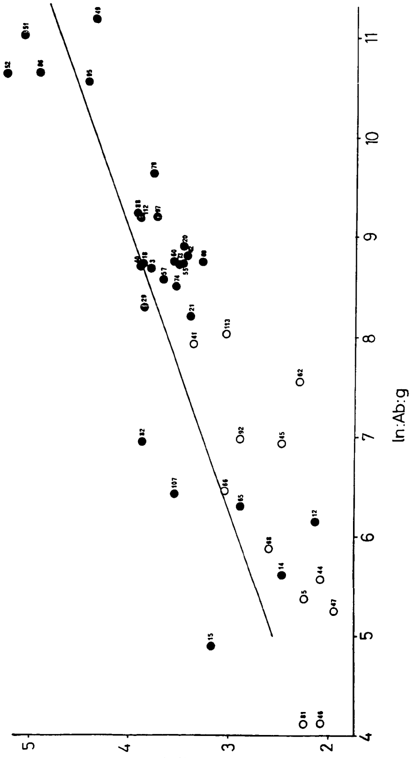
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Figure 20

X-Axis, ln:Ab:g. Natural logarithm of adult female body weight in grams.

Y-Axis, ln:1st Del:d. Natural logarithm of age at first delivery in days.

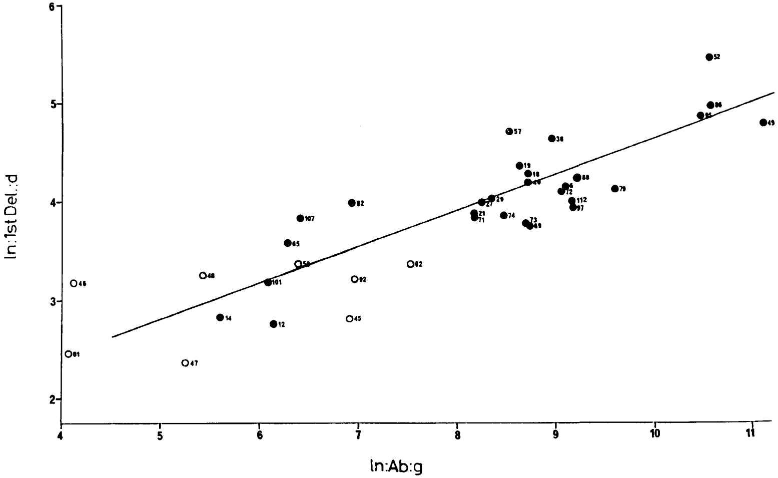
All Primates N = 33, $\bar{x}$ = 8.03, $\bar{y}$ = 3.86
P.A. = 0.36 (0.28, 0.44)
R.M.A. = 0.40, (Linear) Regression = 0.34
r = .85, r^2 = .72

Haplorhines N = 26, $\bar{x}$ = 8.60, $\bar{y}$ = 4.10
P.A. = 0.36 (0.27, 0.46)
R.M.A. = 0.42 (Linear) Regression = 0.34
r = .82, r^2 = .68

Strepsirhines N = 7, $\bar{x}$ = 5.91, $\bar{y}$=2.99
P.A. = 0.13, (-0.11, 0.38)
R.M.A. = 0.32, (Linear) Regression = 0.12
r = .37 , r^2 = .14

Solid line: P.A. (Haplorhines)

This study (c.f. Western, 1977, for ungulate data)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from factors considered in separation from the overall context. Whilst within a group larger adult brain size may be a consequence of extended postnatal development, comparisons between groups in the extent of postnatal brain growth are dominated by the eventual relative size of the brain. A model based simply on the relative proportion of adult brain size at birth applied to all mammals would yield no correlation (data from Sacher and Staffeldt 1974). This major problem in construction of mechanistic models of biological processes arises from the natural evolutionary development of qualitative levels of organization within which generalizations may hold and beyond which are either not correlated or give the opposite conclusion. (These issues are pursued further in the next and last Chapters). Such contradictions are not, however, beyond the scope of Gould's (1977) concept of Heterochrony.

Another important aspect of postnatal brain development, as elaborated in neurophysiological studies, is the supply of nutrients to the developing brain. The rate of supply of energy and essential nutrients to the developing infant brain by the mother and the maintenance of adult brain tissue must reflect in some way the dietary intake of the species and the dietary availability of necessary nutrients (Crawford et al 1977). Harvey (pers. com.) has shown in primate species a statistically valid tendency for relatively smaller adult brain size in folivorous species as compared with frugivores and onmivores (see next Chapter). Whilst the relative size of the whole brain can tell us little of its composition or specific function the correlation clearly indicates a relationship between diet and relative brain development.

In the development of the brain the early period of cell division produces a relatively high concentration of protein in the brain, myelination in later development is associated with a large increase in the fat concentration of brain tissue. If, as in man, primate brain development sees the near completion of cell division by birth then it might be expected that the proportion of adult brain size at birth would be inversely related to the percentage of fat in the milk nutrients. Unfortunately with the data available no such correlation can be found, the calorific percentage of fat in primate milks varies between 26.6 - 60.9% of total calories, with no indication that lower fat concentration is associated with relatively greater proportion of adult brain size at birth, (Buss 1971, Turton et al 1978). This may be due to the probability that the majority of fat consumed by the infant is either catabolized for heat production or stored in body tissues and that the brain requirement for fat is only a small proportion of the total intake. On present information, the gross concentrations of nutrients in the milk tell us little of any relationship between the nutrient intake of the infant and the crude estimates of its brain development.

Another factor, for which even less information is available, is the quality of fats and proteins supplied in the milk in relation to brain development. Certain nutrients are known to be required by the infant in their final form due to the inability of the infant to synthesize them from their components. Whilst they do not comprise a large portion of the total solid intake of the infant they are absolutely necessary, these might include Essential Fatty Acids, certain vitamins and minerals.

Of particular importance in brain development are the Essential Fatty Acids (see p. 181 et sqq). Analysis of these long chained polyunsaturated fatty acids in primate milk is as yet not very thorough, but all analysed primate milks have contained these acids. The analysis of milk lipids of *Callithrix jacchus* (14), *Pongo pymaeus* and man (51/52) has revealed that the whole spectrum of fatty acids is present including the long chained PUFA (Polyunsaturated Fatty Acids). It is not known to what extent the neonate primate is capable of synthesizing EFAs. Adults of certain studied species, such as the cat (Rivers et al 1975) and the turbot (Owen et al 1975), are unable to synthesize FFAs and must obtain them solely from the diet. Slow synthesis in the human adult, placenta and foetus is reported however, Crawford et al (1977).

Crawford et al (1977) estimate that in man between 60 - 70% of the essential fatty acids of the adult brain are acquired by the time of birth (when the brain weighs of adult weight). Whilst there is almost certainly an ability of the human infant to synthesize long chain PUFA required for the brain there is still the production of these substances in the milk, as 1.57% of the total fatty acid content of the milk (Hall, unpublished data, quoted in Turton et al 1978). It is of interest to see that the long chain PUFA (C_{20} and C_{22}) are at a higher concentration in marmoset (*Callithrix jacchus* 14) milk at 5.19% of total fatty acid content (Turton et al 1978). If this difference between human and marmoset milk is eventually found to be significant, then it may reflect allometric factors in both the concentration of stored long chain PUFA in the maternal tissues which is higher in smaller bodied forms (Crawford et al 1977), or the higher specific growth rate of smaller bodied forms of a given taxon. It is to be hoped that many more detailed analyses of these essential constituents of milk will be carried out in the future. As discussed earlier (p. 83 et sqq), the flow of such organized matter will undoubtedly be found to be closely interconnected with gross measures of energy flow, and entropy flow.

Section d) Milk: energetics and composition.

From the period from birth to the first solid food taken by the infant milk provides all the materials for somatic maintenance and growth and the metabolites with which the infant provides the energy for these processes. It is also known that the immune response of the infant is established through priming by the maternal system transferred in the milk, (Brambell 1972). After the initial consumption of solid food by the developing primate infant the proportion of milk nutrients in the diet decreases till weaning.

Several factors must be considered in this period of development; the energetic dependency of the infant on the mother, the supply of essential nutrients and services not immediately related to overall energy demands, (such as the development of the immune system mentioned above) the supply of solid material to be integrated into the somatic tissue of the infant, the spontaneous development of the infant in growth and the overall adaptive features of the species population (the inter-relation of interbirth period and age at weaning for example).

Much of the evidence presented here is contradictory, partially due to innaccuracies in data but also due to inadequacies of the established theoretical models often constructed in isolation from their comparative general implications. When taken together these models fit together imperfectly.

Maternal production. Payne et al (1968) have used Brody's data (1945) for the assessment of maximum stress during lactation, taking stress as a function of the maximum milk energy production of the mother under experimental conditions. For a wide range of size and type of mammalian species the calorific value of maximum milk production is correlated with the metabolic turnover of the animal, at almost twice the basal metabolic rate (Basal Metabolic Rate $\cong$ 70KCal per $Kg^{.75}$ per day, Calorific value of maximum milk production $\cong$ 123 KCal per $Kg^{.75}$ per day). This relationship might be expected under experimental conditions of complete evacuation of all milk in the mammary during the day. It is possible that the absence of milk in the mammary is the main stimulus to production, and that this process when continually stimulated will proceed at the rate of all organic activity under the dominant influence of metabolic rate.

On the other hand let us look at energy demand of the offspring. Brody (1945) published data on oxygen consumption of newborn and growing infants of some mammalian species indicating that under conditions close to thermoneutrality most newborn, regardless of size have roughly 2 times the specific basal metabolic rate expected of adults of that size. Human babies are known to have a B.M.R. almost twice that expected of an adult mammal of a similar weight, under conditions of cold stress this rate may rise extremely rapidly (Dawes 1971). Portman (1970) reports on the heat production of very young rhesus macaques which at about 100 KCal per day is in fact 2.4 times the expected standard adult value for their size. As determined by heat production there appears to be no allometric (Body size dependent) difference in the elevation of metabolic rate in new born infants, which regardless of species size is raised to between 1 and 2 times the adult metabolic curve, for any given body weight. On a log/log plot this correlation would be indicated by a parallel line log2 higher than the standard slope for adults.

However, if the metabolic rate of the young mammal is scaled interspecifically to infant body weight to .75 power, and the weight of the newborn litter and infant at age of first solid food is scaled to approximately the .7 power of maternal weight, then the metabolic rate of the young infant is scaled to about the .5 power of <u>maternal</u> body weight.

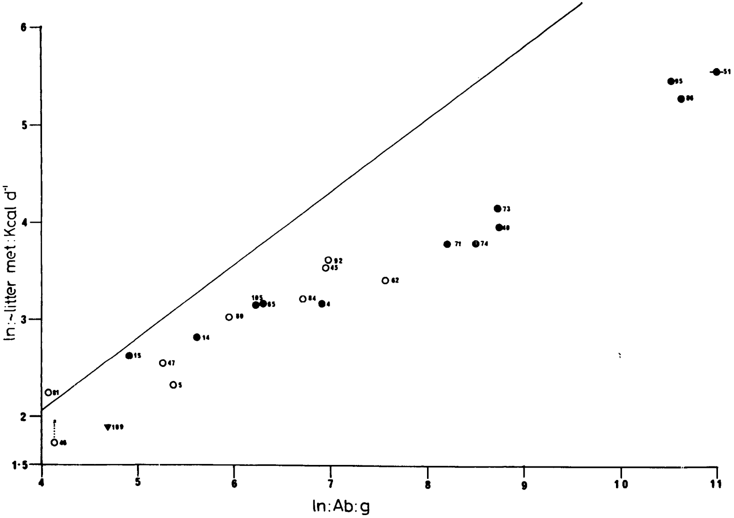
Figure 21 (p 221 - 2) shows the estimated metabolic rate of the litter at age of consumption of first solid food against <u>maternal</u> body weight. The solid line indicates Payne and Wheeler's (1968) correlation of maternal body weight with the energy of maximum milk production. The implication here is that the metabolic rate (of heat production) of <u>larger</u> bodied infants falls far short of the mothers potential energy production in milk. We are not looking at an estimate calorific consumption of the infant in this case and it is possible though unlikely, that the efficiency of milk energy conversion is better for smaller bodied infants.

Figure 21

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:$\sim$ litter met:KCal d^{-1}. Natural logarithm of estimated litter metabolic rate at the age of first consumption of solid food.

Solid line indicates adult female metabolic rate prediction from Kleiber (1961).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In adults this is not the case, Kleiber (1961), where for adult homeotherms ranging in size from the rat to the steer the efficiency of food energy utilization for the production of heat, body tissue and milk is similar regardless of size.

For a few experimental trials with young mammals ranging in size from the rat pup to the calf the actual food energy consumption does tend to increase slightly relative to metabolic size in larger bodied infants (Payne et al 1968). What happens to the 'extra' energy consumed is not known. Even supposing that for infant mammals there is this slight decrease in the efficiency of food energy utilization in larger neonates, it cannot account for the large differences in the larger bodied forms between estimated calorie intake and maximum milk energy production in the mother. For man, the only primate with experimentally determined figures this difference is clearly seen.

Working on the assumption that at the age the infant first takes solid food its requirement for milk is reaching its absolute maximum, we can calculate the difference between energetic demand of the infant and the experimental potential sacrifice of the mother in milk production (from Payne and Wheeler 1968).

The maximum human milk production is ~2670 KCal per day. Taking Brody's (1945) and Kleiber's (1961) values for mammalian cost of milk production (60%-64% efficient) the extra calorific intake of the mother required for maximum milk production would be ~4500KCal per day. On the other hand the infant when first taking solids consumes ~700KCal per day.

Field studies reveal that normal human lactation can be accomplished by an additional intake of about 1000 KCal per day by human mothers (Crawford pers com). This is roughly in agreement with the experimental figure of 700 KCal per day infant intake given above, since with the cost of milk production to the mother taken into account the expected additional maternal intake during lactation would be ~ 1170 KCal per day, once again a quarter of the estimated maternal requirement of 4500 KCal for maximum milk production. It is most likely that the experimental extraction of milk over relatively short periods of time from larger bodied mammals is well in excess of the normal demand made by the growing infant.

Whilst it is well known that for small bodied species of primate such as the marmoset the birth of triplets (normally twins are born) almost invariably results in the loss of an infant under normal conditions of maternal rearing (Hiddleston 1977, Brand pers com). It is also the case that in primitive human societies two infants are not normally suckled simultaneously, the infrequent birth of twins or the close birth of successive infants is often culturally dealt with by infanticide (Lee 1976).

The reduced maternal stress of lactation apparent from Figure 21 (p 221 - 2) is real enough, as is the empirical data quoted for Homo. It is clear however, that the 'stress' on the mother during the reproductive cycle in terms of the real production of viable infants cannot be assessed simply in terms of gross energetic exchange. These contradictions lie at the heart of the understanding of living systems which though exposed still present major problems of interpretation.

Milk composition. The conflicting information on the energetic relations between the lactating mother and the suckling infant present more rather than less difficulty when the composition of the milk is analysed in relation to the uses of milk nutrients in infant maintenance and growth. One problem lies in the data itself; the concentration and composition of mammalian milk, normally assessed in crude measures of total protein, fat and lactose per unit volume, varies between animals of the same species, during the feed and during the period of suckling (Buss 1971).

Nearly all the available figures for primate milk composition have been obtained fairly soon after birth, but are based on small sample sizes. These factors may account for some of the variation in milk composition in the primates, but some allometric trends are clear in the interspecific comparison. For non primates Payne et al (1968) established that larger bodied infants consumed milk relatively less concentrated in digestible protein. The few primate values given in their study reveal the conspicuously low concentration of protein in primate milk. The concentration of total calories in the milk also declines interspecifically for larger bodied infants, but the primate milks are not distinct from other mammalian milks in respect of total calorific concentration of milk.

Over a wide range of infant body sizes (wider than for the primate data in this study) they found that the calorie concentration of milk declines interspecifically to the -.28 power of infant body weight. Payne et al saw this as an indication that the volume of milk consumed daily was directly proportional to infant body weight, and that daily calorie intake would be proportional to infant body weight to approximately the .73 power, a similar scaling of calorie intake for adults relative to body size.

Since the interspecific scaling of protein concentration is similar Payne et al concluded that the protein intake of the infant is directly correlated to the daily growth rate of the infant. The low protein content of primate milks is associated with their relatively slow rate of growth in comparison with other mammals of similar size. In their survey of five mammal species for which complete experimental data is available they show that daily protein intake is related to daily growth rate by a ratio of about one to four, apparently independent of infant body size. The data presented here for primates, haplorhines in particular,largely confirm this picture with the principal exception that no clear correlation is found between total calorific concentration of milk and infant body size. This may be a consequence both of the problems in sampling the constituents of milk and also of a wide natural variation in this value which yields a poor correlation with the relatively small range in primate infant weights as compared with the all mammal sample used by Payne et al (1968). For a sample of 13 haplorhines the total calorie concentration has no significant correlation with infant body weight. However, the concentration of protein in the milk does decline against neonatal body weight, to the power -.34 a value somewhat lower than -.28 quoted by Payne et al for total calorie concentration for mammalian milk, (Figure 22 p 227 - 8).

Figure 22

X-Axis, ln:Nb:g. Natural logarithm of single neonatal body weight in grams.

Y-Axis, ln:pr milk:% total KCal. Natural logarithm of the concentration of protein calories in milk as a percentage of total calories in milk.

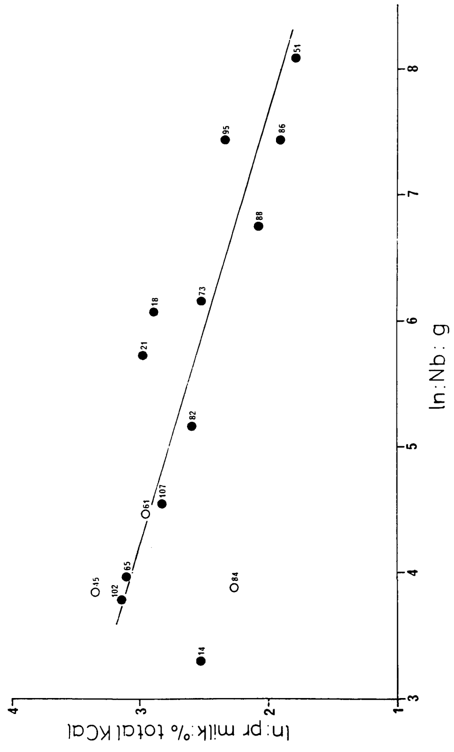
Haplorhines N = 12, $\bar{x}$ = 5.72, $\bar{y}$ = 2.56
P.A. = -0.23 (-0.34, -0.12)
R.M.A. = 0.29 (Linear) Regression = -0.22
r = -0.77, r^2 = .59

Solid line: P.A. (Haplorhines)

For comparison, calculations substituting total litter weight at birth for single neonatal body weight on X-Axis:

Haplorhines N = 12, $\bar{x}$ = 5.89, $\bar{y}$ = 2.56
P.A. = -0.28 (-0.40, -0.16)
R.M.A. = 0.34, (Linear) Regression = -0.27
r = -0.78, r^2 = .62

c.f. Payne et al 1968, additional data in this study.


ln:pr milk:% total KCal
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The assumption made by Payne et al (1968) in the absence of any data on growth rates in early infancy was that growth rate proceeded at a rate determined by infant metabolic rate, i.e. scaled interspecifically to the .75 power of body weight. This appears to hold true for haplorhine species, (see Figure 14 p 193 - 4). This value, and the higher exponent found for strepsirhine species, should be preferred to the values of Case (1978) whose data set is considerably smaller than that used here.

The principal contradiction in the primate data, not apparent in the all-mammal material, is the disimilarity in the lack of scaling of total calorie concentration and the negative scaling of protein concentration in the milk consumed by larger infants. The implications, if such can be drawn from the information available, are that larger bodied infants consume more calories for maintenance than are actually liberated in heat production or that the protein intake is not directly related to growth rate. The latter case would be that smaller infants use some of the protein intake for maintenance, or that for larger bodied infants a larger portion of the non protein element of milk, most likely fat, is used for body weight increase.

This problem of data interpretation could be largely resolved by studies of the milk volume consumption of infants in natural conditions (such as the study by Martin 1968 on tree shrews) and calorific analysis of the excreta of growing infants. These factors in the energetic relationship between the infant and the mother and the duration of the relationship would aid considerably the understanding of the stress of lactation and thus the overall energetic context of life history in related species.

Another issue not dealt with here due to the lack of information is the expected general difference between haplorhine and strepsirhine milks. Since the strepsirhine infant is growing relatively faster than the haplorhine the nutrient requirements are almost certainly reflected in the concentration of nutrients in the milk. The only values for strepsirhine milk, for Nycticebus coucang (84) and Galago crassicaudatus (45) (see Buss 1971), indicate a high proportion of fat calories in the milk, with an inversely lower proportion of lactose calories. The concentration of digestible calories per unit volume is also the highest and fourth highest respectively of all the primate milks analysed (n = 15) which is compatible with the relatively high growth rates of strepsirhine species. Comparative studies of the milks of the strepsirhines, and non-studied primates will aid considerably the understanding of early post natal growth patterns and particularly in clarifying further the nature of the evolutionary division between the haplorhines and strepsirhines.

Section e) Weaning.

The period of weaning represents a further break up in the relationship between offspring and the mother in the course of the development of the life cycle. By the age of weaning the infant is able to survive without either the quantitative energetic contribution of the mother or the qualitative contribution of specific nutrients in the milk such as the essential fatty acids, vitamins and trace elements. This is clearly dependent upon the infant's achievement of the ability, both behavioural and physiological, to seek and identify foods in the habitat, to digest these foods and to synthesise all the required proteins, fats, salts and sugars for metabolism and growth. The immune response of the infant must also be independent of the maternal immune response transmitted through the milk (Brambell 1972). This development of the infant frees the mother of the major energetic load of reproduction.

With these features of weaning in mind it is possible to draw some tentative conclusions from the limited data available for this period. This information includes the weight and age of the infant at weaning, which is analysed in association with the behavioural and physiological development of the infant and the reproductive cycle of the mother.

Figure 17 (p 199 - 200) shows the relation of weight at weaning with adult maternal weight. The solid line is that of identity. The comparison with Figure 8 (p 157- 8) and Figure 16 (p 197 - 8) is instructive in two respects. These are the relation of strepsirhine and haplorhine species and the overall scaling of the relationship.

