Life-history Strategies of Primates

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Abstract

This thesis examines variation in the life-history parameters of primates using comparative techniques. Several theories of life-history evolution are introduced in the first chapter, together with a summary of the previous work on this topic. Scaling methods are used to separate variation in life-history parameters that is correlated with body weight from that which cannot be predicted from an animal's size. These methods are described in detail in Chapter 2.

Chapter 3 describes the variation found in body size and basal metabolic rate and correlations with phylogeny, diet, habitat and other aspects of ecology. Patterns of variation in reproductive parameters, particularly reproductive rates [as measured by the intrinsic rate of natural increase, r_{max}] and reproductive effort [as measured by prenatal and postnatal infant growth rates], are described and compared with patterns reported in other studies. Possible reasons for the scaling relationships found are suggested and the influences of metabolic rate, phylogeny, diet, habitat and other aspects of ecology are investigated. This is carried out for all primates in Chapters 4-6 and in Chapter 7 there is a closer look at the cercopithecine monkeys.

It is suggested that r_{max} is influenced by the predictability of the environment, with more unpredictable environments being associated with a higher r_{max} that more predictable environments. However, this is only found when body weight effects are removed from the r_{max} data. Growth rates do not appear to be correlated with environmental predictability but are mainly correlated with body size and relative metabolic rate. There is some indication that the degree of parental care may also be correlated with relative growth rates.

It is concluded that no single theory of life-history evolution can account for the variation found in primate life-histories, but that some aspects of several theories may be useful in describing the patterns found.

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Chapter 1

Introduction

> ".....the average number of any animal or plant depends only indirectly on the number of its eggs or seeds.
>
> In looking at Nature, it is always necessary to keep the foregoing considerations in mind- never to forget that every single organic being may be said to be striving to the utmost to increase in numbers; that each lives by a struggle at some period in its life; that heavy destruction inevitably falls either on the young or old, during each generation or at recurrent intervals.
>
> Darwin [1872, ch.3]

There were three basic fields of interest that originally led me to undertake this work. Firstly, there was the general feeling, from work that I had done for my degree in biology, that the study of population biology was making an important contribution to our understanding of evolution. Secondly, my doing a short project and the reading of works by Stephen J. Gould and Bob Martin had convinced me that the use of allometric [or scaling] techniques were needed if one was to undertake convincing comparative studies. Thirdly, I wanted to expand my knowledge of the primate group and so was particularly interested in moving into anthropology.

Although there were several previous studies that had looked at the scaling of primate reproductive characteristics [e.g. Rudder, 1979; Leutenegger, 1973] and at comparative ecology [e.g Clutton-Brock and Harvey, 1977], there was little discussion of the ecological factors that could bring about variation in primate reproductive strategies. In his thesis, Rudder [1979] had included a short discussion of the possible causes of different rates of reproduction in primates. However the testing of the questions raised were beyond the scope of his work and several questions were therefore left unanswered. After discussion with Bob Martin I therefore decided to look at the primate life-histories from an ecological point of view, and particularly in relation to the well known theory of r- and K-selection. In this introduction I first give a brief overview of the general theories of life-history evolution and some of the approaches used to look at them, in particular in mammals. There then follows a brief discussion of the characteristics of the primate group and a more specific look at the way in which life-history theories relate to the group. Finally there is an outline of the aims of this study. More details of theory and of work by other investigators are given in the relevant chapters.

Chapter 1

What is a life-history strategy?

When considering the diversity found in nature it is usually diversity of form that comes to mind, and in modern biology this variation is most generally accounted for within the framework of Neo-Darwinism. At the very core of Darwinist theory is the idea that an individual's characteristics are adapted to its particular environment, and that this adaptation has been bought about by the processes of natural selection. Despite the acceptance of the existence of other, non-adaptive, processes that have operated to alter the genotypes and phenotypes of organisms, most biologists today are still of the opinion that adaptation by natural selection has played the major role in the evolution of life. The comparative study of the anatomy and physiology of species and the use of adaptive explanations for differences between these aspects of species has been long established.

However, variation is found not only in form but also in the courses of species' lives or their "life-histories". Although differences in life-histories are greater between the phyla, there are also differences within the groups. Within the Mammalia, some species of rodent are capable of producing many young several times a year [e.g. the black rat produces about 8 offspring 2-7 times a year (Eisenberg, 1981)] whereas others have only one baby at a time which may take several years to raise [e.g. elephants and apes]. If variation in life-histories is to be explained by the processes of natural selection, one must assume that animals have evolved their different life-histories as adaptations to their environments.