Considering the taxonomic relations first, we see that in the post natal growth of the primates from birth to weaning the strepsirhine infants, with their relatively faster post natal growth rate than haplorhine infants, having been lighter than the haplorhine at birth are heavier by the age at weaning, comparative to maternal weight. Another feature of Figure 17 (p199 - 200) is the almost linear relation of size at weaning to adult maternal size (this study). At birth and at the age of first consumption of solid food the scaling of infant weight is closer to .75 power of maternal weight. During the period of nutritional dependence on the mother it was the scaling of litter weight at these periods which was interpreted as a function of the dominant nutritional and energetic relationship between the developing infant and the mother. In the section on milk (p 219 et sqq) it was seen that the maximum production of milk energy under experimental conditions does not agree with the scaling of metabolic rate of the infant litter either at birth or at the age of first consumption of solid food. This is a 'consequence' of the .75 scaling of litter weight to maternal weight at these stages of growth.

However, by definition this nutritional and energetic relationship between the infant and the mother is terminated at weaning. For this reason the scaling of weight at weaning against maternal weight is a reflection of the independent development of the infant and the measure of the level of development in body weight of the single infant as a fraction of the adult weight is of more significance than litter weight at weaning. The weight of the litter at weaning is of less interest since the consequences of the infants size as a member of a litter is no longer dependent upon the energetic contribution of the mother.

Thus the linear scaling of the single infant weight at weaning to the maternal weight cannot be seen as consequence of the maximum energy supply of maternal milk, the incongruence of this information with that of infant metabolic rate remains unsolved (see p 219 et sqq). The linear scaling at weaning is not a feature of nutritional dependency but of the necessary stage of independent development of the infant when it can finally dispense with maternal secretions.

If the supply of maternally synthesized nutrients to the infant is in a sense an indication of the failure of the infants metabolic processes to fulfill these requirements itself, then at weaning the infant has acquired an organized internal regime capable of performing all the basic metabolic processes of adulthood. The brain is both the organizer and the reflection of this organization of the body's metabolic functions. At weaning we would expect that the infant's brain is essentially adult, not in the sense of specific adult social behaviours but in the sense of the physiological organization of the metabolic process. Whilst there is very little information on the postnatal growth of the brain in primates generally, data for human brain growth (Brody 1945) and limited data for rhesus macaque brain growth (Zuckerman et al 1937) shows that approximately 80 - 85% of adult brain size is aquired by weaning age. (There is some difference in the proportion of adult brain size at birth in these two species 50% for the macaque but only 30% for the human).

If the major part of adult brain tissue is established by the age of weaning, then the interspecific proportionality of brain size to body size at weaning is similar to that of the adult. If this is the case it would confirm to some extent the essentially adult form of organization of the weaned infant, though clearly the 'concentration' of neural tissue to body tissue in the weanling would be some generally standard multiple of the 'concentration' of the adult.

The close similarity in the age at weaning and age at independent locomotion of the infant suggests that the co-ordination of neural and muscular activity has reached an essentially adult form by the age of weaning (Figure 23, p 235 - 6).Whilst this similarity may in certain cases arise from the field observer identifying the proximity of a carried infant to its mother with continued suckling, often the sources are different for the two values, and recent authors usually distinguish between the two parameters of independent locomotion and weaning. The identity of the two values for each species is similar for all body sizes, and there appears to be no overall allometric effect in the inter-relation of these two developmental parameters (see also Doyle in press).

Taxonomic implications. Another feature of the Figures dealing with the weaning period is that the strepsirhine infant, whilst generally not taking any greater time to weaning (Figure 18 p 209 - 210) is , as a result of the rapid growth rate, relatively heavier at weaning than the haplorhine in relation to it's own adult weight (Figure 17 p199 - 200). For the strepsirhine species for which information is available all have achieved at least half their adult weight by weaning. The haplorhine species with only a very slight tendency for larger bodied species to be relatively lighter at weaning (this study), have achieved between 1/6 and ½ of adult body size by weaning.

As discussed earlier, the growth patterns of the strepsirhines appear to be adapted for seasonal environments. The relatively large size of the strepsirhine infant by weaning may well be part of this adaptation to seasonality.

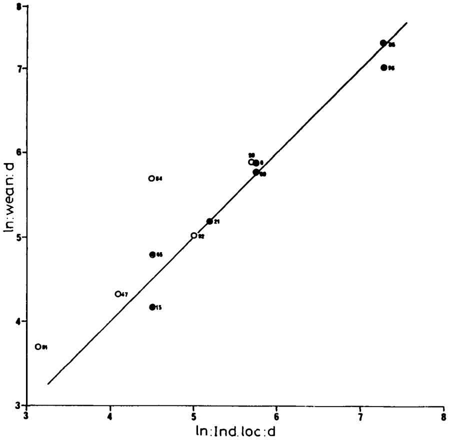
Figure 23

X-Axis, ln:Ind.loc:d. Natural logarithm of age at Infant attainment of independent locomotion in days.

Y. Axis, ln:wean:d. Natural logarithm of age of weaning of infant in days.

Solid line indicates identity.

This study.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For both the Malagasy lemurids and the Asian and African lorisids weaning conincides with the end of the periods of maximum food abundance (Charles-Dominique 1977, Martin 1972, Doyle 1974). The subsequent poor season, which for some strepsirhine species may include very low temperatures and a drastic reduction in food availability may be a critical period in the life cycle. Large body size for the weaned infant may allow both better thermoregulation and the use of stored reserves in extreme conditions.

Weaning and the maternal reproductive cycle. As mentioned earlier the weaning of the infant frees the mother from the major energetic demands of growing infant. In Figure 24 (p 239 - 240) it can be seen that regardless of size, the weaning of the infant is associated with the start of the following pregnancy. The values for interbirth period are from different sources from those of gestation and weaning length. The apparent feature of the primates in the concentration of maternal activity on a single litter till the age of weaning may be a distinguishing feature of the order, certainly it establishes an important aspect of the life cycle in these species, which will be discussed in the next chapter. The exceptions and deviations from this pattern are found only in the small bodied strepsirhine species which are dominated by the seasonality of their habitats which is reflected in their reproductive activity. In laboratory colonies of Microcebus murinus (81) and Galago demidovii (46) two litters a year may be obtained (Glatson pers com, Martin 1972, Andriantsiferana et al 1974, and Charles-Dominique 1977, pers com respectively). Even with this rapid breeding the infant is weaned before the birth of the subsequent litter and, in fact, before the period of maximum maternal stress of late pregnancy. Microcebus murinus (81) has an interbirth interval of 70 days for the female which breeds twice in the reproductive season, the age at weaning is 45 days, thus 25 days of the gestation period of ~60 days is free of nutritional demands of the previous litter. The semi-natural conditions of Andriantsiferana's colony, suggest that some females may have two litters in the breeding season in the wild. For Galago demidovii (46) captive conditions have produced a minimum interbirth period of 108 days (Charles-Dominique, pers com) whilst the previous infant or litter is weaned at 45 days after birth leaving 65 days of the gestation period (normally about 110 days) free from the energetic demands of the previous litter. In the wild however there is no evidence that this species has more than one litter a year.

The necessary adaptations to seasonal environments present the greatest 'problems' to small bodied species and the exceptionality of Microcebus murinus (81) and Galago demidovii (46) in Figure 24 (p 239 - 240) which probably applies to other small bodied strepsirhine species (for which insufficient data exist) reflects the special adaptations required in seasonal environments, (see p 43 et sqq, and p 305 et sqq).

An important consequence of the similarity of interbirth period with the sum of gestation and weaning periods arises out of the differences in the scaling of the two parameters interspecifically. The scaling of gestation period against maternal body weight is roughly proportional to (maternal weight)$^{.1}$ whereas the age at weaning is scaled to (maternal weight)$^{.48}$. Unfortunately

Figure 24

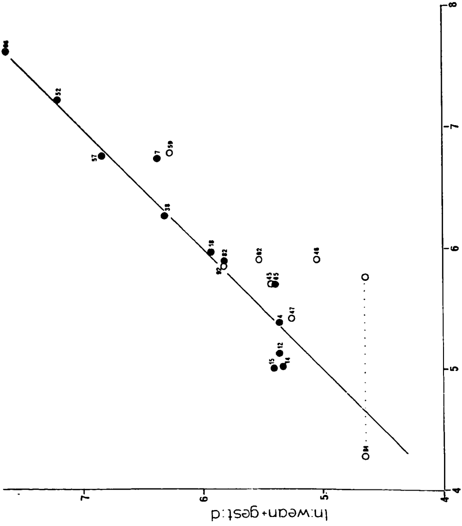
X-Axis, ln:interb:d. Natural logarithm of average period between births in days.

Y-Axis, ln:wean + gest:d. Natural logarithm of period from conception to weaning in days.

Solid line indicates identity.

(*Microcebus murinus* (81), may give birth either once or twice in the breeding season, indicated by the two values joined by the dotted line)

This study.


ln: interb: d
ln: wean+gest: d
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45
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47
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12
15
14
84

it is not known whether this is generally true for other orders of mammals, Kihlstrom (1972) publishes information on the scaling of gestation period varying between .037 - .195 powers of maternal weight for several mammalian taxa. To the authors knowledge no such study is available on the scaling of the weaning period, but it is unlikely that the scaling is as low as the values for gestation.

In the primates where the weaning of the infant is the point to which direct maternal sacrifice to a single litter is taken, there is an allometric relation in the proportion of this period spent with a postnatal infant. A small bodied haplorhine such as the marmoset for example spends 148 days in gestation and 63 days to weaning. The reproductive cycle then returns to conception. A larger bodied species such as the gibbon spends about 228 days in gestation and 730 days till weaning, (sources, Hearn et al 1975 and Epple 1970 marmoset, Voss 1970 and Ellefsson 1967 gibbon). In normal adult life the marmoset female spends only one third of her time in close contact with a free living offspring for the gibbon female however, ¾ of her normal adult life are taken up in close contact and responsibility for her free living offspring.

It is difficult without comparison with other mammalian orders to know to what extent the phylogenetic advancement of the higher and heavier primates is implicated in this effect and how much is a necessary consequence of body size regardless of taxonomy. However, here is a physiological base for the differences in social behaviour found in primates. This will be discussed in greater detail in the final chapter.

This point is made in a slightly different form by Western (1977), in the large mammal he suggests; 'relatively greater postnatal care will be necessary for larger bodied animals to ensure the same relative degree of self sufficiency in the young since they are born a smaller fraction of adult weight. By contrast, the amount of prenatal investment will be correspondingly less. Furthermore, as litter size increases, the ratio of postnatal to prenatal investment will increase.'

We are in a position to define more exactly the basis for this effect, at least for the primates since physiological 'self sufficiency' is clearly the point at which the mother returns to commence her reproductive cycle again. The infant of a particular evolutionary taxon at this point, regardless of body size has achieved a particular fraction of adult size and has achieved all the basic elements of adult physiological control. Why it should be that, as is hinted at by Western though without substantiation, the duration of weaning, or the greater postnatal care, is associated with the infant of a taxon achieving a constant proportion of adult weight is not clear. Nor why the 'same relative degree of self-sufficiency' is associated with the achievement by infants of related species of the same proportion of the adult weight. From the physiological point of view brain development is probably closely associated with this phenomenon. It may also be, depending on the general adaptations of the order, that the infant is prohibited from gathering or capturing the normal adult diet until the 'taxonomically necessary' fraction of adult weight is achieved.

It is also important to note that it is largely the maternal metabolism that dominates the growth rate, during the duration of, and attained size at the end of gestation. It would appear that the postnatal growth to 'self-sufficiency' is largely dominated by infant metabolism. This illustrates the changing roles of the mother and infant within the cycle from conception to weaning, equivalent in the primates to the interbirth interval, a fundamental factor in the population dynamics of the species. These issues are discussed further in the discussion chapter.

Postnatal growth beyond weaning. The data collected for ages at menarchy, first delivery and age at attainment of adult size are not very reliable for the assessment of the interspecific interdependency of these variables. This is a consequence of the long developmental periods of the primates the difficulties of assessing these parameters in the field, and the effects of captive dietary and social conditions on the development of sexual maturity (see data section p 104). It was hoped that some conclusions could be drawn on the significance of adult weight for successful reproduction in primate species other than man. In this species though there is some controversy it appears that the onset of menstruation is associated with the deposition of body fat to a particular level, which is established on average by a weight of 48 Kg (Short 1976). Also of interest is the association of body size with the duration of adolescent infertility which has been noted in seperate studies of the higher primates, (man Doring 1969, chimpanzee Teleki et al 1976, macaque species Hadidian pers com).

Having established the fast, immediately postnatal growth rate for the strepsirhine infants as compared with the haplorhine, it was hoped that the physiological development of menarche and the age at which adult weight is attained could throw some light on the adaptive features of the growth patterns of the two major primate groups.

However, although the information is presented, Figures 19 p 211 - 2 , 20 p 213 - 4 and 25 p 246 - 7), no definite conclusions can be reached on the physiology of comparative timing of these later growth stages. Data obtained from the field whilst more desirable for ecological and most evolutionary studies is often not accurate enough for comparative studies. Whereas accurate times and weights and obtained in captive studies, the effects of captive diet and caging may completely alter the animals normal growth and development. Longitudinal studies are really required for this period especially since the attainment of adult characters appear so sensitive to conditions (see p 103 et sqq).

Data on age of attainment of adult weight, especially for the strepsirhine may in strict terms be quite erroneous. In the light of complete growth curves from Doyle (in press) for Galago senegalensis moholi (47) it can be seen that despite the rapid early growth rate, the last period of increase in weight is very slow. So slow in fact that about 45% of the total period of postnatal growth is spent within the range 90-100% adult weight. If seen in the field during this period though it would be identified as a juvenile its body weight would appear adult.

Briefly, the plots appear to demonstrate that in general the small bodied primates do not reach puberty till adult body size is achieved. For the larger monkeys, apes and man, menarche precedes the attainment of adult weight. By the time of first delivery most of the smaller primates have achieved adult weight, the monkeys generally have just reached adult size and the apes are capable of giving birth whilst still below their adult size. This may be a reflection of the greater immediate stress on the mother during pregnancy and lactation in smaller bodied species. The smaller bodied species possibly must gain all the adult tissue reserves before successful reproduction can be sustained whereas this is not as critical for the larger bodied species.

The problems of captive breeding of strepsirhines make the comparative analysis of the values for late development difficult. This is associated also with the effects of seasonality on the development of reproductive maturity, which especially of the smaller bodied forms, which may tend to disrupt the correlation of physiological maturity with reproductive success, which is not the case for non-seasonal species which may enter the reproductive cycle as and when they mature physiologically. The correlations of the relationships within the strepsirhines for the index of maturity, (Figures 19 p 211 - 2 , 20 p 213 - 4 , and 25 p 246 - 7) are poor. It is of interest to note however, that against body weight the slopes for the Principal axes of distribution are lower than the values obtained for the haplorhines.

Figure 25

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:ageAb:mo. Natural logarithm of age at attainment of adult weight for females in months.

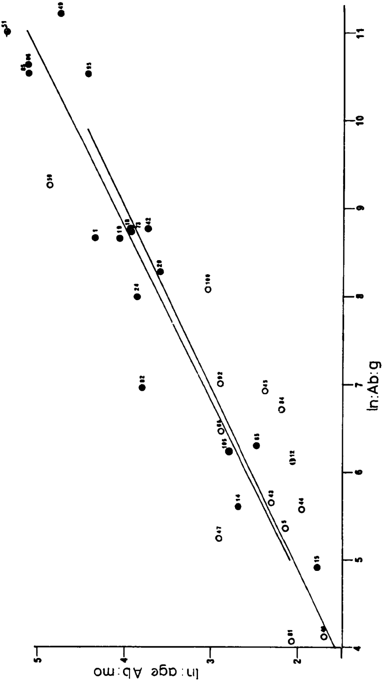
<u>All Primates</u> N = 29, $\bar{x}$ = 7.45, $\bar{y}$=3.31
P.A. = 0.51 (0.44, 0.58)
R.M.A. = 0.53, (Linear) Regression = 0.50
r = .94, r^2 = .88

<u>Haplorhines</u> N = 18, $\bar{x}$ = 8.31, $\bar{y}$ = 3.78
P.A. = 0.51, (0.42, 0.60)
R.M.A. = 0.53, (Linear) Regression = 0.49
r = .94, r^2 = .88

<u>Strepsirhines</u> N = 11, $\bar{x}$ = 6.04, $\bar{y}$ = 2.55
P.A. = 0.49 (0.30, 0.70)
R.M.A. = 0.54, (Linear) Regression = 0.45
r = .83, r^2 = .68

Upper solid line : P.A. (Haplorhines)
Lower solid line : P.A. (Strepsirhines)

This study.

ln: age Ab:mo
2
3
4
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ln:Ab:g
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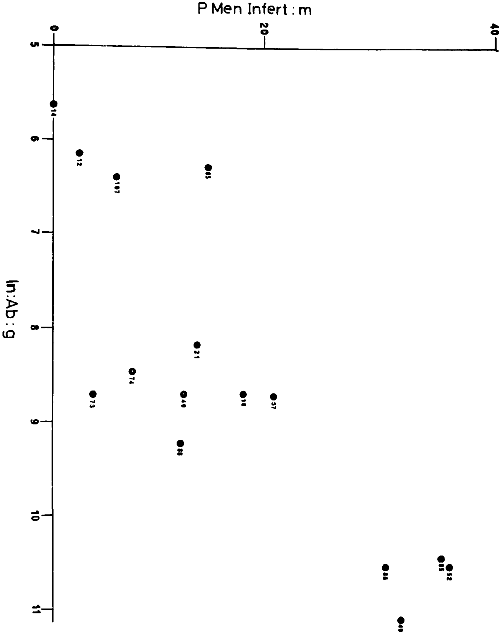
Figure 26

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, P Men Infert. Real values of post menarchal infertility in months.

Figure illustrates allometric tendency in duration of 'adolescent' infertility. (see text p 245).

This study.


P Men Infert : m
0
20
40
ln:Ab : g
5
6
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8
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14
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107
85
21
74
73
40
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57
88
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52
48

Concentrating on the more reliable data for the haplorhines we see that the Principal axes for both age at menarche and age at first delivery against adult female body weight are similar at about .36. The comparison of these parallel slopes shows that in general for all species, the age at menarchy is extended by a factor of .3 to reach the age at first delivery. However, for the small bodied species most or all of this extension is actually in gestation. For the larger bodied species the majority of this extension is in adolescent infertility. The tendency for the greater duration of this period in larger bodied species is represented in Figure 26 (p 248 - 9).

The requirements for a fuller understanding of postnatal growth are principally similar to those suggested in the last chapter (p 181 et sqq). However, experimental work with young growing infants is easier than dealing with foetal growth. Longitudinal studies with monitored nutrition, growth metabolism and temperature regulation would provide a base for profound analysis of the postnatal flow of energy , matter and information.

Summary of Chapter 5

In general, the nature of the postnatal growth of primates as determined by interspecific allometry proves difficult to analyse. This is due in part to the absence of a common pattern of postnatal growth in weight, and as a consequence of the lack of information, a series of apparently contradictory phenomena.

However, the postnatal growth pattern of the strepsirhines, in contrast to the haplorhines, shows a rapid increase in growth rate after birth and a greater proportion of adult size by weaning. This lends further support to Martin's (1972) theory of the seasonal ancestry of strepsirhines.

It also appears that the experimental values of maximum milk production in large species overestimates the demand placed by the litter or infant. The 'missing energy' suggests that the experimental conditions used by Brody (1945) do not represent the normal demands made by infants.

The tendency for longer adolescent infertility in larger haplorhines is reported. A significant factor in the reproductive cycle is that the weaning of the infant is normally associated with the onset of the next pregnancy. However, in larger bodied species the period from birth to weaning exceeds the gestation period, the opposite tendency operates for smaller bodied species.

CHAPTER 6 - REPRODUCTIVE RATES

Section a) Introduction

In this chapter the reproductive turnover of the typical species population is considered. It is on the evolutionary lineage that selection will operate to produce the overall rate and form of population maintenance and gene replacement. This is expressed in the reproductive turnover of the population, which may be considered in respect of the evolution and present ecology of species.

Data on mammae number are also presented since it may be expected to give some morphological reflection of litter size, a component in the reproductive turnover of the population.

The latter part of the chapter deals with the concepts of r and K selection and the concept of 'efficiency' in the use of energy by the population (ecological considerations) and the lineage (evolutionary considerations). It is demonstrated that, comparatively, the primates have a reproductive turnover expected from their apparently K selected evolutionary history (Martin 1975b). In terms of population criteria the primates are further shown to represent the most 'efficient' order of organisms in the maintenance of organized matter.

This leads on to an elaboration and integration of the theoretical concepts presented earlier in Chapter 2 with the results presented in this chapter in particular. This topic is pursued in the final chapter.

Section b) Mammae number

Results of the author's data collection on number of mammae are presented here before the section dealing with the mathematical description of reproductive turnover. Whilst the number of mammae maybe expected to be closely associated with overall reproductive rate, and in particular litter size (Long 1969), it is not incorporated in the mathematical derivations which form the major topic of this chapter.

With the exception of Tarsius all haplorhine genera have only a single pair of mammae with only extremely rare anomalous exceptions (Schultz 1948). The data on Tarsius and strepsirhine species were collected from preserved specimens. Whilst the sample sizes presented in Table 5 (p 363 - 6) are small, the data are supported and corroborated by specimens which, due to dense fur, slight damage or apparent immaturity could not be included with absolute certainty. Such specimens were unfortunately in the majority, yet were apparently no different from those for which there could be no doubt. In view of the rarity of many primate species, the difficulties in restraining live animals for such procedure and the protection of these species in the wild from hunting and trapping small sample sizes are somewhat inevitable. It also appears from the specimens found in museum collections that in general for these species males were more commonly shot than females. Since most species are not markedly dimorphic this is most probably a consequence of the behaviour of the victims rather than of the naturalists.

It may be seen in Table 5 , (p 363 - 6) that the author's findings confirm in general those of Schultz (1948), whilst enlarging the number of species observed. There are some exceptions however; Schultz reports a single pair of mammae in a specimen from the genus Cheirogaleus, in this study two specimens of each species had 3 pairs of mammae. His data give a single pair of mammae for Lemur species, in this study two specimens of Lemur catta had 2 pairs of mammae (this species has the highest proportion of twin litters of the Lemur species, Hill, 1973). Schultz also reports that Varecia variegatus (Lemur v. in his study, see p. 43) has between 1 and 3 pairs of mammae, in this study all six specimens had three pairs.

The most striking feature of the table is the predominance of single pairs of mammae in the Lemuriformes whilst, despite at least four singleton - bearing Lorisiforme species only Euoticus elegantulus has only 1 pair of mammae. Amongst the Lemuridae habitual singleton births are associated with a single pair of mammae. A single specimen of Microcebus coquereli had only a single pair of mammae though in captivity the species may give birth to twins (Pages pers com).

It is also notable that Varecia variegatus is the only species not a member of the Cheirogaleinae that has common multiple births and three pairs of mammae.

Tarsius is the only haplorhine genus with more than one pair of mammae, both this study and Schultz (1948) report a maximum of 3 pairs in this genus. Though Vincent (1969) reports rare cases of 4 pairs of mammae in Galago demidovii, it is believed that 3 pairs is the normal maximum for primate species. In this respect it should be noted that 3 pairs of mammae is the maximum for both haplorhine and strepsirhine species (though Tarsius is the only haplorhine genus with more than a single pair). This observation throws some doubt on Martin's (1975a) suggestion that the ancestral stock of haplorhine species had smaller litters than the ancestral stock of the strepsirhines.

Apart from the general association between litter size and number of mammae it is also possible that both are related to certain behavioural adaptations seen in the strepsirhine species, and body size (small species tend to have larger litters). Certain strepsirhine species and possibly Tarsius species exhibit the 'baby parking' phenomenon described by Martin (1972), (Charles-Dominique 1977). The infants may be left either in a nest or clinging in foliage during the activity period of the mother. This does not occur in Lemur species, or amongst the Indridae. Amongst the other Lemuriforme genera, Microcebus, Phaner, Cheirogaleus, Varecia, and Daubentonia all leave infants in constructed nests or tree hollows. Lepilemur and Hapalemur are known to leave their infants in tree hollows or epiphyte cups, especially during the early life of the young when the mother is active.

Amongst the African Lorisiformes all the Galago species construct or use nests of some sort, Arctocebus and Perodicticus 'baby park', Euoticus apparently 'baby-parks' but is not known to use nests in captivity (Charles-Dominique 1977). Manley (1966) reports that the Asian lorisiforme Nycticebus carries it's young from birth in captivity.

For species which leave their infants for part of the day the suckling period is necessarily concentrated. It is possible that the intermittent demand on the mother for milk in such species is best provided by more than a single pair of mammae. The obvious exceptions to this suggestion are Daubentonia, Euoticus and possibly Microcebus coquereli if the single specimen examined is normal.

Another possible association of mammae number is with body size, this is of course associated with litter size as well. The smaller bodied forms give birth to relatively heavier infants. It is possible that the infant will consume a daily volume of milk proportional to its body weight (see p. 225 et sqq). As a proportion of adult weight this will be greater in smaller bodied species. It is possible that the distribution of the relatively larger bulk of milk in smaller bodied animals is more efficiently distributed between a number of mammae. This might be the best explanation of the multiple mammae in Tarsius species which habitually produce only single young. Once again there are exceptions, including Microcebus coquereli, Euoticus elegantulus with reduced number of mammae and Varecia variegatus with three pairs of mammae though weighing 3 Kilos.

None of these possible correlations for mammae number in primates is entirely satisfactory (those of litter size, baby parking, and body size). However, the morphological nature of mammae number is being compared with possibly more 'flexible' (over evolutionary time) characters; namely, egg releases per oestrus, maternal behaviour and body size. The concept of mosaic evolution would lead us to expect some anomalies. Furthermore, general evolutionary tendencies may in future be inferred from such mosaics following the concepts elaborated by Gould 1977

These results are discussed further in the discussion chapter (p 305 et sqq). The remainder of this chapter is devoted to extant values of reproductive rate.

Section c) Theory: rates in population reproduction

In the previous two chapters the comparative physiology of primate growth and development have been discussed. It has been seen that information such as gestation length, or age at menarche, reflects some necessary energetic factors in the growth of the individual animal. The developing individual may be considered however, as both the member of a population or as the member of an evolutionary lineage. The rate of growth of the individual as it is transformed from the product of the previous generation to the producer of the next is therefore a fundamental property of the population and the lineage. The rate and pace of renewal of the population and gene pool reflects both the ecological conditions in which the species survives and also the evolutionary history of the lineage.

In this chapter the information available on primate reproductive parameters is used to extend the analysis from the comparative physiology of individual members of a species to the questions of species and population survival. The two subjects are inseparable, and as far as the survival of a species is concerned, express both the form of the unity of physiological factors and population dynamics and also of the contradictory interaction of these two factors in the adaptions of the evolving species to a constantly changing environmental conditions. In the discussion chapter this inter-connection of physiology and population is extended further to the consideration of the separate primate species as representatives of a particular level of organization in the development of terrestrial life.

Consideration of the energy exchanges in the process of development and survival of organisms was indispensible for the discussion of the individual as a unit in the previous two chapters, and so it will be in the discussion of the primate order as a whole in the following chapter. The same applies to this chapter, in which the population of a species is taken as a unit.

In general the conclusions from the analysis of the population survival of species given here are speculative. The relatively long life of primates makes studies of population dynamics difficult. In any given locality the particular prevalent conditions may give an 'abnormal' picture of the population dynamics of the whole species. In certain localities the species may be rapidly colonizing or in others declining, it may have been a particularly good or bad period for the local population in terms of disease, food availability, predation or weather. In general it is assumed that any given species population remains relatively stable over long periods, and that death rate is balanced by birth rate. Two studies from the field exemplify the difficulties in extrapolating from the rare field reports on population dynamics to evolutionary considerations for the whole species. Gautier-Hion (1971) reports an average population increase of 20% per annum over seven years for a group of Miopithecus talapoin in the wild. Altmann (1974) reported an increase of a population of about 41 Papio cynocephalus by five new members in the course of a years study. In many areas however, primate populations are declining under pressure from human populations. Such rates of population increase and decrease cannot be considered as normal in terms of the long periods of evolutionary development of the species.

Such studies are in any case rare in the literature, and for the purpose of discussing the long term and evolutionary aspects of species population maintenance populations are assumed to be constant. This is a general practice for such considerations (see Fenchel 1974 and Cole 1954). In this study the potential for population growth is determined crudely from information on lifespan, litter size, age at 1st female delivery and interbirth period. Most of this information comes from captive studies, under conditions where maximum survival of individuals is the intention of the captors. In general it may be assumed that such conditions produce abnormally high rates of population increase as compared with the wild condition. Some primate species are, however, notoriously difficult to maintain and breed in captivity (for example the Tarsier, and leaf eating monkeys), and for these species captive studies may reveal lower reproductive rates than those for wild living animals. In general the species represented in the literature may be considered good breeders. Although it is not necessarily so, the available data for analysis, may not be truly a representative 'cross-section' of primate species in respect of reproductive rate.

Theory. As with the previous chapters on data analysis some discussion and clarification of theory is necessary. The study of populations and particularly human demography has established a long history of mathematical methods for the interpretation and analysis of population data and life history variables. Early studies of human population growth include those of Malthus (1798) and Verhulst (1838). The development of mathematical analytic methods has continued since the work of Gompertz (1825) and Lotka (1907a, 1907b) and there are many recent theoretical studies (e.g. Hutchinson and MacArthur 1959, Demetrius 1978). As Cole (1954) pointed out in an important paper there has been a mutual tendency on both the part of theoreticians and biologists to ignore the interdependence of mathematical technique with field research for the advancement of both. This problem, whilst perhaps being rectified to some extent in very recent studies (e.g. Western 1977, and Fenchel 1974), is exemplified by the inadequate or inappropriate use of mathematical concepts in dealing with biological data (e.g. Schultz 1938, Goss-Custard et al 1972), and the generation of evolutionary theory based on mathematical models without a material context (see Demetrius 1975, Williams in press and p. 345 et sqq).

The implications derived from mathematical considerations of population dynamics for life history studies are discussed in some detail by Cole (1954) and Lewontin (1965) and are most important for the correct evaluation of the significance of life history variables in the reproductive strategy of the species.

Under conditions of food abundance, with suitable habitat available and without predation and disease, populations are capable of exponential growth (Fenchel 1974, MacArthur and Connell 1965 Chapter 5). When this kind of population growth is continuous, the population N increases at a rate which is a constant proportion of the population at any time, thus;

$$\frac{dN}{dt} = rN$$

where r is the Intrinsic Rate of Natural Increase (IRNI). At any time t after time t_o and population N_o , the population N_t is determined from the integration of the rate equation above.

$$N_t = N_o e^{rt}$$

Under natural conditions the average population size remains constant over long periods of time. The field ecologist with knowledge of age apecific birth and mortality rates is able to determine the replacement rate R_o for the normal wild condition, with a roughly stable population and a stable age structure.

$$R_o = \sum_{x=0}^{\infty} l_x \; m_x$$

where for any specific age interval x to x + 1 the birth rate is m_x and the survivorship l_x. The replacement rate, R_o, is the value which reflects best the overall reproductive renewal of any population, but field data on age specific birth and survivorship rates are very rare in the literature, and would, as mentioned earlier, reflect local and perhaps temporary conditions which are unlikely to represent long term evolutionary population conditions. A value which it is possible to estimate is the value r. Whilst early studies on human population growth determined r from empirical data on the population growth rate in the United States during the period from the first European colonization, the value of r is now generally understood to be the maximum potential growth rate of a population (Cole 1954), and is given the notation r_m as the maximum potential value.

In wild populations, even under extremely favourable conditions, it is unlikely that the proportional rate of population growth ever reaches r_m as determined from laboratory studies (as quoted in Fenchel 1974), or as determined in this study following the method of Cole (1954). Nevertheless, calculation of the maximum value of r, or the use of laboratory values of r from the equation $\frac{dN}{dt} = rN$, can be of some use in assessing the physiological potential for population increase. The value r_m is an estimate of r for a population that has no mortality intervening between birth and maximum lifespan. This potential, whilst not reflecting normal conditions must reflect the inherent ability of the population to maintain its evolutionary status. A parallel can be drawn with Sacher's (1976) use of maximum longevity in his study described in detail earlier (p 79 et sqq). Sacher employs values of maximum longevity for his study since he is concerned with the importance of the entropy relations of the organism in maintaining its homeostatic systems from decay.

In this study, which has concentrated on physiological and energetic relations of reproduction, it is the potential regenerative ability of the species which is likely to be most closely associated with these underlying entropy factors.

Another quality of r_m in relation to evolutionarily stable populations is indicated by Fenchel (1974). If it is generally the case that one female replaces another under natural conditions, then during a given period individuals are being removed from the population at a rate ${}^{rm}/t$, assuming a stable age distribution, where t in this case is the average period of female replacement.

The value of r_m per day used by the author in this study and Fenchel (1974) is thus a measure of the production of individuals in excess of the stable production per day. These are then lost to the population with a certain energetic cost to species, as measured by the energetic content of the 'dying' individuals, or perhaps more properly the energetic sacrifice in construction (see p 300 et sqq). The value of $^{r}m/t$ can indicate, then, something of the physiological resiliance of the species, and also of the evolved patterns of response to either long periods of pressure on the species population, or periods of relatively advantageous conditions.

Of the wide range of life history patterns exhibited by living organisms the mammals and the primates particularly fall into one extreme, with repeated reproduction and relatively small litter size.

Many lower organisms exhibit semelparity, the production of a single litter in the life of the organism. Usually these litters are large, though in the case of bacteria and some unicellular organisms the division of the parent cell into two daughter cells represents the smallest litter size for a semelparous species enabling population growth.

The production of single offspring necessitates iteroparity, the production of more than one litter per life,,to ensure the potential for population growth. In many large mammals and the larger bodied primates this is the normal litter size. For sexual species, where the average litter size is one,two births per female per life (assuming no intervening mortality) are required simply to maintain the population, assuming that on average the sex-ratio is 50:50 at birth. With the primates, we are dealing with a group that is both sexual and has small litter sizes, iteroparity is necessary for population maintenance of those species with single offspring per litter, and for those producing twins iteroparity is necessary to increase the population.

The ability of a species to maintain itself in the wild where there will be more or less fluctuation in mortality patterns and rates, and to have the potential to colonize new habitats requires a potential value of r greater than 0. The rate of r_m per day is a consequence of the absolute and relative values of the interbirth period, age at first delivery, litter size (number of females per litter for sexual species) and number of litters per life time. The significance of any one variable in the life history pattern is dependent on the relations of the other variables. Whilst mathematical models of the adaptive significance of changes in one or more of the variables may give the impression that life history patterns are the arbitrary property of a species as long as the 'required' r_m for survival is maintained, this is not the case.

As we have seen in the previous chapters, the rates of growth and development of the individual organism are closely correlated with some of the most basic variables of the living matter of mammals, in particular, brain size, body size, and metabolic rate. A feature of the non-linear scaling of these properties in related forms is the necessary variation in the proportions of organ sizes, and the rates and durations of the phases in development. These fundamental factors extend, as expected, into the field of life history strategy.

The principal relationship discussed in this chapter is that between body size and r_m per day in the primates. (Figures 27 p 270 - 1 , and 28 p 272 - 3). Having established the general form of this relationship it is possible to examine the types of adaptation of life history variables (within the limitations of size and physiology) to ecological conditions, with the aid of the mathematical models available (especially Cole 1954). This discussion will include data on the primates presented in this form for the first time. These data include those on average litter size, age at first delivery, age at menarche, lifespan, and sex ratio at birth.

In introducing the correlation between r_m and body weight for primates a description of the assumptions of method of calculation is required. The data is used based on the assumption of stable age structure and that the female survives to the maximum physiological age whilst still breeding (apparently the case, in primates with the exception of man, and the chimpanzee for which age at menopause is considered the maximum). It is also assumed that a female on reaching reproductive maturity maintains a regular reproductive pattern. Other values used are means taken largely from captive studies. In this sense the only drastically 'unnatural' assumption made in the calculations is that mortality does not exist until senility. The obtained values are potentially those possible under laboratory breeding conditions, and whilst the figures given here are extrapolated from different sources the values are essentially equivalent to the empirical values of non primate organisms given by Fenchel (1974).

The estimation of r_m, following Cole 1954, is based on the generalization of Thompson's (1931) method. Assuming maximum survivorship and summing the numbers of offspring at each interbirth interval over the length of a generation, the value of r can be determined by an iterative procedure from the following identity

$$e^{r\alpha} = b(1 + \bar{e}^{r} + \bar{e}^{2r} \ldots \bar{e}^{r(n-1)}) \qquad \text{(Eq. 19)}$$

where the interbirth period is 1 unit, α is the age at first delivery, n the number of litters per life and b the average litter size (average number of females per litter for sexual species). The equation in fact represents the identity of the infinite equation

$$dN/_{dt} = rN$$

with the finite values obtain over a particular period, so that on average, and with large enough population, the population sizes at intervals x and x + 1 are related in the ratio

$$\frac{f(x+1)}{f(x)} = e^{r}$$

The sum of the series on the right hand side of equation 1 is,

$$\frac{1 - e^{-rn}}{1 - e}, \left(\equiv \frac{e}{b}\right)$$

This is the form used to approximate r. The value r_m per day is simply the value of r obtained with interbirth period taken as unity, divided by the interbirth period in days.

The calculations are made on the assumption that the sex ratio at birth is 50:50, i.e. that b = ½. For all primate species for which there is any information this appears to be case, with the possible exception of the tamarin species reported by Wolfe et al (1975) (see Table 6 , p 367). It may be that the predominance of male offspring in some studies of marmosets and tamarins (Wolfe et al 1975, Kleiman 1977) is a product of particular breeding stocks and conditions. For the lion marmoset the apparent high proportion of males in Kleimans colony is not seen in the report of Bridwater 1972 from many sources.

<u>r and K selection</u>. At this point it is worth describing briefly the concept of r and K selection as first elaborated by Robert MacArthur (MacArthur and Wilson 1967). The potential ability of a population to grow at an exponential rate is essential to this concept. In an environment of a given finite abundance of food and other resources required by a particular species an introduced population may be expected to grow at an exponential rate r until it approaches the carrying capacity of the environment, K, when the population stabilizes at about this value. (This model assumes, however, that the age structure does not change. The pattern of mortality has important consequences both for the model, and for the difference between potential and actual reproductive rate of the population, see Demetrius 1978, and this study p. 293 et sqq, p 341 et sqq). However, the stability of the environmental conditions over long periods of time have important consequences for the type of natural selection exerted on the species population. In environments where K is subject to fluctuations, within or between years, selection will favour those genetic combinations and mutations which increase the value of r. In such environments the majority of evolutionary history of the species will be spent under conditions where the

population is below the carrying capacity. The survival of the species through the harsh periods will depend on the ability of the species to colonize other niches rapidly.

The general features of species with a history of r selection are summarized by Wilson (1975). These include rapid development, high r_m, early reproduction, small body size and a tendency to semelparity, short life, an emphasis on productivity in energy use, and unstable population structure. Species which exhibit such features may be described as opportunistic.

Those species evolving under more stable environmental conditions are subject to selective pressures of the opposite sort. The species population will spend most of its evolutionary history close to the carrying capacity of the environment. Selection will favour those genetic combinations and mutations which increase the efficiency of resource exploitation. This is associated with a reduction in r_m, slow development, late reproduction, large body size, repeated reproduction and stable population structure. These species may be described as specialized. MacArthur et al (1967) suggest that stable environments favouring K selection would include tropical rain forest where season change is small. r selection would tend to operate in environments subject to sudden and possibly catastrophic changes, in arid regions or non equatorial environments for example.

Section d) Results

Figure 27 (p 270 - 1) gives the values for $\underline{r_m}$ <u>per day</u> for those primate species for which reliable data are available. Most of the data are derived from captive animals. With the exception of <u>Hylobates lar</u>, captive breeding figures yield a slightly higher value of $\underline{r_m}$ <u>per day</u> than figures from the wild. For this gibbon species however, field estimates give a very slightly higher rate than captive breeding.

The values for the !Kung bushmen(52) give the range between the lower value of nomadic hunter gatherers and the upper value for the same genetic type living in sedentary agricultural settlements. The three values given for caucasian <u>Homo sapiens</u> (51) give the lower value based on the estimated real $\underline{r}$ of the population growth an 18th and 19th century America, the middle value of real r_m of the modern Hutterite population which has a cultural restraint on breeding till the 22nd year and the upper value an estimate of the potential r_m were this cultural impediment on breeding to be lifted. This upper value represents possibly the highest attainable value of r_m of modern western <u>Homo sapiens</u>. A separate section is given to the discussion of the human data (see p 336 et sqq).

As mentioned earlier, estimates of both wild and captive r_m per day given here are based on the assumption of maximum captive longevity of the females. Calculated differences in r_m per day for wild and captive values are thus due to differences in interbirth period and age at first delivery. Whilst accurate information on wild ages at first delivery is very rare, there is

Figure 27

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:rmd^{-1}. Natural logarithm of estimate of maximum potential Intrinsic Rate of Natural Increase per day.

<u>All Primates</u> N = 31, $\bar{x}$ = 7.37, $\bar{y}$ = -7.17
P.A. = -0.35 (-0.42, -0.29)
R.M.A. = 0.39, (Linear) Regression = -0.34
r = -0.88, r^2 = .78

<u>Haplorhines</u> N = 19, $\bar{x}$ = 8.13, $\bar{y}$ = -7.48
P.A. = -0.39 (-0.48, -0.31)
R.M.A. = 0.42, (Linear) Regression = -0.38
r = -0.91, r^2 = .82

<u>Strepsirhines</u> N = 12 $\bar{x}$ = 6.17, $\bar{y}$ = -6.67
P.A. = -0.15 (-0.26, -0.04)
R.M.A. = 0.24, (Linear) Regression = -0.14
r = -0.60, r^2 = .36

Solid line: P.A. (Haplorhines, except Man (51/52))

species distinguished between forest types (diamond enclosed) and non-forest types. See text p 293 et sqq.

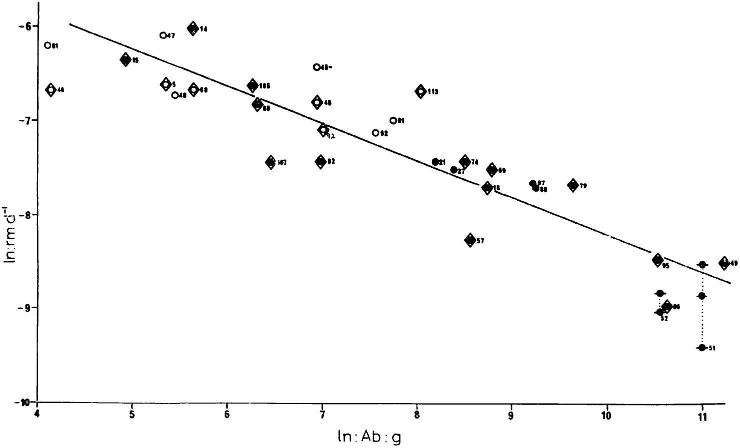

ln:rm d^{-1}
-6
-7
-8
-9
-10
ln:Ab:g
4
5
6
7
8
9
10
11
81
44
15
47
14
5
48
68
105
65
107
45
92
82
62
81
113
21
27
74
69
18
97
88
79
57
95
96
52
51
49

Figure 28

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:rmd^{-1}. Natural logarithm of estimate of maximum potential Intrinsic Rate of Natural Increase per day.