That there is no one life-history that maximizes fitness is clear from the apparently limitless variation seen in the life-histories of plants and animals. A species' life-history can be described by certain parameters that provide information on the course of its growth and development. For mammals, examples of such parameters include gestation length, growth rate, weight at birth, length of time that young are dependent on parental care, age at sexual maturity, number of young born in a litter, birth rate, longevity, and so on. It has frequently been noted that such life-history characters tend to vary together with small organisms tending to have rapid developmental times and high birth rates and large organisms developing and breeding more slowly. The fact that some traits appear to be linked has led to the idea of life-history strategies. The idea of a strategy is that of a set of coadapted characteristics. These characteristics are bought about by natural selection in response to particular ecological problems.

The linking of small body size, rapid development and fast breeding [and the opposite set of parameters] has given rise to the idea that these life-history characters are selected together to adapt organisms to different types of environment. The problem is then to determine which environment will select for a "small and fast" species and which for a "large and slow" species.

Addressing this question has given rise to two commonly invoked adaptive theories of life-history evolution [known as r- and K-selection and bet-hedging, respectively] which are discussed in some detail below. Additionally other, adaptive and non-adaptive, reasons for the covariance in life-history traits have been suggested, and these ideas are also discussed.

Theories of life-history evolution

Darwin's theory of natural selection predicts that any heritable character that increases an organism's contribution to forthcoming generations will be selected. This has often been taken to mean that selection will operate to increase fecundity to the maximum that is possible, given the constraints of genetic variability and the environment [e.g. Cole, 1954]. However, as noted by Darwin [1872, see quote at the beginning of this chapter] it is not always the case that the production of larger numbers of young leads to increased representation in future generations. Modern sociobiological theory tends to explain this phenomenon in terms of "trade-offs" between "investments" in young and investments in survival ability [e.g. Trivers, 1972; Wilson, 1975; Dawkins, 1979]. To briefly summarise the ideas of 'trade-offs": an organism has access to a limited range of resources, and selection may therefore favour a particular pattern of investment of these resources. The organism may invest resources in offspring. Alternatively, it may put resources into itself so as to enable it survive for a longer period of time, and produce offspring at a later date. In addition it can may produce many small offspring or a few large offspring. Which of these strategies is selected will depend on the environment in which the organism is found. Adaptive theories attempt to explain life-history evolution using these ideas.

The following is a summary of the theories that are most generally invoked to explain variation in life-history characters. The first two theories have two features in common. Firstly, they are "adaptive" in their explanation, in that they assume that life-histories are primarily determined by natural selection and therefore adapt a population to a certain environment. Secondly, they both attempt to relate the evolution of life-histories to the degree of environmental variability. There then follows a discussion of other possible explanations for variation in life-histories, some of which place emphasis on factors other than adaptation.

Two points about the presentation of the various theories need to be made here. Firstly, I have deliberately chosen to take the theory of r- and K-selection [r/K theory] as my starting point, talking of alternative ideas with reference to their similarities and differences to r/K theory, and this course is followed throughout this thesis. This is not because I felt that r/K theory was the correct viewpoint, against which all other ideas should be judged, but more because it is a widely quoted and generally well known concept. This has meant that a large number of researchers have accounted for their results in terms of this theory and it has been widely developed and elaborated on, in a way that has not yet occurred with the alternative explanations of variation in life-history evolution. Many of the alternative ideas have, in fact, been developed using r/K theory as a starting point and my work reflects this. In addition, I felt that to use r/K theory as the framework for this work would give it a coherence and line of argument that could not otherwise be developed. Secondly, the theories are presented separately, not because I believe that they are necessarily mutually exclusive, but for the sake of clarity.

The theory of r- and K-selection

For the last twenty or so years a central idea in the theories of how life-history strategies evolve has been that of r- and K-selection theory [r/K theory]. This idea was first explicitly proposed by MacArthur and Wilson [1967] in their influential book "Island Biogeography". Building on the work of Dobzhansky [1950], who suggested that selective forces forces differed in quality between temperate and tropical zones, and on the more mathematical work on population ecology [see Appendix I] MacArthur and Wilson developed a theory that endeavoured to explain the processes of island colonization.

Their analysis of the selection pressures on an island population starts by discussing the characters that will be selected if a small number of animals colonize an island. Given that the island contains the necessary resources for the species in question, and that no other species is utilising the same ecological niche, those individuals that produce the most descendants, in the shortest period of time, will be the most successful [i.e. such individuals will have a greater number of copies of their genome in the forthcoming generations]. It is clear that, assuming that the characters that produce such rapid breeding are inherited, a colonising species in a uncrowded habitat where resources are not limiting will be selected to produce many young rapidly. The mother that produces her offspring in the shortest period of time will have a selective advantage, as her offspring will be the first to colonize the new area. Colonizing species will therefore be expected to put a relatively large proportion of their available resources into reproduction so as to produce many young in a short space of time, i.e. they will have a high reproductive effort. [Reproductive effort, [RE] is accordingly defined as the proportion of total available resources put into reproduction.] The parameters that will be primarily selected for can be found by analysis of the factors which alter the rate of increase of a population and increase reproductive effort.