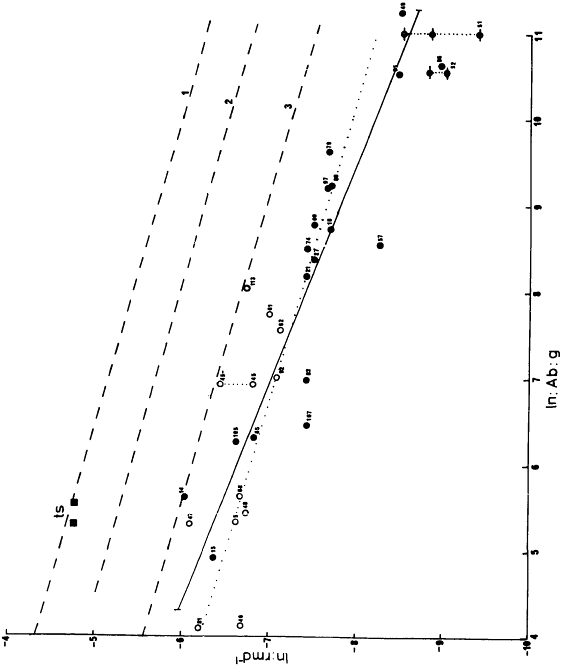
See Fig. 27 for statistical interpretation.

Solid line: P.A. (Haplorhines)
Dashed Lines: 1) Extrapolated regression of 'mammalian' allometry of r_m from Fenchel (1974)
2) Extrapolated regression of heterothermic metazoan allometry of r_m from Fenchel (1974)
3) Extrapolated regression of unicellular allometry of r_m from Fenchel (1974).
Dotted line: parallel to Fenchel's slopes passing through mean primate values of r_m/day and body weight.

ts indicates values for two tree shrew species (see p 296).

For further explanation see text (p 293 et sqq).

This study (following Fenchel 1974).


ln:rmd-1
ln:Ab:g
-4
-5
-6
-7
-8
-9
-10
4
5
6
7
8
9
10
11
1
2
3
ts

evidence that wild interbirth periods are similar to those obtained in captive studies. For species represented in Figure 27 (p 270 - 1) for example; _Callithrix jacchus_ (14) has a captive interbirth of about 160 days (Hearn 1975) wild estimates from Stevenson pers com are similar, _Saguinus_ species (101-105) have average captive interbirth periods of 240-280 days (Wolfe et al 1975), wild reports collated by Hershkovitz (1977) suggest an annual birth peak in some areas but captive animals in semi-natural conditions have been known to breed biennially. _Saimiri sciureus_ has an interbirth interval of 414 days average (Rosenblum 1972) in captivity, Hershkovitz (1977) reports annual births in Peru. Cercopithecoid species are generally reported to breed annually in the wild, captive studies reveal a similar picture. Captive gibbon species breed naturally about every 2½-3 years (Haggard 1965) wild estimates of 2-2½ years (Ellefson 1967) suggest roughly similar interbirth values for wild and captive conditions. In general, average interbirth values are preferable and may give slightly longer values than values for wild inter-season values.

However, the effect of captive conditions on the age at sexual maturity (see p 104 et sqq) appears to result in a reduction of this value. It is probable then that estimates of r_m from wild obtained values may underestimate the potential value which might be obtained under captive conditions.

Unfortunately the values for the great apes are all based on wild figures, however, the exclusion of these values from the correlation of r_m per day against adult body weight for haplorhine species does not greatly alter the value of the slope. The difficulties associated with captive breeding of the great apes (see Keeling et al 1972) suggests that captive breeding might not increase the value of r_m per day by a great deal.

The correlation for the haplorhine species except man is given with Figure 27 (p 270 - 1). All the strepsirhine figures given fall within the range of distribution for the more numerous haplorhine figures. The declining slope of interspecific correlation of r_m per day and adult body weight is in agreement with the findings of Fenchel (1974), although the negative slope is somewhat steeper than the values he obtained for unicells and poikilotherms. The implications of the primate data in relation to Fenchel's work will be discussed later (p 295 et sqq). Some general consequences for the survival strategy of primates, and implied for all groups of organisms may be deduced from the data on r_m, interbirth period, lifespan, and age at first delivery as correlated with body size. (Respectively Figures 27, 28, p 270 - 1 , p 272 - 3 , Figure 29 p 281 - 2 , Figure 30 p 283 - 4 , Figure 20 p 213 - 4).

Both interbirth period and age at first delivery are scaled to a higher power of body weight than lifespan. A a proportion of the physiological potential for life, a factor limited by the genetic potential of the organism to reduce the irreversible disordering processes accompanying normal metabolism, the reproductive period is shorter for larger bodied species.

As the interbirth period is also a greater fraction of life span in larger bodied species it may be concluded that under natural conditions the mortality pattern of large and small bodied primates differs considerably.

A schematic representation of three types of life table is given in Diagram 3 (p 277 - 8), (after Demetrius 1978). ω is the maximum lifespan along the time axis, and $l(x)$ is the age specific survivorship. Type I, with maximum survivorship up to the maximum physiological lifespan is the type, assumed for the calculation of r_m in Figure 27 (p 270 - 1), and is not generally approached under wild conditions, though may be in good captive breeding colonies. Types II and III are more likely to be found in natural populations and may be generally distinguished at least for the primates in relation to body size. It is suggested that the smaller bodied species tend towards type III generally and the larger bodied forms tend toward type II. The expected difference in age structure is associated with the necessity for larger bodied species to survive well into their potential lifespan in order to achieve even the replacement of the population. If reproductive potential starts relatively earlier or later in life it is still possible for both types to have a similar total pre-reproductive mortality though the pattern of age-specific survivorhsip must differ.

The importance of a natural survivorship into later life for the population maintenance of large bodied species is indicated by some manipulation of the r_m per day values assuming for all species a halving of number of births per life time. For the smaller bodied primates with high number of potential births per life and a relatively early age at first delivery the value of r_m per day is almost unaltered. For the larger bodied species however, the value of r_m per day drops considerably reducing the slope of the correlation with adult

Diagram 3

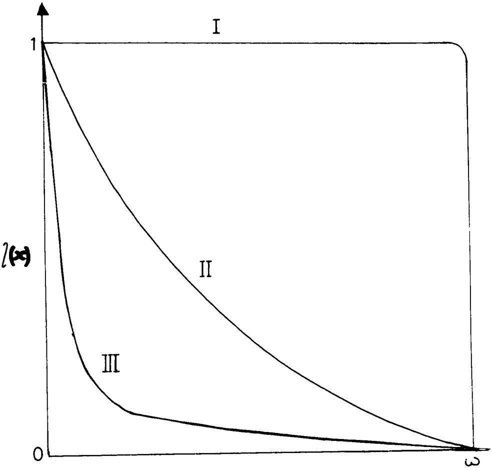
X-Axis: Age of population member to maximum longevity ω.

Y-Axis, l(x). Age specific survivorship.

Type I curve. Indicates semelparous type with breeding at ω. Assumed survivorship for calculation of r_m. Intrinsic entropy is zero, $H^* = 0$.

Type II curve. Indicates iteroparous type and survivorship tendency of large body size (see text p 276 et sqq). Intrinsic entropy maximum, $H^* = 1$. Mortality is age random.

Type III curve. Indicates iteroparous type and survivorship tendency of small body size (see text p 276 et sqq). Intrinsic entropy > 0, $H^* = \frac{1}{2}$. Mortality is age specific, higher infant mortality.


I
1
l(x)
II
III
0
ω

body weight from ~ -.393 (for found number of births per life) to -.564 (for calculation halving number of birth per life).

Another indication of this trend is to estimate the average length of life required by the female members of the population to replace themselves. This age is equivalent to age at first delivery for species habitually delivering twins and age at second delivery for species habitually delivering singletons, assuming an equal sex ratio at birth. For haplorhine species the correlation of this value against Adult female body weight yeilds a slope of .429 (.280 - .587) $r^2 = .613$. Further discussion of these results follows later, (see p 293 et sqq).

Adaptive value of life history. As can be seen from the form of the equation for estimating r_m, the separate components of interbirth period, age at first delivery litter size, b, and potential litter number per life, n, are interdependent in their contribution to r_m. The significance of this interdependence is emphasized in Cole's (1954) article in which he indicates the altered adaptive values of each component with differing values of the others.

It should be mentioned that Cole assumes that the evolutionary tendency in all species is to increase r_m, this is however not the case as explained by MacArthur's concept of r and K selection described earlier (see p 267 et sqq). This does not of course detract from the value of Cole's theoretical analysis, since the varying effect of the differing components on the value of r_m applies whether the selective advantage is for the increase or decrease in r_m.

From this study it is clear that the various components alter interspecifically with body size; Litter size: (see Figure 31, p 285 - 6) with the notable exception of Varecia variegatus (113) multiple litters are frequent only in species below about 1Kg adult weight.

Potential number of litters per life: declines with increasing body size (Figure 32 p 287 - 8).

Age at 1st delivery: (Figure 20 p 213 - 4), generally increases with increasing body size for haplorhine species, (strepsirhines show very poor correlation).

An Interbirth interval: (Figure 29 p 281 - 2) generally increases with size, though as mentioned the strepsirhine species tend to have longer interbirth periods, apparently constrained by seasonality in the smaller forms.

In the discussion of the general consequences of size the author will consider primarily the haplorhines, since the strepsirhine correlations are relatively poor, this will be discussed subsequently.

Cole's findings may be summarized as follows: the influence of litter size on r_m decreases with increasing age at first reproduction, where number of litters per life is held constant (this effect is not greatly altered when number of litters per life declines with increasing age at first reproduction, the case in primate species, interspecifically). The influence of number of litters on r_m is very great for low numbers in species with early 1st delivery, The influence declines as the number of births increases.

Figure 29

X-Axis, ln:Ab:g. Natural logarithm of adult female body weight in grams.

Y-Axis, ln:Interb:d. Natural logarithm of average interbirth period in days.

<u>All Primates</u> N = 39, $\bar{x}$ = 7.76, $\bar{y}$ = 6.06
P.A. = 0.25 (0.19, 0.32)
R.M.A. = 0.32, (Linear) Regression = 0.24
r = .76, r^2 = .58

<u>Haplorhines</u> N = 29, $\bar{x}$ = 8.17, $\bar{y}$ = 6.08
P.A. = 0.33, (0.26, 0.41)
R.M.A. = 0.38, (Linear) Regression = 0.32
r = .86, r^2 = .74

<u>Strepsirhines</u> N = 10, $\bar{x}$ = 6.55, $\bar{y}$ = 6.01
P.A. = 0.18 (0.06, 0.30)
R.M.A. = 0.26, (Linear) Regression = 0.17
r = .67, r^2 = .45

Solid line: P.A. (Haplorhines)

This study.

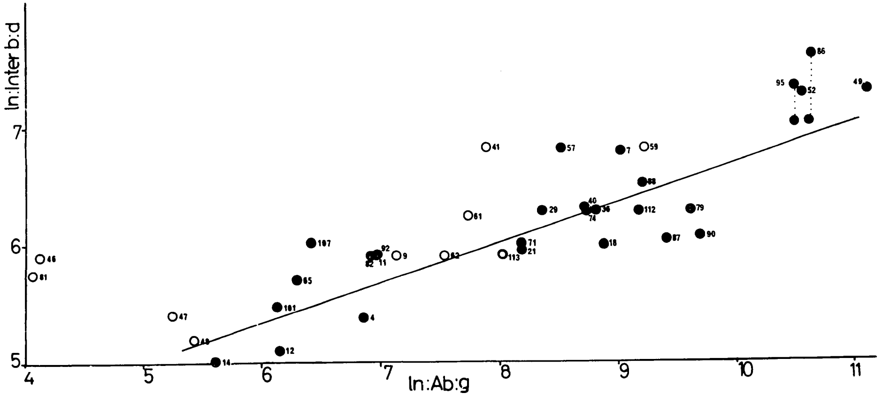

ln:Inter b:d
5
6
7
ln:Ab:g
4
5
6
7
8
9
10
11
86
95
52
49
41
57
7
59
40
29
36
112
79
74
61
107
71
21
18
87
90
46
92
9
62
113
82
11
81
65
47
101
4
12
14

Figure 30

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:life:yr. Natural logarithm of maximum recorded female lifespan in years.

<u>All Primates</u> N = 40, $\bar{x}$ = 7.56, $\bar{y}$ = 2.94
P.A. = 0.23 (0.17, 0.28)
R.M.A. = 0.28, (Linear) Regression = 0.22
r = .78, r^2 = .62

<u>Haplorhines</u> N = 30, $\bar{x}$ = 8.10, $\bar{y}$ = 3.04
P.A. = 0.25 (0.18, 0.32)
R.M.A. = 0.31, (Linear) Regression = 0.24
r = .77, r^2 = .59

<u>Strepsirhines</u> N = 10, $\bar{x}$ = 5.96, $\bar{y}$ = 2.66
P.A. = 0.26 (0.11, 0.41)
R.M.A. = 0.33, (Linear) Regression = 0.24
r = .73, r^2 = .54

Solid line: P.A. (Haplorhines)

(calculations exclude values for man, 51, 52, where upper points represent max. potential lifespan joined by dotted lines to lower points representing maximum female reproductive lifespan)

c.f. Sacher 1959, additional data in this study.

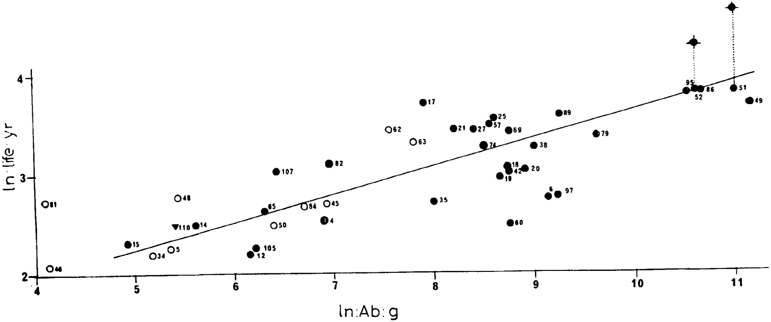

ln life yr
4
3
2
ln:Ab:g
4
5
6
7
8
9
10
11
81
46
15
34
5
48
110
14
65
107
105
12
50
84
45
4
82
62
63
17
35
21
27
57
25
74
69
18
42
19
20
60
38
6
97
89
79
95
52
86
51
49

Figure 31

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, Average litter size. Real values of average number of neonates per birth, on logarithmic scale.

All species of primate with female body weight greater than 8,000 grams habitually deliver singletons.

This study.

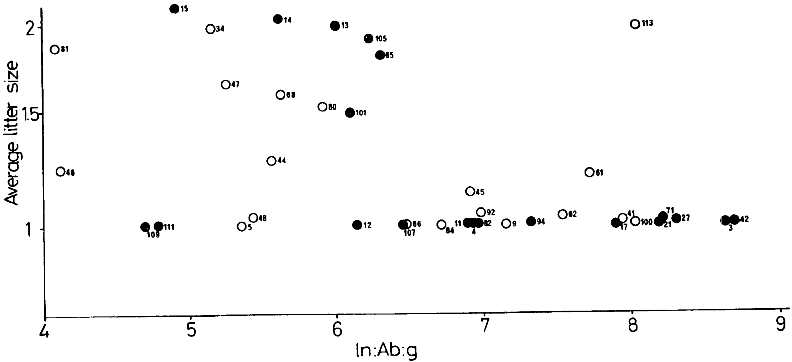
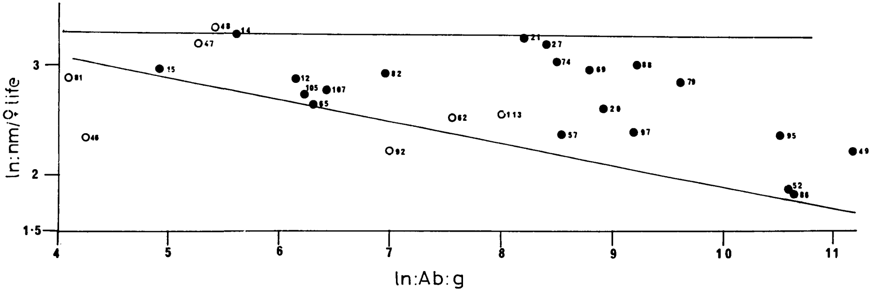

Average litter size
2
1.5
1
4
5
6
7
8
9
ln:Ab:g
15
14
13
105
65
113
34
81
47
68
80
101
44
46
61
45
92
48
62
41
71
27
42
109
111
5
12
66
107
84
11
4
82
9
94
17
100
21
3

Figure 32

X-Axis, ln:Ab:g. Natural logarithm of Adult female body weight in grams.

Y-Axis, ln:nm/ life. Natural logarithm of the maximum potential number of offspring in a females life.

Solid lines enclose haplorhine values along major axis.


3
2
1·5
ln:nm/♀ life
4
5
6
7
8
9
10
11
ln:Ab:g
48
14
47
15
81
12
105
107
65
46
82
92
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113
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27
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57
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95
49
52
86

For species with late age at first delivery the influence of variation in number of litters is lower for those with early age at first delivery, but the influence is maintained for greater total litters. For any given total litter number the value of r_m is greatly affected by age at first delivery.

If it is assumed that the variation in the two components total litter number and litter size are a reflection of the adaptations of species to obtain optimum values of r_m for their particular ecological niches, then the data presented here confirms Cole's hypotheses.

1) From Figure 31 (p 285 - 6) it can be seen that small body size (early first delivery, Figure 20(p 213 - 4) is associated with the greatest variation in litter size.

2) From Figure 32 (p 287 - 8) it can be seen, with the notable exception of *Galago demidovii* (46), that the variation in potential litter number is greatest in larger bodied species (those with later first delivery). The variability in the components for estimating n, potential litter number,

$$\frac{\text{Lifespan} \quad - \quad \text{Age at 1st delivery}}{\text{Interbirth period}}$$

for strepsirhine species can be seen in the Figures 30 (p283- 4), 20 (p 213 - 4) and 29 (p 281 - 2), noting especially the poor correlations for strepsirhine interspecific allometry of age at 1st delivery and interbirth period. In Figure 32 (p 287 - 8) the two solid lines denote the increased variability of n with with large body size for haplorhine species.

Following the concepts of 'r' and 'K' selection discussed earlier (p 267 et sqq) summarized by Wilson (1975) it might be expected that the distribution of r_m per day given in Figure 27 (p 270 - 1) would reflect the environmental conditions of the different species. There are however some problems with the generalized conception of r and K selection which are dealt with in this chapter and the next. The problems can be divided into three main issues.

1) The value of r_m (the rate of population increase under optimal conditions) and K (the mean density of the population) are only properly understood in relation to energy. The evolutionary implications of the value of r_m are best interpreted in the form of the ratio between energy of maintenance and energy of reproduction, the method of Fenchel (1974).

2) r and K are inadequate demographic parameters for populations with age structure (i.e. iteroparous species). Selection acting on species in variable environments will not operate solely on values of r and K but will tend to favour an increase in the ability of the population distribution to resist disruption from environmental perturbations (Demetrius 1975).

3) The values of r_m and K are dependent on body size (Fenchel 1974, Western 1977 see p. 292 et sqq). In this section of the discussion we shall consider the distribution of r_m values within the order primates, although the three problems mentioned are significant at this level the main theoretical discussion is reserved for later sections (on evolution of primate values of r_m; problems 1) and 3) p. 295 et sqq,)

For the purposes of this section we shall refer to particular instances of these three problems which are dealt with in general later.

In reference to : 1) The comparative variability of strepsirhine metabolic rate and the relative invariability of haplorhine metabolic rate (see p 52 et sqq) 2) The calculation of r_m per day is an estimate of the maximum rate expected in captive studies, following Fenchel this is assumed to be an estimate of r under optimal conditions equivalent to the r_m of Wilson (1975). (It is probable that were all the species to be bred in large captive colonies and r_m estimated from the rate of population growth, they would fall lower than values given in this study, due to captive breeding inadequacies and genetic failure not accounted for in the present estimate, see next section p 299 et sqq). The estimate of optimal conditions eradicates the variation experienced in the natural conditions of both

a) maximum potential population density, K_m, of the environment over time, and

b) mortality between age classes (which may however be stable over time).

The variation in carrying capacity of the environment is associated with seasonal and other variable ecological conditions, classically selecting for high r_m. Variation in age specific mortality of a population may apply to species in either variable or stable environments and will depend on the agencies of mortality. It is possible that in a stable environment a species may be subject to high pre-reproductive mortality, due to the predation of infants, or lower infant resistance to disease. This type of mortality is associated with a survivorship curve of type III (Diagram 3 p 277 - 8). As explained earlier (p 262) the estimation of r_m per day assumes a survivorship of type I.

A species adapted to maintain a stable population under stable conditions of high infant mortality will exhibit a higher r_m per day than a related and similarly sized species which normal suffers stable conditions of age independent (or random) mortality (Type II curve).

This means that the value of r_m per day may be high for either or both of two factors, firstly as a consequence of adaptation to unstable environmental conditions, and secondly as a consequence of adaptation to high infant mortality, whether in stable or unstable environmental conditions. 3) Fenchel (1974) demonstrated that when the experimental values of r_m per day were divided into the respiratory types 1) homoiotherms 2) heterothermic metazoa 3) unicellular organisms, there was an interspecific decline in the values for each group with increasing body weight. The three groups gave distinct distributions, and for each group the relationship was of the form:

$$r_m \text{ per day} \propto (\text{Adult Body Weight})^{-.275}$$

The Principal Axis obtained from the haplorhine distribution has a greater negative slope

$$\text{P.A.} = -.39 \qquad r^2 = .82,$$

the linear regression method (used by Fenchel) yields a correlation with slope -.38. This difference will be discussed later (p 335), but for the purposes of analysing the distribution within the primate order we shall refer to both the findings of Fenchel and those presented here.

An important point central to further aspects of Fenchel's analysis is that the interspecific exponent of -.275 for each respiratory type is very similar to the exponent of body weight proportional to specific metabolic rate (in kCal/g, day) for the same groups of species, -.25, (Hemmingsen 1960, Zeuthen 1947).

Adaptive variation in r_m per day in Primates. Figure 27 (p 270 - 1) shows the plot of log. species r_m/*day* against log. mean adult (female) weight. In order to assess empirically the relationship between r_m/*day* and environmental stability species are distinguished not only between haplorhine and strepsirhine species but also between those primarily inhabiting tropical forest zones and those which are generally found inhabiting a wider range of habitats (assumed to be subject to greater environmental instability), including woodland savannah, thornveldt, grassland savannah. This is a crude classification based on Napier and Napier (1967), Martin (1972), Charles-Dominique (1977) and Hershkovitz (1977). It can be seen that there is no clear-cut relation between either absolute or relative value of r_m/*day* and habitat stability within the primates. The lowest relative values of the distribution about the Principal Axis, those of *Galago demidovii* (46), *Saimiri sciureus* (107), *Miopithecus talapoin* (82) *Hylobates lar* (57), *Pan troglodytes* (86), (and *Homo sapiens* (52) nomadic !Kung value) are all tropical forest types (except *H. sapiens*). However two of the four highest relative values of the distribution are also tropical forest types, *Callithrix jacchus* (14), *Varecia variegatus* (113), unlike the two southern, thornveldt populations of *Galago crassicaudatus (umbrosus)* (45-) and *Galago senegalensis (moholi)* (47). The central area of the distribution is mixed. The same picture obtains when considering the distribution about Fenchels slope (see above p. 292) passed through the mean values of the distribution with the exception that the forest living *Pongo pygmaeus* (95), and *Gorilla gorilla* (49), join those species with relatively low values.

This result need not be confusing, but does seem to demonstrate a problem with the generalized *r* and *K* selection schema. As previously discussed the primates may be generally considered as the most K selected of terrestrial homoiotherms. The lower values of r_m/day within the primates may in fact be some of the lowest known. (it should be remembered that these estimates are likely to overestimate the values which might be obtained in laboratory colonies empirically; there are still many problems in successful breeding of primates in captivity). It is most likely that for these extremes of the homoiothermic spectrum only conditions of both environmental stability and type II survivorship (p 276) will produce such low relative values of r_m/day However higher values of r_m/day may be a consequence of either instable environments, stable environments with high infant mortality (Type III survivorship, p 276) or a mixture of both, (see next section and Chapter 7 for further discussion of the evolutionary position of the primate order).

The two species most obviously out of place in terms of the generalized *r* and *K* selection theory are

Callithrix jacchus (14) and *Varecia variegatus* (113). Both these forest living species would be predicted to have relatively high infant mortality for primates of their size, despite forest stability of the environment. If Fenchel's slope is used for comparison, the prediction of abnormally high infant mortality, as compared with other primates of similar size, might be extended to include the tamarins and marmosets generally.

The variation of r_m/day values about the correlation, suggests variation in life expectancy for the species. This is generally associated with size, where, as discussed earlier (p 276 et sqq) life expectancy of smaller bodied species is expected to be a smaller proportion of potential lifespan than for the larger bodied forms. Further, for any given body size relatively high values of r_m/day suggest low relative value of life expectancy, though the low value of expectancy will be dependent on both the losses through mortality due to environmental instabilities and also relatively high infant mortality (independent of gross environmental changes).

Before moving on to the next section it is interesting to note once again the relatively poor correlation of strepsirhine values in Figure 27 (p 270 - 1). The range of strepsirhine r_m/day values is similar for a range of adult sizes from 60-3,000 grammes.

General position of primates. It is of some interest to compare the values of r_m/day for primates given in this study with those of other organisms given by Fenchel (1974). In Figure 28 (p 272 - 3) the regressions obtained by Fenchel for; 1) a few Mammalia (genera Rattus, Mastomys and Bos),

2) heterotherms

3) unicellular organisms

are superimposed on the primate distribution. Fenchels values were obtained from laboratory colonies, whereas those given for primates are estimated, and almost certainly overestimate the values that might be obtained from long term breeding of colonies. Thus, if the primate values were obtained from an equivalent source to Fenchel's they would be lower than the estimates given here, by how much is hard to judge and would depend on the particular captive breeding problems of any particular species.

The most striking feature of the primate distribution is that the primates have, for their size, possibly the lowest known rates of potential population growth.

This might not be expected from the comparison of the results given by Fenchel which demonstrate that for any given body weight heterotherms have a higher r_m/day than unicells and that the few mammalia studied had a higher r_m/day than the heterotherms of given size. However a more expected pattern, expressing the evolutionarily 'advanced' character of the primates is revealed when metabolic rate is taken into account (following Fenchel 1974).

Two values for the tree shrew species Tupaia belangeri and T. glis are estimated from Martin (1968a). Both lie outside the range of the primate distribution (see Figure 28 p 272 - 3), but interestingly lie close to the regression found by Fenchel (1974) for mammalia (slope 1).

r_m/day and metabolic rate. Fenchel (1974) considers a population growing exponentially at the rate r_m, and that at an achieved population of N' individuals are removed at a rate $N' r_m$ so as not to disturb the age distribution. Thus the population remains at N' individuals (c.f. the assumption of roughly stable species population size over long periods), and the yield or production is $N' r_m W$ per unit time, where W is the average body weight of the population.

'Thus r_m can be interpreted as a measure of the potential productivity per unit weight of a population. The fraction - r_m/metabolic rate perunit time - measures how much energy an organism spends for production relative to how much it spends for maintenance.... The ratio 'production/respiration' of populations takes a maximum value of the magnitude 1-2; i.e. ½ - ⅔ of the assimilated energy is spent for production, values which are found in microorganisms, whereas higher organisms are known to have lower values for this ratio.'

Fenchel proceeds to demonstrate that for a given size a heterotherm metazoan has an r_m/day about twice that of a unicell (the difference between line 2 and line 3 of Figure 28 (p 272 - 3), however the metabolic rate of the heterotherm metazoan will be on average 8.3 times higher than the unicell. When comparing heterotherm metazoa and homoiotherms the latter (for Fenchel's species) have an r_m/day about 1.7 times the former (the difference between slopes 1 and 2 of Diagram 6:) and a metabolic rate about 28 times the former.

Fenchel says; 'Accepting r_m as a measure of potential population productivity the present results would indicate that the ratio 'production/metabolic rate' is about 28/1.7 or 16.5 times higher for heterotherms than for homoiotherms.' Field values for the ratio of production to respriation for several heterotherms and homoiotherms (McNeill and Lawton 1970) show a difference of a factor of 23 times between the ratio of 'production/respiration' for heterotherms and homoiotherms. This difference between the two values is probably a consequence of the fact that 'metabolic rate' employed by Fenchel is the resting value - Basal Metabolic Rate (B.M.R.), whereas field values come closer to an active metabolic rate, higher than the B.M.R.

Following Fenchel once more, a similar estimate is now possible for the primates or at least the haplorhine species, for which Basal Metabolic Rate is accuratley predicted by Kleiber's (1947) curve for most homoiotherms (see Hildwein and Goffart 1975). The mean value of $\underline{r_m/\text{day}}$ for haplorhine primates, is, for standard body size, about half that of unicellular organisms, ¼ that of heterotherms, and about 1/6.8 that of the homoiotherm mammals studied by Fenchel.

This suggests that the ratio of 'production/metabolic rate' of primates is about 1/6.8, (14.7%), that of other homoiotherms, about 1/(16.5 x 6.8), (.89%) that of heterotherms and about 1/(16.5 x 6.8 x 4.1),(.22%), that of unicellular organisms.

The unicellular organisms use between ½ - ⅔ of their assimilated energy on production, on this basis we may roughly assess that for haplorhine primates, exhibiting as a group probably the lowest known ratio of 'production/respiration' in energy flow of between

.22% - .44%

This ratio is an inverse measure of the efficiency of the species population in the use of energy. The 'production' side of the ratio is in fact a material and energetic loss or 'waste' to the population, or to the evolutionary lineage (assuming roughly constant populations over the majority of evolutionary history). Such tissue, and the energy contained in it (dead members of any age) is sacrificed by the constant population. The primates thus emerge, as might be intuitively expected, as probably the most efficient users of energy living (a concept to be further discussed p 327 et sqq).

In general, the use of the concept of energetic efficiency clarifies the apparently confusing distribution of $\underline{r_m/\text{day}}$ values for all respiratory classes and the primates. The low value of the primates is thus seen not simply as an apparent regression to low $\underline{r_m/\text{day}}$ but much more significantly as a progression in the apparently evolutionary trend of increasing energetic efficiency.

There are two principal inconsistencies in the analysis which whilst not altering the value of the concept, may render the fine detail of the phylogenetic relationships innaccurate until further data becomes available.

1) There is an assumption that the energetic cost of maintenance of tissue is equivalent to the cost of creating new tissue in the form of the foetus or infant. (See chapters 4 and 5 for discussion of the interrelations of foetal and infant growth and metabolism with maternal metabolism).

2) Properly, neither adult weight or adult metabolic rate should be employed for the correlations, but rather population means of these parameters. As a proportion of adult weight it would be expected that higher infant mortality in the smaller bodied species of any group would tend to reduce mean population member weight, (see p 276). Due to slightly higher specific metabolic rate in mammalian infants, a higher population mean specific metabolic rate, as a multiple of adult specific metabolic rate, would be expected in smaller bodied species. In fact the expected errors generated by the use of adult values for body weight and metabolic rate are mutually contradictory. That is to say that as far as the obtained values of the ratio of production/respiration given in this study and Fenchel (1974) are concerned the errors may be found to cancel each other out, leaving such values unaltered.

Three further issues worth considering in the discussion of r_m/day values given here are:
1) The steep negative slope of the haplorhine correlation as compared with those of Fenchel (see p 292).
2) The poor correlation of strepsirhine values and
3) Age at first delivery, principal component of the reproductive potential of the population.

1) Unlike the correlations obtained by Fenchel (1974) there is a marked difference between the interspecific slope of metabolic rate and that of r_m/day. The latter being -.39 as compared with the expected metabolic slope of -.25. This result for the haplorhine distribution indicates that the larger bodied species within the group use a smaller portion of metabolic energy in reproducing themselves. Fenchel had noted the same

effect within the three groups he studied (see p 292) but the difference in exponent between the r_m/day and metabolic allometries was of the order of $\sim$ .026 whereas for haplorhine species the difference is closer to .14. It is of interest that this tendency should be most marked in the order with the greatest 'efficiency' of reproduction. This factor will be discussed in greater detail later (p et sqq).

2) The poor correlation of the strepsirhine values of r_m/day against female body weight suggests once again some relection of the metabolic variability of these species (see p 52 et sqq). Although 'average' annual metabolic rates of these species may be comparable with haplorhine species it is possible that strepsirhine species have the potential for a sophisticated form of heterothermy (not as extreme as that of hibernating mammals which are themselves more homoiothermic than the true heterothermic organisms). If this is the case then perhaps the average annual metabolic rate of the strepsirhine species is generally lower than that of haplorhine species. Therefore, whilst both strepsirhine and haplorhine species have comparable rates of r_m/day for a given body size they may in general have slightly higher values of the ratio production/respiration, or slightly lower efficiency of reproduction than haplorhine species. Further discusssion follows (see p 305 et sqq).

3) As demonstrated by Cole (1954) and Lewontin (1965), the most important variable in the intrinsic rate of natural increase is the period from birth to first delivery in the female. The low values of primate r_m/day, as compared with the other mammals considered by Fenchel (see Figure 28 p 272 - 3), is largely a consequence of their relatively late age at

first delivery. As an order the primates show a later age at first delivery than all other mammals of a given body size (Western 1977). In fact most heterothermic organisms show a later age at first reproduction than mammals, probably due to relatively slower metabolism and growth rates. The primates however, for a given size, despite their homoiothermy and raised metabolism common to all mammals, delay first delivery till as late as some heterotherms.

Further consideration of these topics follows in the next, final, chapter.

Summary of Chapter 6

The chapter is primarily concerned with long term reproductive potentials. For this reason data on the number of mammae are discussed. In general the number of mammae may be associated with litter size, nesting habits and body size.

However, the major topic concerns estimates of r_m, the maximum potential exponent of population growth. This measure is strongly associated with the concepts of r and K selection, which are briefly described, though pointing out the failure of the value r to incorporate information about the age structure of the population. r_m is estimated for primate species following Cole (1954). The value is lower in larger bodied species. A crude estimate of the environment identifies an expectation of relatively high infant mortality in Varecia and the marmosets and tamarins generally. Two values for Tree shrew species lie outside the primate range. Whereas most homoiotherms have a generally higher r_m for a given size than heterothermic metazoa and unicellular organisms, the primates have a lower value still. This indicates that primates are possibly the most efficient organisms in the use of energy absorbed.

CHAPTER 7 - GENERAL CONCLUSIONS

In the course of this chapter the author intends to bring together some of the issues raised earlier in a condensed form. This applies to both the data on the primates and the theoretical perspectives developed earlier. Some reference will be made to Tables 7, 8 and 9 (p 368 - 372) which give a qualitative representation of the comparisons of strepsirhines with haplorhines, primates with other eutherian mammal orders, and members of the Hominoidea with haplorhines primates in general, for many of the bivariate relations discussed earlier.

The organization of the chapter has presented something of a problem. The author was concerned to summarize the immediate form of the results before elaborating more speculative aspects of theory. The subject of human evolution has been placed after the theoretical discussion since the outlook presented depends upon the thermodynamic considerations. Whilst the author's most recent academic experience does not allow an authoritative discussion of human evolution, it is proposed that the thermodynamic nature of human activity deserves more attention by those primarily concerned with the subject. The final section is concerned with the development of research in the future. Methodology is reconsidered and aspects of study which, in the author's opinion, may yield fruitful results, are listed.

The Primates

Section a) Comparison of groups within Order Primates.

In the introductory chapter a broad perspective of the evolution, ecology and physiology of the primates was given, partly in support of the decision by the author to treat the two groups, Haplorhini and Strepsirhini, separately in the analyses. In general the results given confirm the distinctions already presented in the literature, and enlarge upon the range of opposing tendencies exhibited between the two major primate taxa. It should be recalled that the fossil evidence suggests that both groups arose from radiations about 40 million years ago, and that the two lineages had probably been divirgent for almost the same length of time prior to these radiations. Table 7 (p 368 - 370) presents a visual comparison of the strepsirhine distributions as distinct from the haplorhine pattern. The table is not statistically tested and represents a preliminary examination, (see explanatory note preceeding Table 7). For some factors there appears no general distinction. In fact, low relative values of a_w and a_w brain (a, b), high neonatal encephalization (e), late first delivery (o) and long life (s), factors which show no difference between the two major groups are considered as characteristic of primates in general (see Table 8 and next section). However, the values for r^2 are often poor for strepsirhine analyses, especially those that measure specific rates or developmental periods. In general it is proposed, that these values reflect the 'flexibility' of the strepsirhine forms in both individual and specific adaptations to ambient temperature and seasonal conditions.

The most noticeable of the general differences between the two groups are associated with tendencies that are most apparent about the time of birth, with the exception of adult encephalization (f). Whilst the high characteristic foetal brain/body ratio is shared by both groups, the strepsirhines can only maintain this ratio for isometric growth to a neonatal weight $\sim \frac{1}{3}$ that of haplorhines relative to female adult weight (C). This may be associated with low rates of oxygen or nutrient diffusion through the eiptheliochorial placenta of strepsirhines. (It will be recalled that the time and growth rate parameters are poor predictors for birth see p. 154 et sqq, and maintenance factors are probably more involved).

It seems likely that the high characteristic foetal brain/body ratio of both haplorhines and strepsirhines was a feature of the ancestral primate stock. The isometric growth of brain and body during the foetal period of all mammals (Holt et al 1975) gives the ratio special significance. It would appear, however, that this is an element of structure which is dependent in its eventual form (in adult encephalization) on the relative rates of development in the pre and postnatal periods. It is in these rates that the strepsirhines differ markedly from the haplorhines. Having achieved only $\sim \frac{1}{3}$ of the body weight advancement of haplorhines by birth, the strepsirhines infants undergo an acceleration in growth postnatally (h), so that by age at weaning they are further advanced than haplorhine infants in proportion to adult weight (l). However, the advantages of the intrauterine environment for the development of encephalization are lost and the adult encephalization is finally lower than that for haplorhine species.

These features of the strepsirhine developmental pattern support Martin's (1972) contention that seasonal conditions during evolutionary history have constrained the reproductive pattern of these species. In most species gestation covers, at least in part, a period of relatively poor resource availability. The peak nutritional demand of the mother and infant, during lactation, falls during the period of maximum food abundance and the infant is weaned just prior to the onset of a further period of relatively poor food availability. The slow growth of the foetus as compared with the rapid growth to weaning (with a greater body weight advancement at weaning) in strepsirhine species as opposed to the haplorhine pattern, appears strongly adaptive to seasonal conditions. The haplorhines on the other hand are generally exposed to more favourable conditions in extant forms. The development in utero is more rapid than the strepsirhines (with the notable exceptions of Microcebus murinus, Cheirogaleus spp. and Varecia variegatus), whilst retaining the high characteristic foetal brain/body ratio of primates. This gives the haplorhine neonate a greater body advancement at birth. It seems most likely that both faster growth and greater weight attainment at birth in haplorines are associated with the highly invasive placental type, haemochorial placentation. There is no sudden alteration in growth rate at birth and relative to both infant and maternal weight the postnatal growth rate is lower than that of strepsirhine species. Infants are capable of self support in digestive physiology at a relatively poorer advancement in weight than strepsirhines.

The general picture may be summarized as follows: In absolute time there are no general differences in the periods of gestation, lactation, age at first delivery and total lifespan, relative to weight between haplorhines and strepsirhines. However, during the intrauterine period of high structural advantage (i.e. isometric brain and body growth), but low absolute demand, the haplorhines have relatively accelerated growth, and strepsirhines relatively decelerated growth. In the postnatal period of poorer structural advantage to development, but higher absolute demand the haplorhines have relatively decelerated growth and the strepsirhines have relatively accelerated growth. These tendencies may be understood as adaptive reflections of environmental tendencies operant during the evolutionary history of the two groups. Esentially, following Martin (1972), this seems to be due to a relatively dry period in the area of the ancestral stock of strepsirhine species about 40 million years ago. At that time the ability of small bodied (i.e. less than 8 Kg) strepsirhines species to live in harsh seasonal conditions was either created or relatively permanently established and is maintained in both extant Lemuriformes and Lorisiformes. It may be proposed that following the initial arboreal adaptation of all ancestral primates the haplorhines lineages remained, all inclusively, within forest conditions. The growth pattern of the haplorhines shows no major disjunction at birth, and the relative acceleration of the intrauterine period and deceleration of postnatal growth suggests that environmental conditions may have been relatively good and stable over the whole period from conception to weaning, and probably beyond. For larger bodied species this would mean almost aseasonal and highly productive environmental conditions of food availability.

Recalling the general pattern of modern primate distributions and the overview developed in the first chapter, the adaptive form of the two major groups of primates suggests two significant features relevant to general theory.

Firstly, whilst certain structural similarities may exist between the two groups long term adaptation appears, in a relative sense, to have restrained the potentialities of strepsirhines (seasonal conditions - harsh), and enhanced the potentialities of haplorhines (aseasonal conditions - luxuriant). Adaptation in the former has acquired the character of an incorporation of environmental contingencies into the pattern of development. Or to put it the other way round the overall nature of the group has tended to become flexible in the face of strict, inflexible conditions. This tendency is equivalent to a poor homeostasis, and dominance by the environment. On the other hand the haplorhines, within a flexible environmental contingency have evolved a more specific form, demonstrated most clearly in higher adult encephalization and metabolic inflexibility. This tendency is towards good homeostasis and dominance over the environment.

Secondly, many of the reasons for the present, and possibly past, conditions of strepsirhine species may be associated with their poor competitive status against haplorhines (extant and ancestral) for occupation of the forest, (see p 48 et sqq). In this sense the potentialities of the strepsirhine species on the Old World mainland have been 'suppressed', on Madagascar, under different conditions, primarily without haplorhines, these potentialities found much greater expression.

The second example, is however, incomplete since in South America there are haplorhines and no strepsirhines, and it is here that the only monkeys below 1Kg are found. It seems certain that the evolutionary history of the marmosets and tamarins included a period when singleton births were normal as with _Tarsius_. Whereas _Tarsius_ retained multiple pairs of mammae the Callithricids lost the trait. Unlike strepsirhine species with bicornuate uteri, all the haplorhines have a simplex uterus. The haplorhines have also lost the tapetum, a specialization for nocturnal activity. Following Charles-Dominique 1975, we can see that small body weight ($<$ 1Kg) and diurnal habits would be unusual for strepsirhine species, and primates in general. This might lead us to expect an enhanced competition for these small species with bird species. Furthermore, of all primate species, predation is most commonly referred to, and sighted in the wild for the Callithricids (c.f. Charles-Dominique, Hershkovitz 1977, and Napier and Napier 1967). The predators are diurnal hawk species. In comparable environmental conditions, i.e. equatorial forest, nocturnal strepsirhine species of a similar size generally breed annually and give birth to single offspring. In adapting to a small body size niche the diurnal Callithricids, presumably under the pressure of predation, have been forced into twin litters and at least the potential for biennial breeding (reported for semi-natural, and captive conditions Hershkovitz 1977, Hearn et al 1975). This gives the Callithricids high r_m, which when compared with the 'normal' metabolic rate of these species suggests a relatively high value of production to respiration. This tendency suggests that whilst the absence of strepsirhine species has permitted the development of small size potentiality in the haplorhines, this has generally required an evolutionary regression of form. The only exception to this tendency appears to be the genus Callimico, which deserves special attention. It is important to note that the significance of twin-bearing in the Callithricids is only understandable in terms of its effect on r_m, and r_m may be further interpreted in relation to energy flow.

Section b) Comparison of Primates with other Mammalia.

Having discussed a few of the features which distinguish groups within the primates in terms of basic ecology, energy flow and reproduction we may now consider those features which serve to delineate primates from other orders. In a qualitative sense the notion of primates as an extremely 'K' selected group in the spectrum of extant animals is already familiar (Martin 1975b). This concept is given a quantitative basis in the analysis of allometric trends describing important thermodynamic aspects of the primates. The primates emerge as efficient users of the energy which flows through the living form, both at the level of individual physiology (see Sacher 1976 and next section) and in terms of the population in the ratio of production/maintenance (see Chapter 6 and next section). In most respects these feature of the primates are expressed only in relative values of basic physiological and reproductive parameters which lie at the extremes of the ranges known for all animals, of a given size. However, as we have seen (Fenchel 1974, Chapter 6) the rate at which energy is metabolised at a particular body weight is an important specification of a living object. Many of the 'extremes' demonstrated by the primates in relation to body size, for example late age at first delivery, long lifespan, slow growth rate etc., are extremes only in relation to mammals. Reptiles and other heterotherms may live longer, deliver first later, and grow slower. (Some birds may live relatively long but as pointed out by Sacher, 1976, this factor is associated with body temperature, as well as energy flow, see next section). However, in relation to the rate of energy flow through the living individual, (for any given size the mammalian metabolic rate is ~ 28 times higher than that of heterotherms, Hemmingsen 1960), these developmental parameters are proportionally much longer and slower in mammals, and at an extreme in primates.

The general similarity of the relation between energy flow and body weight for all mammals allows the qualitative evaluation of the significant features of primates as compared with mammals, all with a standard energetic base, Table 8 (p 371). The essential character of the primates, in relation to both size and in general to energy flow as revealed by this comparison may be summarized as follows; primates have the slowest foetal growth at the highest foetal cephalization, with latest age at 1st delivery in the female, lowest reproductive potential, longest potential lifespan and lowest ratio of production to respriation. Other factors which are also represented in Table 8 (p 371) which show some apparent distinction between the two groups of primates are also mammalian extremes; Low foetal growth weight at birth (strepsirhines), high adult encephalization (haplorhines), slow postnatal growth (haplorhines). These factors are also clearly associated with the relatively low entropy production of adults (Sacher 1976).

At present these tendencies are presented merely as a correlation, later a theoretical basis for a functional interelation is discussed, (see p 314 et sqq).

We may however, briefly point out the expected relationships that are based on theoretical issues already discussed. On the basis of r and K selection theory the primates may be seen to fulfil some general conditions of species with a K selected evolutionary history listed by Wilson (1975). Though noting that these are only absolutely satisfied in relation to the rate of flow of energy. (Letters refer to Tables 7, 8 and 9).

1) Slower development - as seen with low foetal and postnatal growth - (a, i).
2) Delayed reproduction - late age at 1st delivery -(O).
3) Longer life - (s)
4) Emphasis on efficiency in energy utilization - (r)
5) Small colonizing ability - low r_m - (q).
6) Climate fairly constant - predominance of forest living in extant forms, locomotor adaptations to forest living.

Sacher's (1976) identification of the entropy factors in aging have been described earlier, they primarily associate the long life of primates (s) with high adult encephalization (f) through the factor of thermodynamic energy production of metabolism as mediated by the negentropy of the structure through which metabolic energy is released.

Sacher et al 1974 identified the significance of foetal brain growth in the rate of foetal somatic growth, they established the association of low foetal growth (a, d) and high foetal encephalization (e) in the primates.

The relatively low concentration of protein in haplorhine milk (insufficient data to include strepsirhines) has been associated by Payne et al (1968) with the relatively low rate of postnatal growth of these species (i).

Further discussion of these relationships which have their extreme expression in primate species will arise within the following section.

Theory, with some additional reference to Primates.

In the following part the author will examine, and attempt to draw together some aspects of general theory that have been briefly described and referenced, see Chapter 2 and p 295 et sqq. It has already been pointed out that this aspect of research was forced upon the author during the course of research which was initially aimed at a more particular subject (p 15 et sqq). In the author's knowledge no truly integrated analysis of biological theory that extends beyond essentially only qualitative discussion, or mathematical derivations is available in the literature. Whilst authors such as Engelgardt (1978) have given a general qualitative account of the essential features of living systems, few authors have attempted to demonstrate these qualities within empirical observations. A major exception would include the work of Sacher (all cited references). Were more general theoretical treatises available much of the particular research presented here might have been more profoundly examined. As it is, much effort was expended in examining general theory and some of the conclusions of this examination are reported here. In general the form of this discussion is attributable to the author, though the bases for discussion have followed the literature referenced in Chapters 1 & 2

The author will refer often to concepts and papers discussed and presented in Chapter 2. The reader may care to re-examine that chapter briefly at this point.

Section a) Aspects of energy flow in living systems.

It has been asserted earlier that three essential flows are united within the processes characterizing living systems, the flows of matter, energy and information. The'unity' of these three processes is expressed in their interdependence. It is clear from modern physics that none of these three forms of the movement of matter may exist without the other two. Matter flows essentially only in the form of attraction or repulsion (e.g. gravity and heat), response to gravity (attraction) results in the loss of energy (potential) of the system, whilst repulsion (against gravity) requires an input of energy (kinetic). Energy is thus generally used as an expression of repulsive motion(Engels 1934). The flow of information expresses the relative conditions of the relationship between the flows of energy and matter. In the thermodynamics of gases for example the flow of information is determined by the relationships of change in mass, thermal energy and temperature over time (Wesley 1974). The nature of these changes with respect to time gives us the term 'flow'. The movement of matter be it apparently passive (e.g. the orbiting of the electrons in a 'stationary' mass) or active (the falling of such a mass in a gravitational field) only ceases at absolute zero. A condition that is unobtainable in practice and by all accounts theoretically impossible due to the resonance expressed in any object, no matter how cold, which is generated by the continual motion of the universe about it, (Bondi 1965, Schrodinger 1945).

Thus the characteristics which are postulated above for the essential nature of living systems do in fact apply to all forms of the continual movement of matter. This is the thermodynamic corrolary of the assertion of modern evolutionary biochemists that there is no absolute distinction between living matter and non-living matter (Bernal 1967, Pirie 1937). However, let us consider the essential distinction formulated by Wesley (1974) and Engelgardt (1978) with respect to the second law of thermodynamics (see p. 73 et sqq). This definition is based on the assertion of Clausius' law, that there is a universal tendency for increase in entropy over time. In recent years empirical observation has lead to a restatement of this law to include the possibility that the total measure of entropy is, in fact, in balance universally, thus the second law becomes $dS \text{ (universe) } \geqslant 0$, Wesley (1974, p.8). However, brief consideration of the possibility that entropy increases universally would indicate that at some point entropy was at a minimum and will in course reach a maximum universally. The initial start of the tendency and its 'correction' in

due course implies an impulse from <u>outside</u> the universe, clearly an untenable position (Engels 1934). If then on theoretical grounds we assert the universal balance of the total sum of positive and negative entropy i.e. $dS(\text{universe}) = 0$
on what basis does the essence of living systems rest? In any particular 'system' the tendency may be for loss or accretion of entropy, the continual movement of matter necessitates this effect. Certain sections of universal matter collapse, at the centre of this collapse the tendency for attraction dominates, whilst simultaneously large amounts of matter are repelled by the heat generated in attraction. This summarizes the history of our solar system. On Earth, lying close to, but not at the centre of this collapse the tendency for attraction dominates, this is expressed in the slow cooling of the Earth as a whole. Thus, in our part of the universe all processes and movement are associated with the relative tendency of increased collapse (attraction) and heat emission (entropy production). However, the transitional relation of the earth in respect of the outer reaches of the solar system and the centre is one that necessitates great interplay of the two processes that characterize the development of the solar system.

The two features discussed, firstly the overall tendency of attraction and the 'activity' of the planet Earth are expressed by processes that are of great consequence to the evolution of life. Firstly, a general tendency of cooling of the planet over long periods of time (a process that takes many forms and may be apparently discontinuous in form e.g. loss through low or high energy radiation etc). Secondly, in the short term, an energy flux passing into and away from the earth, (heating by the sun, and reradiation from the Earth) with no short term increase or decrease in total heat energy.

Even in the simplest interactions however, energy and matter undergo changes in form. An important feature of the short term rapid energy flow through any planetary system is that in general the flux of absorbed energy is four times that of radiated energy. This transformation of energy mediated by the planet is a simple consequence of the ratio of the area of incidence to energy radiated by the sun, πr^2 where r is the radius of the planet, to the total surface area of the planet $4\pi r^2$. Whilst this 'average' law must hold if the planet remains, in the short term, in thermal equilibrium, further properties of the terrestrial system, particularly its surface allow some highly complex chains of transformation to occur. The form of many of these transformations, those that are of particular interest to the biologist, are chemical. (This is not the case in other parts of the solar system, at the centre nuclear transformations predominate, at the periphery, mechanical transformations of particles predominate). The chemical nature of many transformations of the form of absorbed solar energy prior to reradiation is a consequence of surface temperatures and the particular ratios of the elements that make up the Earth.

To refer again to the basic transformation of energy at the surface of a thermally stable, revolving planet moderately close to a star, we see that energy must be 'stored' during the process in order that thermal balance may be maintained. For a cool revolving planet composed of dense matter of low volatility the storage will be in the form of heat, which is slowly reradiated, especially from the 'dusk', 'night' and 'dawn' of the planet.

The particular characteristics of the Earth's matter and temperature allow a different form of storage, that of chemical bonding. Over relatively short periods the energy stored is equal to that lost, the net change in energy being zero for thermal equilibrium.

In the complex chemical transformations incorporated in the living tissue of organisms this must also be true. In the course of a day in the life of a dog for example the total amount of energy liberated in digestion is expended in heat and work. However, the storage of energy in chemical bonds and its subsequent release may proceed at different rates within the evolving system. Furthermore under certain conditions the transformation from stored to liberated energy may be suddenly disturbed from an equilibrium. For example the relatively stable form of stored energy in the cellulose of a tree may within the gut of a wood boring grub be suddenly transformed to heat and mechanical work. The nature of the differential rates of storage and release or absorbtion and reradiation within living tissue are of great importance, we shall return to this point later.

It has long been recognized that the origin of the energy that passes through living systems is derived ultimately from the sun. In general the total energy flux through any particular ecosystem is dependent upon the total flux of absorbtion in photosynthesis. The first step in this absorbtion is the only non-chemical part in the whole subsequent series of energetic transformations (excepting here the only other known involvement of radiant energy transformed to stored energy in photoreception or light perception). This primary step involves the transformation of photon energy into chemical energy through the changes brought about in light-sensitive substances especially chlorophyll. All subsequent transformations are chemical both within and beyond plant tissue until subsequent re-radiation at lower flux (see above).

In general then the transformations of energy in all heterotrophic organisms may be considered as chemical in nature. Furthermore, in the common origin of all stored energy in the results of photosynthesis expresses an essential unity of all the varied forms of reaction that constitute the activity of living matter. A particular aspect of this unity lies in the nature of the energy rich phosphate bonds of ATP (adenosine triphosphoric acid), which are not only the form through which radiant energy is transformed in photosynthesis but are a necessary stage in the transformation of all energy released in exothermic metabolic reactions. Not all the reactions within the organism are exothermic (giving out heat) however, but the endothermic reactions that constitute the formation of living tissue must take place in close proximity to these energy releasing reactions for greatest efficiency.

The radiation of thermal energy is not,however, the only transformation of chemical energy that occurs in living tissue. All types of motion are associated with conversion of chemical energy into mechanical work. The movement of water and dissolved substances require the performance of osmotic work in active transport. Nervous activity requires the transformation of chemical energy into the co-ordinated movement of electrons. All these non-thermal expenditures require,however, special configurations of organized matter for their release. This feature of all forms of living matter expresses an essential integrated feature of the endothermic and exothermic reactions that occur within the living system. However, in the life of any individual this integrated aspect is a measure of the differential rates of exothermic and endothermic reactions. The background configurations that mediate the release of energy are themselves only slow endothermic reactions. These reactions are themselves unstable and subject to the effects of the exothermic reactions, which in the course of activity disturb and degenerate their performance. In general the somatic tissue that surrounds the release of energy in the course of the individuals life is itself a *mediating* tissue between the two extreme elements in the opposed tendencies of living matter. At one extreme the slow but necessarily continuous (for all extant reactions) endothermal crystalization of the aperiodic crystals (Schrodinger, 1945) that constitute the genetic material of the organism. And at the other extreme the reradiation of originally solar energy, that is the essential nature of catabolism and decay.

We have necessarily covered this argument rapidly, omitting many important features of the evolution, and nature of life. One particular feature of life is its tendency to continually create the potential for new forms of activity, though this is expressed even within the life of the individual in the interaction of the three levels of reaction we have described. Even in this interelationship is seen the feature of somatic configuration in allowing completely novel activity in the life of the individual. However, there is no space for this discussion here. Briefly, the author has attempted to establish the following bases for further discussion:

1) The interelation of the continual, though differential rates of the flows of matter, energy and information.
2) The nature of energetic transformation in terrestrial environments.
3) The chemical nature of energy transformation, in all but the first step in absorbtion of solar energy, in living systems.
4) The three levels of chemical transformation in genetic crystalization, endothermic somatic configuration, and re-radiation of solar energy in catabolism and decay. The interelation of these three levels.

These considerations allow the author to return to the analysis of Sacher (1976) and some evidence presented earlier in this study.

Section b) Re-examination of heterotrophic form and activity.

On re-examination, Sacher's important paper (1976) does not seem so difficult to incorporate into theory as it may first have appeared. The analysis itself is based on mammalian systems and in general we must be limited in discussion to these forms of life. The most significant step he makes is the treatment of living activity within the context of the thermodynamics of chemical reaction rates (Eq 15 p 80). This is entirely compatible with the essential nature of energy transformation in living systems as we have seen.

The form of Sacher's results as considered in relation to the general equation for reaction rates is, broadly speaking, an identification of the two opposed tendencies described earlier (p 322 et sqq). The form of the slow endothermic reactions which constitute form of the somatic tissue of the organism and the rate and form of the exothermic reactions which are largely reflected in the metabolic rate of the organism. The former is equated by Sacher to the configuration entropy of the organism and the latter to the activation entropy of the metabolic processes. It is clear however, that these two measures are not entirely independent of each other. This is most forcibly expressed in the context of the evolutionary tendency to low values in both configuration and activation entropies in higher forms of life (Sacher 1976, p77). Even within the context of mammalian activities this interrelation must operate, since despite the generality of Kleiber's rule many mammals either hibernate or have variability in metabolic rate and temperature. Such variability is expressed in important differences in the form of endothermic structural reactions (e.g. the low melting point of brown fat in hibernating mammals, not found, for example, in the fats of man which are viscous at much higher temperatures) see below for further elaboration of this point. For the purpose of discussing short term processes in general however, the separation of these two components is entirely permissible and necessary at this early stage in the development of theory.

Reconsidering the relationship of Lifespan to the cephalization and metabolic factors we are able to see that the general form of the differential rates endothermic and exothermic reactions within any group of mammals takes a form that is biologically acceptable. The lifespan of the organism is, we might expect from earlier consideration, a measure of the stability of the slow endothermic reactions that constitute the form of somatic tissue. Statistically, this measure is strongly correlated with two orthogonal measure of the form and activity of the somatic tissue. Restating Eq 14 (p 79)

$$L = 8K_c^{0.6} K_m^{-0.5},$$

we see that of the two orthogonal terms K_c and K_m, K_c the encephalization of the organism, is known to be relatively constant for members of a given order of mammals (e.g. Bauchot et al 1969). The common features of morphology, physiology and general adaptation within orders suggests that the measure K_c is a reflection of the general form of a particular group of organisms that must be contained within shared properties of the genetic material of the group. K_c, is then strongly reflective of the form of the slowly changing structures that mediate the exothermic reactions of energy release. It is largely independent of the rate of activity. On the other hand the K_m term is essentially an expression of the rate of activity, dependent upon both body size and body temperature. It is important to note however, that the form of the K_m (eq 10 p 79) term indicates that a change in T_b by a factor of 10 is equivalent to a change in M.s by a factor of only 1.1. That is to say that the effect of Temperature on the K_m term is relatively insignificant, (though see below), important factor is the rate of release of energy per unit gram of tissue. The higher this rate the greater the rate of disordering, or aging of the 'innate' configuration.

The principal variation in M.s with any fixed value of K_c (that is within an order of mammals) arises from variation in adult body weight. This is an indication of the activity or 'regulatory' (Gould 1977) nature of body size within any order of mammals which appears less constrained by essential structure (K_c) in evolution. (Rensch (1959) points out that most major radiations are associated with a basic form followed by wide evolutionary variation in body size, generally towards larger size). To return briefly to the significance of Tb to the metabolic factor in mammals, it may be inferred from consideration of heterothermic and unicellular respiratory groups that the temperature of the system is also closely related to the performance of the configurational component, a point made above (p 323) in reference to the interdependence of the configurational and activational components in the chemical reactions of living matter. Whilst the regulatory relation between metabolic rate and body mass still operates in the lower respiratory groups, at any given body size they do not achieve the metabolic rates known for homoiotherms. The density of energy flow in these lower organisms, of standard size, is lower, suggesting that the configurational component is of higher entropy. The failure of homoiotherms to function under permanent low temperature conditions is further confirmation of the relationship of required temperatures for specific configurations.

In chemistry this feature of compounds is well known, temperatures of fusion and dissociation for certain compounds are, under conditions of constant pressure and volume, fixed and definite. It is known under modern theory that these definite thermal energies of transformation reflect the 'quantized' nature of energy in atoms and molecules. The nature of the configuration term, and its requirement for specific temperatures of activity in order to maintain configuration allows us to draw an analogy between the levels of encephalization found in living orders and the quantized energy states of orbiting electrons. We suspect that the configuration term is associated with structural aspect of the slow, endothermic reactions that create the 'background' to the exothermic reactions of energy release, (p 320). This anabolic process derives largely from the synthesis of proteins from the genetic template. The nature of genetic matter is such that quantized effects are the principal form of change. This is a consequence of the small scale of the genetic material which may not undergo continuous change but responds to external effects by discrete 'jumps' in arrangement. This feature of genetic material is of great significance of evolutionary theory, a point to which we shall return, (p 343 et sqq). For our present purpose we may merely note the analogy between the configurational term and quantized, discontinuous levels, and mention one further point made by Schrodinger (1945), which expresses another important feature of the relationship between temperature and (genetic) configuration. It is simply that an increase in temperature around the genetic material increases the rate of mutability of this structure. (A decrease may, as pointed out above 'solidify' it, thus impeding its interaction with its

medium). As Schrodinger suggests this thermodynamic effect must be very significant in the apparent acceleration of evolution in homoiothermic forms. Before extending these features of the individual's thermodynamic performance to that of the population let us briefly re-capitulate the perspective elaborated.
1) The relative independence of the Kc factor from body size, its dependence upon taxon, and its reflection of the configuration of 'structural' genes.
2) The relative dependency of the 'rate' term or metabolic factor Km, upon body size. This activity as a reflection of relatively flexible regulatory components in genetic material.

Section c) The population, the extension of the individuals thermodynamic form.

In Chapter 6, following Fenchel (1974) it was shown that the ratio of production to respiration was very low in the primate order, it was asserted that the primate value is the lowest in nature. In general, following Fenchel, it can be seen that for the major respiratory groups, that this ratio is constant, regardless of the individual size of the organism, and of the rate of energy flow through the population. In its derivation this ratio is an average measure for a population under conditions of unperturbed age structure. The form of the derivation, and the problems discussed earlier (p 295 et sqq), make this ratio only a very crude estimate of the real relationship in nature. During the course of the chapter the term high 'efficiency' was used to indicate the large proportion of assimilated energy that, rather than being lost to the system in the stored chemical energy of dead tissue, is transformed into the motion of heat or work.

In general, however, low efficiencies are found in the respiratory groups of lower metabolic activity at standard body size. This relationship is similar to the evolutionary association of low configuration entropy and low activational entropy (see p 80). In fact the author believes, pending more exact analysis, that on an intuitive basis the terms derived by Sacher for the individual are entirely compatible with the pattern described by the population. It is clear that a low value of r_m for a species requires in particular a late age at first delivery. In the context of environmental conditions of stability, relatively high productivity i.e. 'K' type, the organism itself must have a homeostatic mechanism allowing absolutely long life expectancy, and long potential lifespan (see Sacher 1975b). Intuitively speaking then, if the replacement rate of the population is absolutely low in time, the survival of the organism must be absolutely long in time. Clearly the population expresses the nature of the individual in this basic fashion. Just as the K_c factor, within orders, is independent of size, i.e. rate of energy flow per unit mass, so is the ratio of production to respiration. Furthermore, despite the differences in metabolic rate per unit mass between the major respiratory groups it can be seen that both K_c and the 'efficiency'.of energy use are greatest in the higher orders of life. This proposed relationship requires further examination. It may be further seen that whilst the K_c term and the efficiency term generally are roughly constant within orders that the rates of aging, and the rates of population turnover are dependent upon the same exponent of body size as the rate of energy flow per unit mass, i.e. proportional to

$$\text{Body Weight}^{-.25}$$

within orders. It is clear from this effect that, as we might expect, the nature of the individual and the nature of the population reflect each other in a very close manner. On average the total ratio of stored and expended energy of the average total life of an individual will yield a similar result to that of the entire population over the same period. This allows us to generate a very general schema of the possible allocations of total energy budget to the biological system, at the level of the 'average' individual or the population. This is presented in Diagram 4 (p330-1). It must be first stated that this scheme does not indicate the relationship of rate of flow to efficiencies of the energetic transformations at levels I, II and III. In general the rate of flow may be expected to have the most significant effects on transformations II and III whilst transformation I is most closely associated with the configurational or productive efficiency terms that are roughly constant within orders, and independent of rate of energy flow within orders. The 'efficiencies' at levels I, II and III are simply ratios of two opposed results of each transformation. The two opposite results are not entirely independent of each other, and at each level the interaction of the opposite tendencies introduces an element that mediates the two tendencies. An important point to be made is that whilst this diagram attempts to express the form of energetic transformations within living tissue, i.e. within the 'system', these transformations emerge only as adaptations to environmental conditions. This is the case for all but one process which the author has labelled 'active work (enhancement)' which it is proposed, and only under certain conditions is a measure of the potential of living matter to create the conditions for

Diagram 4

Schematic representation of energy flow in living systems. See text for explanation.

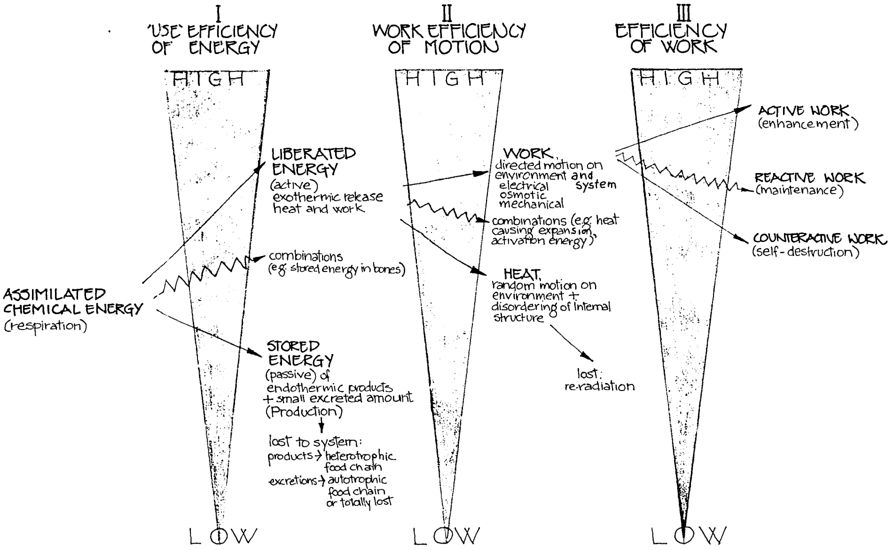
I
'USE' EFFICIENCY OF ENERGY
II
WORK EFFICIENCY OF MOTION
III
EFFICIENCY OF WORK
HIGH
HIGH
HIGH
LOW
LOW
LOW
ASSIMILATED CHEMICAL ENERGY (respiration)
LIBERATED ENERGY (active) exothermic release heat and work
combinations (e.g. stored energy in bones)
STORED ENERGY (passive) of endothermic products + small excreted amount (Production)
lost to system: products → heterotrophic food chain excretions → autotrophic food chain or totally lost
WORK, directed motion on environment and system electrical osmotic mechanical
combinations (e.g. heat causing expansion, activation energy)
HEAT, random motion on environment + disordering of internal structure
lost: re-radiation
ACTIVE WORK (enhancement)
REACTIVE WORK (maintenance)
COUNTERACTIVE WORK (self-destruction)

DIAGRAM 4

the development of higher and novel expressions of life (which it is clear has been a dominant aspect of evolution). Finally it is not proposed that these transformations occur in temporal succession, for example heat may be generated at every transformation. The diagram is more an indication of the hierachy of form that energy assimilated may take whilst it remains within the scope of the system.

However, let us work through these transformations from their initial form in assimilated chemical energy. At level I the distinction is made between energy liberated in motion from exothermic reactions, and the energy absorbed and eventually lost to the system in the products of endothermic reactions. The interaction of these two tendencies may be expressed in the use of stored components in the motion of the system, an example might be the limb bones of mammals which contain essentially dead matter which is employed in the release of motive energy.

At level II we are concerned with only that portion of assimilated energy that is liberated in motion. This takes the form either of work performed internally or externally to the system in the electrical, osmotic or mechanical forms referred to earlier. The opposite tendency is the energy of motion lost in heat. As we have seen this has a disordering effect on the endothermic reactions that is the metabolic factor in aging. The interaction of these two tendencies may be seen in the requirement of heat in the activation of the whole resp. atory process and possibly heat energy resulting in expansion of tissues to perform work. The efficiency of this transformation(II) appears to be associated to be associated with rate in that within orders lower rates per unit mass of tissue are associated with larger body size and the requirement of a greater proportion of liberated energy to perform work against gravity (Kleiber 1969, Kelly et al 1966).

However, the proportion of liberated energy resulting in work is not in itself a measure of the value of that work to the organism since it may produce either an advantage or a detriment. In general over long periods of evolution in the past the balance of this work results in maintenance. In some situations it may result in death and extinction. One can imagine for example a terrified and disorientated rabbit running straight into the jaws of a predator. However, in some lineages it is clear that the activity of the system, within relatively unaltered environmental circumstances has created, through work, conditions for its own enhancement. This process has been extremely slow in the past, but with humans has achieved a rapid and important development that may be said to be a unique feature of human activity. It it this 'efficiency' that is expressed in level III. We shall return to this in due course.

In general we see that the three levels of efficiency have a multiplicative effect. That is to say that the proportion of active work attained from assimilated energy may be increased by an improved efficiency at all three levels. It is clear that the maximum of the total proportion of assimilated energy available for active work may only be approached by maximization of the level I efficiency regardless of maximized efficiencies in levels II and III. High rates of evolution are thus associated with a high configurational efficiency (I), large body size (II) and efficient use of available work (III). The conditions for such efficiencies are related to factors which range from highly structural characters common to a large taxon level (I), size characters which are related to metabolic activity and appear to be slightly more flexible in evolution level (II) (see p 327), and essentially behavioural characters (level III) which have the highest flexibility (relative to the other factors).

It would seem that the advances in efficiency in energetic transformations that arise in adaptation allow the advance of the other efficiencies as well. Although, due to the nature of the three levels as described above, the impact of any advance in level III is largely determined by the attained levels of primarily I and secondly II. This is expressed, once again within the general stability of the solar system, as an accelerative function reflecting the multiplicative effect described above. It might be termed as a 'postiive feedback system' or an 'explosive' relationship. This effect becomes clearer if we re-consider the primates.

It may be seen that as a group the primates, and particularly haplorhines, are relatively advanced in respect of level I in this scheme. In fact it appears that whereas the configurational status of other organisms is dependent largely on respiratory categories (in both cephalization Jerison 1973, and level I efficiency in population production/respiration ratio, Fenchel 1974) within the single <u>order</u> Primates we see a major departure from this respiratory type constraint. Whilst the significance of its alteration largely in r_m and the Kc factor rather than in K_m is not yet clear, it would appear that this departure and advance by a single order in the short space of 70 million years is an expression of the continuing progressive acceleration in the advanced forms of life. It is worth pointing out that the three respiratory categories that in general indicate the advancement of the configurational term have had in evolution successively shorter periods of dominance. Unicellular organisms appear at about 3,500 million years ago (MYA) and dominate for a span of just under 3,000 MY until 570 MYA upon the earliest appearance of heterothermic metazoa. The emergence of homoiotherms may be traced to 200 MYA following 270 MY of heterothermic dominance. If we consider the emergence of primates to signify a new departure, only 70 MYA of primate dominance has elapsed following a general homoiothermic dominance of about 130 MYA.

In fact it appears that during the period of level II expression in the primates, i.e. size radiation (from a small ancestor), further advance has become very rapidly established in relation to size. In the author's opinion this tendency is expressed in the tendency to higher Kc in larger haplorhines (not apparent in other orders where Kc is similar regardless of size, i.e. brain to body allometry is close to a power of $\frac{2}{3}$ of body weight, Bauchot et al 1969). This tendency is further corroborated in this study by the steep negative slope of the r_m to body weight allometry see Figure 28 (p 272 - 3) and p 295 et sqq, as compared to the 'expected'slope of Fenchel of about -.25. Both tendencies indicate a higher level I efficiency in larger haplorhines, an unusual effect by comparison to lower orders.

The true 'explosive' and accelerative effect is seen most clearly with respect to humans however. Though, as the author will attempt to point out the tendencies are, in many respects, contradictory.

Human Evolution.

As stated earlier, the author is no authority on the detailed evidence pertaining to the evolution of Homo sapiens. However, in respect of the considerations given here some discussion is presented. Reference will be made to Table 9 (p 372) and Diagram 4 (p 330 - 1). The nature of large bodied haplorhines at a period about 20 - 15 MYA may in a general sense be approximated by comparison with the modern apes. Fossil evidence from that period suggests that the 'proto hominid' forms of Ramapithecus were essentially ape like. True bipedalism was not yet evolved and the fossils are associated with a fauna characteristic of riverine forest areas interspersed with areas of more open territory (Simons 1972 Molleson pers com). Unfortunately there is a dearth of hominid fossils between the period of the ramapithecines and the almost sudden appearance in the fossil record no earlier than 4 MYA of a fully bipedal ape, with a slight advance in encephalization over extant apes (Sacher 1975b), and incipient tool use. Needless to say, much speculation has arisen concerning the nature of the evolutionary development of the hominids during the intervening period (Ardrey 1976). In contrast to the large body of literature that postulates a slow but direct migration of forest forms to the savannah, little attention has been given to the hypothesis put forward by Hardy (1960) that hominid evolution in this period was mediated by a period of semi-aquatic life and concomitant adaptation.

(This hypothesis has been championed by Elaine Morgan in her stimulating book Descent of Woman, Souvenir Press 1973). The hypothesis has certain features that make it more attractive than the 'savannah' hypothesis. Apart from all the corroborative evidence of morphology and physiology provided by Hardy for his theory, one particular aspect is especially significant. The primates in general are adapted to highly productive environments of long term stability. The strepsirhines, many adapted less favourable conditions, have lower encephalization, variable metabolic rates, and as suggested earlier as a consequence of the variable energetic factor probably a low level I efficiency (Diagram 4 p 330 - 1). Other savannah primates, members of the haplorhines, are the baboons with a higher body size they may survive on less nutritious food than smaller monkeys but as may be seen from Figure 28 (p272 - 3) they have a relatively high r_m as compared with for example gibbons and the other forest living apes. It seems improbable on ecological grounds that savannah conditions result in anything but a deterioration in the level I efficiency for primates. This would not be a characteristic feature of an evolutionary advance, (Martin pers com). In respect of Hardy's hypothesis two further phenomena deserve some consideration. Aquatic conditions appear to allow the development of high cephalization, this process in the evolution of the dolphin is well-known. A more striking example may be found in the higher encephalization of extant fishes than that of extant reptiles (Jerison 1973). Aquatic conditions may also have allowed the neotenous tendency described by Gould (1977, from Holt et al 1975) of maintenance of the normally only foetal isometric growth of the brain and body.

The aquatic theory provides the possibility of a biological impetus to advancement that must be considered less likely under the savannah hypothesis.

However, such hypotheses may be finnaly verified only by the location of fossils from the 'missing' period in littoral deposits.

By 4 MYA or thereabouts, bipedalism was well established, the hands must have been freed from their role in locomotion for some time. We do not know how long this period lasted, but the perfection of the hand was clearly well advanced since by about 3 MYA tools, although primitive, appear in the fossil record. For the purpose of the rest of this section two periods, that appear to have had marked effects upon the physiology of the organism, will be distinguished. Firstly, the long period of almost 3 million years that stretches up to the emergence of agriculture, and secondly the period that follows. The author intends to concentrate on factors in human evolution that relate to energy flow and may only be discussed by analogy with living communities. Such considerations are thus speculative.

In the first period the major expansion of the brain occurred (Passingham 1975a, b), under the impetus of a slow development of socialized labour. This activity created the requirement for speech. By the end of the dominance of the hunting and gathering way of life, human animals had undergone a transformation entirely novel in the evolution of life. Folowing Gould we may refer to Engels (1934 p.308) for a succinct definition of the unique nature of human activity that is labour,

'The most that the animal can achieve is to collect; man produces, he prepares the means for life, in the widest sense of the words, which without him nature would not have produced.' (emphasis in the original).

By the time of incipient agriculture the enhancement permitted by the activity of labour in the provision of chemical energy appears to have had the effect of lengthening lifespan, development of the brain (which may be considered to have attained modern size by about 100,000 years ago, Sacher 1975b), and the general delay in onset of sexual maturity, with low values of r_m relative to size. This appears to be the present day case for hunting and gathering communities in comparison with the apes (Table 9 p 372). (It should be stated here that the author is not intending to demonstrate any marked difference in the genetic constitution between the !Kung communities and Industrial communities. On the contrary, such differences that do exist are believed to be completely insignificant. The author merely wishes to demonstrate the effect of development in human activity upon elements of physiology that in other contexts might take millions of years to alter).

It appears that the period from the emergence of labour till incipient agriculture whilst generating unprecedented evolutionary development of the brain and longevity was still slow enough to be traced by these configurational factors. Following agriculture, to the present day the development of human activity and its increasingly rapid enhancement of the chemical energy assimilated in modern industrial communities, the opposite tendencies have developed (Short 1976, Frisch 1978) but they are essentially non-configurational. This may be seen in Table 9 (p 372). The impact of agriculture on a fundamental measure of potential population growth, r_m, may be seen in Figure 28 (p 272 - 3). The low value of !Kung (52) is from hunting and gathering communities, the upper value comes from those members of the same tribe who have recently moved to sedentary farming communities. The lower value for Industrial communities (51) is an achieved rate, r, during the nineteenth century. The middle value is the achieved rate for American Hutterite communities (with 2 year interbirth period, and breast feeding but cultural restraint on breeding till the 22nd year). The upper value is an estimate of r_m for breast feeding Hutterite communities with no restraint on early breeding. It can be seen that this latter value demonstrates an extraordinary effect of post-agricultural development. This tendency is seen also in animals fed with high concentrate diets, though human activity intervenes in this case also.

The significance of the agricultural revolution is that whereas earlier hominids were capable of applying the principles of non-biological laws to the world about them, in tool use etc., the source of chemical energy itself remained outside their control. With agriculture all that is changed, human activity enters into a new relationship with nature in the development of new forms of life. In agriculture and the domestication of animals the evolution of life may be seen once again to have created the conditions for its own continuous and novel enhancement.

Suggestions for future research.

Before concluding this report certain issues concerning the development of the subject will be very briefly elaborated.

Section a) Theory.

The work of Demetrius (1975, 1978) deserves special consideration in that the crude use of r_m in this study may, with suitable data, be elaborated to incorporate the nature of the variability of the contributions of the age classes to the stable age structure. Demetrius demonstrates most elegantly the inadequacy of r and K selection theory to account for the evolution of iteroparity. This is due to the failure of r to fully characterize the 'adaptive fitness' of the population which is more exactly in his term - the population 'entropy'. Diagram 3 (p 277 - 8) illustrates three main types of survivorship curve, which for the theoretical descritiion (1978) of a fixed and constant fecundity of age classes (not found in nature) are found to have intrinsic entropies H* of, for type I curve $H^* = 0$, II $H^* = 1$ (maximum) and III $H^* = \frac{1}{2}$. The total 'entropy' of the population may be defined as $H^* + \log_e e_o$ where e_o is the mean life expectancy. With accurate data on survivorship and age specific fecundity the 'entropy' of the population may be accurately defined. This will greatly aid the interpretation of the relationship between the 'homeostatic' nature of the population under given conditions and the 'homeostatic' nature of its individual members as expressed crudely in the Kc and Km terms of Sacher (see p 331 et sqq). Brief consideration of the expected primate population 'entropy' indicates the highest value amongst mammals. This may be adduced from the data of Western (1977) on values of e_o obtained for ungulates. The age at first delivery in primates is, at any body size, later than e_o for ungulates. However, it is possible that in absolute time some heterotherms may exceed primate population entropies. This latter observation indicates that the model will require the incorporation of a physical parameter other than time, in particular energy flow. This is an example of the necessity of incorporating an element of real, physical attribute of living matter into all purely mathematical models (see further discussion p 345 et sqq).

In general, Sacher's (1976) analysis is only able to give an abstract guide to the morphology of living (and extinct forms). This is expressed in the configuration and activation entropies of reaction and the ratio of energy flow to mass. The identification of the K_c term will be of great value in the 'reconstruction' of the activities of extinct forms. Gould's considerations (1977) approach Sacher's from the outlook of a palaeontologist. Gould in his notion of Heterochrony has bridged the gap between form (morphology) and function (reproductive activity or rate) in his identification of the significance of age at sexual maturity in the growth patterns of extant (and by extension, extinct forms). Gould's method promises to be most fruitful in the development of palaeontology since he introduces the element of energy flow (in reproductive rate). As has been demonstrated here (p 330 et sqq), reproductive activity reflects individual activity. However, care must be taken in three respects neglected by Gould. Firstly, whilst age at sexual maturity plays the dominant in the measure of r, interbirth period, number of females per litter, and mean lifespan also contribute to the value r (Cole 1954). Secondly evolutionary rates are expressed only in relation to energy flow, extension from living forms may be permissible, but as yet we have no certain evidence that respiratory rates have not undergone evolutionary change. Thirdly, as evidenced by Demetrius (1975, 1978), r does not describe fully the performance of a population in response to environmental perturbations from equilibria.

In respect of the sociobiological theory of the 'selfish gene', the author fully supports Gould et al (in press) in their attack on the 'Adaptationist programme'. Whilst, as Gould et al state, the determination of the hereditary nature of 'altruistic' behaviour in insect societies represents an important advance in biological knowledge, simple inferred extrapolation of these mechanisms to higher organisms must be viewed with deep suspicion. This proper, scientific, critical outlook is further confirmed by the tendency of many authors (Dawkins 1976, Holliday et al in press, Kirkwood, New Scientist, 29 March 1979, p 1040, amongst others) to credit genetic matter with attributes which have no basis in our scientific knowledge of this substance. With respect to Schrodinger (1945) (see p 321 et sqq), we note that genetic matter takes the form of an aperiodic crystal, undergoing slow endothermic replication in mitosis within somatic tissue, which is lost to the system. Meiotic divisions and recombinations are <u>chemical</u> reactions which proceed at a rate equivalent to the reciprocal of mean life expectancy. The exact material, energetic nature of the gene requires that it may change only in discrete, discontinuous, quantised leaps. This aspect of genetic matter is entirely <u>inconsistent</u> with the adaptable, versatile continuous nature with which it has been credited by the authors above. Furthermore, in no circumstances may genetic matter be equated with 'architect's plans' (Dawkins, 1976, p.23). Nor may the relationship between genetic matter and the somatic reactions involved in absorbtion and release of chemical energy be described as the relationship between genes and 'survival machines' (Dawkins, 1976 p.22 etc.). This description serves only to mystify and obscure those <u>physical</u> attributes of the essence of life that despite difficulties are being approximated by authors such as Sacher (all cited references). In particular, the theories of aging proposed by Kirkwood, see above, which propose that senescence is inflicted on living tissue by its genetic content; 'The distant ancestors of our genes, in obediance to the dictates of natural selection, learnt to build 'disposable' bodies by trading eternal youth for a cheaper product' and later 'If the 'disposable soma' theory is correct; and its predictions are fairly easy to test it provides an exquisite example of the 'selfishness' of our genes. The fundamental answer to the perennial question of why we grow old may simply be that to do otherwise, to stay forever young, would require us to invest resources in somatic maintenance, that, from our gene's selfish point of view, are better spent on reproduction.' If such theoreticians would care to examine the material nature of the substance they describe, and some basic thermodynamics, they might discover that 'eternal youth' is no easy task for living matter, bombarded and irradiated as it is by the continuous randomn motion about it, and within it. Secondly examination of Fenchel (1974) would reveal that the most recent forms of life, the highest forms of living matter, have a low ratio of production/respiration. In the jargon of Kirkwood 'disposability' is therefore a feature of the lowest forms of life. The author fully supports Sacher's (1976) call for the abandonment of non-meterialistic theories of aging.

Section b) Method.

In allometric study: In general the author supports Sacher et al's (1974) method of bivariate examination prior to multivariate analysis. Sacher (1976) demonstrates that multivariate analysis may only be properly performed when the variables are all physical magnitudes measured on ratio scales, and may properly have power-function relations to one another. It is proposed that the descriptive value of multivariate analyses be tested by submitting each point to the transformations derived from the group and examining the residual pattern. This practice would help identify any significant patterns of deviation from the general trend. There are dangers in the method of reduction in variance in multivariate analyses (as proposed by Gould 1966). This danger lies in two aspects. Firstly reduction of variance studies may incorporate factors which assume a similar value as a result of opposing tendencies. For example in this study, low r_m of primates arises from the advanced nature of primate efficiencies and should not be confused with the comparable values of unicells, for given size (see chapter 6). Secondly the criterion of low variance will exclude important adaptive variations that do exist in nature. In general the significance of the parameters to the activity of the biological system should be assessed first on a broad theoretical basis. Statistical and empirical tests of 'fit' and high correlation must be compared with the result expected on theoretical grounds. The comparison of categories should always be examined within the context of the processes which mediate their relationship (see p 67 et sqq). The value of statistical methods must be assessed with reference to the conditions required of the data (see p 109 et sqq). An important and under employed value of allometric analysis is that coincidences in development and correlation may be distinguished from necessary associations by the comparative method.

A consideration of general biological theory. The development of scientific knowledge extends beyond the limited categories of activity considered by the historical schools of the natural sciences. The indentification of the flow of energy matter and information as inter-connected features of the essence of life leads to an important conclusion. "Biological' processes are, properly speaking, a category within the broadest field of processes, those that encompass all known attributes of the movement of matter. Thus, in general mathematical models require at least one physical parameter in order to ensure application to the system.

Section c) Some proposed lines of enquiry.

General topics:
Examination of the interconnection of the different respiratory levels of plants and animals with respect to the unified features of terrestrial life.

Examination of the significance of body weight ranges within and between orders, their absolute and relative values.

Further consideration of the scaling of metabolic rate following Kleiber (1969).

Examination of the energy, temperature and weight parameters of the entire growth period, so as to approximate the flow of energy, matter and information more exactly for the wide population.

The energy relations of sexual dimorphism.

Examination of the allometric factors in species behaviours, for example, the relative dominance of the suckling period in larger bodied primates (p 243 et sqq).

Physiology:
Examination of the effects of captive nutrition on reproductive function.

Examination of the nature of nutrient and oxygen transfer across the placenta, including comparative study of oxygen tensions in relation to placental type.

Further information on milk constituents, particularly Essential Fatty Acids.

Examination of _Cheirogaleinae_ and _Varecia variegatus_ with respect to their high foetal growth rates.

Ecology:

Examination of wild mortality and fecundity with respect to age class, in reference to Demetrius 1975 (see p 341).

Examination of the species Varecia variegatus and the Callithricids in respect of the predicted high mortality, despite forest conditions.

Summary of Chapter 7

The chapter serves as a conclusion to the report. The results of the analyses are presented together, with a non statistical analysis. The distinction between haplorhine and strepsirhine reproductive function is associated with the rates of growth around birth. Strepsirhine growth patterns appear to be adapted to seasonal conditions. The haplorhine pattern is less discontinuous around birth and suggests adaptation to aseasonal conditions. The primates are compared with other mammals indicating their high efficiency in the use of energy.

The nature of energy transformations in living systems are examined. Chemical transformations are the principal form of energy flow in living tissue. The methods of Sacher (1976) and Fenchel(1974) are re-examined and the thermodynamic nature of the individual is seen to reflect the nature of the population. A schematic representation of the energy transformations in living systems is given. The evolution of the Primates is reconsidered in the light of this scheme. Some aspects of the evolution of human reproduction are presented.

In conclusion, in respect of the future of this type of study, issues of theory,method and particular lines of research are briefly elaborated.

Table 1 - Species key

1	Allouatta caraya
2	Alloutta seniculus
3	Alloutta villosa
4	Aotus trivirgatus
5	Arctocebus calabarensis
6	Ateles fusciceps
7	Ateles geoffroyi
8	Ateles paniscus
9	Avahi laniger
10	Cacajao rubicundus
11	Callicebus moloch
12	Callimico goeldi
13	Callithrix argentata
14	Callithrix jacchus
15	Cebuella pygmaea
16	Cebus apella
17	Cebus capucinus
18	Cercocebus albigena
19	Cercocebus galeritus
20	Cercocebus torquatus
21	Cercopithecus aethiops
22	Cercopithecus albogularis
23	Cercopithecus ascanius
24	Cercopithecus cephus
25	Cercopithecus diana
26	Cercopithecus lhoesti
27	Cercopithecus mitis
28	Cercopithecus mona
29	Cercopithecus neglectus
30	Cercopithecus nictitans
31	Cercopithecus pogonias
32	Cercopithecus pygerythrus
33	Cheirogaleus major
34	Cheirogaleus medius
35	Chiropotes chiropotes
36	Colobus badius
37	Colobus guereza
38	Colobus polykomos
39	Colobus verus
40	Cynopithecus niger
41	Daubentonia madagascarensis
42	Erythrocebus patas
43	Euoticus elegantulus
44	Galago alleni
45	Galago crassicaudatus
46	Galago demidovii
47	Galago s. moholi
48	Galago s. senegalensis
49	Gorilla gorilla
50	Hapalemur griseus
51	Homo s. (caucasian)
52	Homo s. (bushman)
53	Hylobates agilis
54	Hylobates concolor
55	Hylobates hoolock
56	Hylobates klossi
57	Hylobates lar
58	Hylobates moloch
59	Indri indri
60	Lagothrix lagotricha
61	Lemur catta
62	Lemur fulvus
63	Lemur macaco
64	Lemur mongoz

65 Leontideus rosalia
66 Lepilemur mustelinus
67 Lepilemur ruficaudatus
68 Loris tardigradus
69 Macaca arctoides
70 Macaca assamensis
71 Macaca fascicularis
72 Macaca fuscata
73 Macaca mulatta
74 Macaca nemestrina
75 Macaca radiata
76 Macaca sinica
77 Macaca sylvana
78 Mandrillus leucophaeus
79 Mandrillus sphinx
80 Microcebus coquereli
81 Microcebus murinus
82 Miopithecus talapoin
83 Nasalis larvatus
84 Nycticebus coucang
85 Pan paniscus
86 Pan troglodytes
87 Papio anubis
88 Papio cynocephalus
89 Papio hamadryas
90 Papio papio
91 Papio ursinus
92 Perodicticus potto
93 Phaner furcifer
94 Pithecia pithecia
95 Pongo pygmaeus
96 Presbytis cristatus
97 Presbytis entellus
98 Presbytis obscura
99 Presbytis melalophos
100 Propithecus verreauxi
101 Saguinus fuscicollis
102 Saguinus geoffroyi
103 Saguinus midas
104 Saguinus nigricollis
105 Saguinus oedipus
106 Saimiri oerstedi
107 Saimiri scuireus
108 Symphalangus syndactylus
109 Tarsius bancanus
110 Tarsius spectrum
111 Tarsius syrichta
112 Theropithecus gelada
113 Varecia variegatus

Table 2

Taxonomic affinity and Vernacular name, and key number for species used in study, following Jolly (1972), with exceptions discussed in Chapter I.

Strepsirhini

Infra order	:Lemuriformes		
Superfamily	:Lemuroidea		
Family	:Lemuridae		
Subfamily	:Lemurinae		
Genus	:Lemur		
Species	:catta	Ringtailed lemur	61
	:fulvus	Brown lemur	62
	:macaco	Brown or Black lemur	63
	:mongoz	Mongoz lemur	64
	:Hapalemur		
	:griseus	Gentle lemur	50
	:Lepilemur		
	:mustelinus	Sportive lemur	66
	:ruficaudatus	Sportive lemur	67
	:Varecia		
	:variegatus	Variegated or Ruffed lemur	113
Subfamily	:Cheirogaleinae		
	:Cheirogaleus		
	:major	Greater dwarf lemur	33
	:medius	Fat tailed dwarf lemur	34
	:Microcebus		
	:coquereli	Coquerel's mouse lemur	80
	:murinus	Lesser mouse lemur	81

	:Phaner		
	:furcifer	Forked lemur	93
Family	:Indriidae		
	:Indri		
	:indri	Indri	59
	:Avahi		
	:laniger	Woolly lemur	9
	:Propithecus		
	:verreauxi	White Sifaka	100
Super family	:Daubentonioidea		
Family	:Daubentoniidae		
	:Daubentonia		
	:madagascariensis	Aye-aye	41
Infra order	:Lorisiformes		
Family	:Lorisidae		
Subfamily	:Lorisinae		
	:Loris		
	:tardigradus	Slender Loris	68
	:Nycticebus		
	:coucang	Slow Loris	84
	:Arctocebus		
	:calabarensis	Golden potto	5
	: Perodicticus		
	:potto	Potto	92

Sub family	:Galaginae		
	:Galago		
	:senegalensis.s.	Lesser bushbaby	48
	:senegalensis moholi	(southern form)	47
	:crassicaudatus	Thicktailed bushbaby	45
	:alleni	Allen's bushbaby	44
	:demidovii	Demidoff's bushbaby	46
	:Euoticus		
	:elegantulus	Needleclawed bushbaby	43

Haplorhini

Infra order	:Tarsiiformes		
Family	:Tarsiidae		
	:Tarsius		
	:bancanus	Horsefield's tarsier	109
	:spectrum	Spectral tarsier	110
	:syrichta	Philippine tarsier	111
Super family	:Ceboidea		
Family	:Callitrichidae		
Sub family	:Callitrichinae		
	:Callithrix		
	:argentata	Silvery marmoset	13
	:jacchus	Common marmoset	14
	:Cebuella		
	:pygmaea	Pygmy marmoset	15

	:Saguinus		
	:fuscicollis	Brown headed tamarin	101
	:geoffroyi	Geoffroy's tamarin	102
	:midas	Redhanded tamarin	103
	:nigricollis	Black-and-red tamarin	104
	:oedipus	Cottontop tamarin	105
	:Leontideus		
	:rosalia	Golden lion tamarin	65
Sub family	:Callimiconinae		
	:Callimico		
	:goeldi	Goeldi's marmoset	12
Family	:Cebidae		
Subfamily	:Aotinae		
	:Aotus		
	:trivirgatus	Owl monkey	4
	:Callicebus		
	:moloch	Dusky titi	11
Subfamily	:Pithecinae		
	:Pithecia		
	:pithecia	Paleheaded Saki	94
	:Chiropotes		
	:chiropotes	Bearded saki	35
	:Cacajao		
	:rubicundus	Red uakari	10

Sub family	:Alouattinae		
	:Alouatta		
	:caraya	Black howler	1
	:seniculus	Red howler	2
	:villosa	Mantled howler	3
Sub family	:Cebinae		
	:Cebus		
	:apella	Black capped capuchin	16
	:capucinus	White throated capuchin	17
	:Saimiri		
	:oerstedi	Redbacked squirrel monkey	106
	:scuireus	Squirrel monkey	107
Sub family	:Atelinae		
	:Ateles		
	:fusciceps	Brownheaded spider monkey	6
	:geoffroyi	Blackheaded spider monkey	7
	:paniscus	Black spider monkey	8
	:Lagothrix		
	:lagotricha	Humbolt's woolly monkey	60
Super family	:Cercopithecoidea		
Family	:Cercopithecidae		
Sub family	:Cercopithecinae		
	:Macaca		
	:arctoides	Stumptailed macaque	69
	:assamensis	Assamese macaque	70
	:fascicularis	Crabeating macaque	71
	:fuscata	Japanese macaque	72
	:mulatta	Rhesus monkey	73
	:nemestrina	Pigtailed macaque	74

Sub family :Cercopithecinae continued

:radiata	Bonnet macaque	75
:sinica	Toque macaque	76
:sylvana	Barbary ape	77
:Cynopithecus		
:niger	Celebes black ape	40
:Cercocebus		
:albigena	Graycheeked mangabey	18
:galeritus	Agile mangabey	19
:torquatus	Whitecollared mangabey	20
:Papio		
:anubis	Olive baboon	87
:cynocephalus	Yellow baboon	88
:hamadryas	Sacred baboon	89
:papio	Guinea baboon	90
:ursinus	Chacma baboon	91
:Mandrillus		
:leucophaeus	Mandrill	78
:sphinx	Drill	79
:Theropithecus		
:gelada	Gelada baboon	112
:Cercopithecus		
:aethiops	Vervet	21
:albogularis	Sykes monkey	22
:ascanius	Redtail	23
:cephus	Moustached monkey	24
:diana	Diana monkey	25

	:Cercopithecus continued		
	:lhoesti	L'Hoest's monkey	26
	:mitis	Blue monkey	27
	:mona	Mona monkey	28
	:neglectus	De Brazza's monkey	29
	:nictitans	Spotnosed monkey	30
	:pogonias	Crowned guenon	31
	:pygerythrus		32
	:Miopithecus		
	:talapoin	Talapoin	82
	:Erythrocebus		
	:patas	Patas monkey	42
Sub family	:Colobinae		
	:Presbytis		
	:cristatus	Silvered leaf monkey	96
	:entellus	Hanuman langur	97
	:obscura	Dusky leaf monkey	98
	:melalophos	Banded leaf monkey	99
	:Nasalis		
	:larvatus	Proboscis monkey	83
	:Colobus (Piliocolobus)		
	:badius	Red Colobus	36
	:Colobus (Procolobus)		
	:verus	Olive Colobus	39
	:Colobus (Colobus)		
	:polykomos	King Colobus	38
	:guereza	Abyssinian Colobus	37

Super family	:Hominoidea		
Family	:Hylobatidae		
	:Hylobates		
	:agilis	Agile gibbon	53
	:concolor	Black gibbon	54
	:hoolock	Hoolock gibbon	55
	:klossi	Kloss's gibbon	56
	:lar	Lar gibbon	57
	:moloch	Silvery gibbon	58
	:Symphalangus		
	:syndactylus	Siamang	108
Family	:Pongidae		
	:Pongo		
	:pygmaeus	Orangutan	95
	:Pan		
	:troglodytes	Chimpanzee	86
	:paniscus	Bonobo	85
	:Gorilla		
	:gorilla	Gorilla	49
Family	:Hominidea		
	:Homo		
	:sapiens	(values for Industrial man)	51
	:sapiens	(values for !Kung bushman)	52

Table 3

subsidiary data on the allometry of gestation period.

X-Axis, natural logarithm of Adult female body weight in grams.

Y-Axis, natural logarithm of gestation period in days.

<u>All Primates</u> N = 53, $\bar{x}$ = 7.63, $\bar{y}$ = 5.05
P.A. = 0.11 (0.08, 0.14)
R.M.A. = 0.16, (Linear) Regression = 0.11
r = .69, r^2= .48

<u>Haplorhines</u> N = 34, $\bar{x}$ = 8.27, $\bar{y}$ = 5.17
P.A. = 0.08 (0.06, 0.10)
R.M.A. = 0.10, (Linear) Regression = 0.08
r=.77 r^2 = .60

<u>Strepsirhines</u> N = 19, $\bar{x}$ = 6.50, $\bar{y}$ = 4.83
P.A. = 0.09 (0.00, 0.19)
R.M.A. = 0.22, (Linear) Regression = 0.09
r= .40, r^2 = .16

Table 4a

subsidiary data to Fig 8 (p 157 - 8)

X-Axis, natural logarithm of Adult female body weight in grams.

Y-Axis, habitual litter weight in grams (following Leutenegger's technique, 1973)

<u>Haplorhines</u> N =46, $\bar{x}$ = 8.21, $\bar{y}$ = 5.76
P.A. = 0.69 (0.65, 0.73)
R.M.A. = 0.69, (Linear) Regression = 0.68
r = .98, r^2 = .96

<u>Strepsirhines</u> N = 19, $\bar{x}$ = 6.38, $\bar{y}$ = 3.76
P.A. = 0.65, (0.55, 0.75)
R.M.A. = 0.66, (Linear) Regression = 0.63
r = .95, r^2 = .90

Table 4b

subsidiary data to Fig 8 (p 157 - 8)

X-Axis, natural logarithm of Adult female body weight in grams.

Y-Axis, natural logarithm of average litter weight in grams.

Haplorhines N = 43, $\bar{x}$ = 8.35, $\bar{Y}$ = 5.84
P.A. = 0.70, (0.65, 0.74)
R.M.A. = 0.70, (Linear) Regression = 0.69
$r = .98$, $r^2 = .96$

Strepsirhines N = 18, $\bar{x}$ = 6.35, $\bar{y}$ = 3.73
P.A. = 0.64, (0.56, 0.74)
R.M.A. = 0.65, (Linear) Regression = 0.63
$r = .96$, $r^2 = .92$

Table 5

No. Mammae pairs and distribution in strepsirhine species, with litter size values of callithricid haplorhines for comparison.

Abbreviations for distribution

P = Pectoral.
M = Midway on Ventral surface.
A = Abdominal

This study, c.f. Schultz, 1948

Table 5

Genus	mammae				litter size	
Species	Position	n	Position	n	mean	range
LEMURINAE						
Lemur						
catta	P	2	P M	2	1.2	1-2
macaco	P	25			1.0	1-2
mongoz	P	7				1-2
rubriventer	P	4				
Varecia						
variegatus	P M A	6			2.0	1-3
Hapalemur						
griseus	P	2	P M	2		1-2
Lepilemur						
mustilenus	P	6				1
ruficaudatus	P	2				
CHEIROGALEINAE						
Cheirogaleus						
major	P M A	2			2	1-3
medius	P M A	2			2	
Microcebus						
murinus	P A	1	P M A	1	1.9	1-3
coquereli	P	1			2	1-2
Phaner						
furcifer	P M	1	P M A	1		

Table 5

Genus Species	mammae Position	n	Position	n	litter size mean	range
INDRIIDAE						
Indri						
indri	P	5			1	
Avahi						
laniger	P	5			1	
Propithecus						
diadema	P	5			1	
verreauxi	P	6			1	
DAUBENTONIIDAE						
Daubentonia						
madagascariensis	P	1			1	
LORISINAE						
Loris						
tardigradus	M A	5			1.6	1-2
Nycticebus						
coucang	P M	11			1	
Arctocebus						
calabarensis	P M	2	P M A	2	1	
Perodicticus						
potto	P M A	15			1.1	1-2

Table 5

Genus	mammae				litter size	
Species	Position	n	Position	n	mean	range
GALAGINAE						
Galago						
crassicaudatus	P M A	52			1.1	1-2
senegalensis	P M A	40				1-2
demidovii	P M A	5			1.2	1-2
alleni	P M A	4			1.3	1-2
Euoticus						
elegantulus	P	7			1	
TARSIIFORMES						
Tarsius						
spectrum	P M A	2			1	
bancanus	P M	1			1	
CALLITHRICIDAE						
Callithrix						
argentata						1-2
jacchus					2.1	1-3
Cebuella						
pygmaea					2.1	2-3
Saguinus						
fuscicollis					1.5	1-3
illigeri					1.6	1-3
oedipus					1.9	1-3

Table 6

SEX-RATIO AT BIRTH

Arctocebus calabarensis	est.	50: 50	(juv)	Charles-Dominique 1977
Callithrix species		138:132	birth	Hampton et al 1972
Cercopithecus aethiops		28: 26	birth	Valerio et al 1975
Galago demidovii	est.	50: 50	(juv)	Charles-Dominique 1977
Gorilla gorilla		31: 43	birth	Groves 1971
Leontopithecus rosalia		23: 8	birth	Kleiman 1977
Leontopithecus rosalia		62: 53	birth	Bridgwater 1972
Macaca mulatta	(n=294)	96:100	birth	Koford 1965
Macaca mulatta		150:161	birth	Van Wagenen 1972
Macaca nemestrina		211:187	birth	Sirianni et al 1975
Macaca fascicularis		81:83	birth	Valerio et al 1975
Perodicticus potto	est.	50: 50	(juv)	Charles-Dominique 1977
Saguinus oedipus		59: 31	birth	Wolfe et al 1975
Saguinus fuscicollis		126: 99	birth	Wolfe et al 1975
Saimiri sciureus		100:116	birth	Rosenblum 1972

Explanatory note to Tables 7, 8 and 9

These tables are based on visual examination and are not statistically tested. They represent a preliminary analysis of many of the bivariate relations given earlier.

Column I: gives a letter to each factor by which they are identified in the text.

Column II: refers the reader to the Figure from which the visual estimate is made.

Column III: indicates: the vertical axis (Y) of the bivariate plot/horizontal axis (X).

Column IV: gives a visual interpretation of the relative increase or reduction of the group considered in relation to the general pattern of another group. The comparisons are as follows:

Table 7: Strepsirhines (Strep.) as compared with Haplorhines.

Table 8: Primates as compared with other Mammalia. Where there is some distinction between Haplorhine(H) and Strepsirhine (S) tendencies these are indicated also, relative to Mammalia.

Table 9: 4 species of Ape and post - and pre-agricultural values for humans as compared with the general Haplorhine pattern.

The discrimination gives minus values for relatively low values in the vertical component, i.e. the Y Axis or first parameter in Column III, and positive values for relatively high values in the vertical component. No visual difference is indicated by 0. In cases where data are lacking no value is given. + + + or - - - indicate extreme values.

<u>Column V</u>: in Table 7 gives comparison of r^2 statistic (the proportion of variance in one variate attributable to variance in the other) for each bivariate analysis. (In certain cases the Strepsirhine (S) value is both poor, .5, and considerably lower than that obtained for Haplorhines (H). The effect of the Strepsirhine data may be seen in the comparison with r^2 for all Primates (P)).

Table 7

I	II	III	IV	V		
				r^2		
Factor			Strep.	P	H	S
a)	Fig 4	a_w/Nbl	0	.62	.76	.39
b)	Fig 7	$a_w$brain/Ne	0	.72	.85	.31
c)	Fig 8	Nb/Ab	-	.93	.96	.96
d)	Fig 9	Ftgr/Ab	-	.89	.95	.79
e)	Fig 10	Ne/Nb	0	.98	.97	.91
f)	Fig 11	Ae/Ab	-	.93	.93	.92
g)	Fig 12	Ne/Ae	-?	.98	.98	.98
h)	Fig 13	Pgr/Ft	+	-	-	-
i)	Fig 14	Pgr/Nb	+	.69	.86	.75
j)	Fig 15	Pgr/Ab	+	.78	.86	.93
k)	Fig 16	Wt.1stSol/Ab	0	.96	.99	.88
l)	Fig 17	Wt.wean/Ab	+	.96	.97	.98
m)	Fig 18	wean d/Ab	0	.83	.86	.71
n)	Fig 19	Men/Ab	-?	.72	.56	.48
o)	Fig 20	1st Del/Ab	0?	.72	.68	.14
p)	Fig 25	age Ab/Ab	-?	.88	.88	.68
q)	Fig 27	rmd^{-1}/Ab	0	.78	.82	.36
r)	Fig 29	Inter b/Ab	+?	.58	.74	.45
s)	Fig 30	life/Ab	0	.62	.59	.54

c.f. Factor a) Frazer et al 1974, Factor c) Leutenegger 1973, Factor d) Payne et al 1968, Factor f) Bauchot et al 1969, Factor s) Sacher 1959

Table 8

I	II	III	IV		
Factor			Primates	H	S
a)	Fig 4	a_w/Nb	- - -		
c)	Fig 8	Nb/Ab		0	- -
d)	Fig 9	Ftgr/Ab		- -	- - -
e)	Fig 10	Ne/Nb	+ + +		
f)	Fig 11	Ae/Ab		+ + +	+ +
g)	Fig 12	Ne/Ae		+ +	+
i)	Fig 14	Pgr/Nb		- -	0
o)	Fig 20	1st Del/Ab	+ + +		
q)	Fig 27	rmd^{-1}/Ab	- - -?		
s)	Fig 30	life/Ab	+ + +		
u)	Fig 32	nm life/Ab	- - -?		
v)	text p.	production/ respiration		- - -	- - ?
w)	text p.	litter size/Ab	- -		
x)	text p.	adult entropy production/metab. consumption		- - -	- -

c.f. Factor a) Payne et al 1968, Factor c) Leutenegger 1977, Factor d) Payne et al 1968, Factor e) Sacher et al 1974, Factor f) Jerison 1973, Factor g) Sacher et al 1974, Factor i) Case 1978, Factor o) Fenchel 1974, Factor q) Fenchel 1974, Factor s) Sacher 1959, Factor u) Author's estimate, Factor w) Frazer et al 1974, Factor x) Sacher 1976,

Table 9

I	II	III	IV					
Factor			57	95	49	86	51	52
a)	Fig 4	a_w/Nb	-	-	0	-	0	
c)	Fig 8	Nb/Ab	0	0	-	0	+	+ +
d)	Fig 9	Ftgr/Ab	-	-	- -	-	0	
e)	Fig 10	Ne/Nb	+	0	0	-	+	
f)	Fig 11	Ae/Ab	0	-	- -	0	+ + +	
g)	Fig 12	Ne/Ae	0	+	0	- - -	- -	
i)	Fig 14	Pgr/Nb	+	+ +	0	0	-	
k)	Fig 16	Wt 1st Sol/ Ab		+ +		0	+	
l)	Fig 17	Wt wean/Ab		+ +		+	0	
m)	Fig 18	Age wean/ Ab	+ +	0		+		0
n)	Fig 19	Men/Ab	0	0	-	+	+	+ +
o)	Fig 20	1st Del/Ab	+ +	0	-	0		+ + +
p)	Fig 25	age Ab/Ab		- -	- -	+	+	
q)	Fig 27	rmd^{-1}/Ab	- - -	0	+	- - -	0	- - -
r)	Fig 29	Interb/Ab	+ +	+	+	+ +		+ +
s)	Fig 30	rep life/ Ab	+	0	-	0	0	0
t)	Fig 30	life/Ab	+	0	-	0	+ + +	+ +
u)	Fig 32	nm life/ Ab	-	0	0	- -	0	- -

57 Gibbon

95 Orang

49 Gorilla

86 Chimp

51 and 52 Man

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