The breeding rate can be measured by the natural rate of increase of a population. This variable can be estimated when there is a predictable schedule of births and deaths in a population. The variables that are needed for its calculation are the multiplication rate per generation [R_0] and the mean generation time. R_0 is calculated quite simply by the following equation:

$$R_0 = \frac{\text{no. of daughters born in generation } t+1}{\text{no. of daughters born in generation } t}$$

An estimate for the intrinsic rate of natural increase [r] can then be made using R_0 and the generation time [G].

$$r = \log_e(R_0) / G$$

[See Appendix I for a further discussion of this derivation of r, and for a more accurate method of calculation].

Both from these equations, and intuitively, it can be seen that r will be increased by either:

1) Increasing the number of young produced in a given period of time, i.e. increasing the birth rate.

2) Increasing the number of breeding seasons, i.e. increasing age at last reproduction or decreasing age at first reproduction.

3) Decreasing generation time, i.e. decreasing age at first reproduction.

Cole [1954] discussed the ways in which the alteration of the different variables affected the value of r. Using an equation that in fact calculates r_{max}, or the maximum intrinsic rate of increase [see Chapter 2 and Appendix I], he found that the variable that has most influence on r_{max} is the age at first reproduction, with the birth rate also having a strong influence on r_{max}, but with age at last reproduction having a virtually negligible influence.

As colonising species are selected for the capacity for rapid breeding, they will be expected to have a high rate of increase or are said to be "r-selected". This high value of r can be produced by having an early age at first reproduction, a high birth rate and a long breeding life [w]. However, selection for a long breeding life will be very weak, due to the very small influence that age at last breeding has on r_{max}, and will be counteracted by the positive relationship found between age at first reproduction and life expectancy. This positive relationship is due to the fact that by reproducing early a female is putting her resources into breeding, and not into enhancing her own ability to survive. She will therefore be more likely to suffer from predation, disease, etc. Similarly, a negative correlation is expected to be found between birth rate and life expectancy, as a high birth rate will also make demands on a female's resources. If selection is strong for an early age at first reproduction and a high birth rate, the decrease in life expectancy that this implies will mean that selection will not be able to operate to increase breeding life. As an individual that possesses the genetic capacity to live for longer than the average will rarely be able to live long enough to gain any advantage, genes for long life will not become fixed in the population. Hence, r-selected species will be predicted to have short lifespans.

Although the work of MacArthur and Wilson was initially dealing with the ecology of islands, it can be extended to other, more general, situations in which a population is found in a situation where it is expanding into a habitat [and where resources are not limiting]. This is found with weed species that are in basically the same situation as island colonisers, as they are also colonising new unexploited areas, and the same characteristics will therefore be selected for. The second "type" of population that will be expected to be r-selected are those that suffer periodic, but unpredictable, "crashes" in numbers [e.g. due to an unpredictable climate which causes high mortality at irregular intervals]. For a survivor of such a catastrophe, a high rate of increase will mean that its descendants will rapidly fill the "space" left by the demise of the majority of its competitors. Slower breeding survivors will be at a disadvantage, as by the time they are produced the offspring of rapidly breeding organisms will already be occupying the available niche space. The uncertainty of surviving to the next season to breed also means that it is advantageous for the individual to put as much as possible into one breeding attempt as resources held "in reserve" for the next may be wasted if [say] a fluctuation in resource levels kills it, i.e a high reproductive effort will also be selected for in such species.

No habitat is infinite and for any given species there will be a limit to the number of individuals that it can support; this limit is known as the carrying capacity [K]. In the absence of new areas to colonise, or periodic population depletions, a colonising species will eventually expand to "fill" the available niche space. Unlike the situation when a population is not at the carrying capacity of its habitat, the resources in a "full" habitat are limiting the growth of the population. Thus, there is a high incidence of density dependent mortality, i.e. mortality due to competition for limiting resources rather than stochastic events. Individuals are therefore affected more by the others around them, and the ability to compete for resources becomes a vital factor in the determination of the survival and reproductive success of the organism. Such species will therefore be selected for different attributes than those needed for a colonising species. In particular, MacArthur and Wilson reasoned, selection will favour individuals that use the available resources most efficiently, so increasing their ability to out-compete less efficient individuals. This selection for increased efficiency will mean that the number of individuals that can be supported by the habitat will be maximized i.e. a high K will be selected.

To achieve this efficiency in the use of resources organisms must devote a larger proportion of their resources towards increasing their competitive ability. This could be done in many ways, but some of the more obvious ways for animals are increasing body size, searching more systematically for food, and defending territories to exclude others from food sources. This diversion of resources towards competition will mean that less resources will be available for reproduction and such "K-selected" species will therefore be expected to put a smaller proportion of their total available resources towards reproduction [i.e. they will have a low reproductive effort].

In addition to this, K-selected species will also be selected to produce young that have a high competitive ability. To do this the parent must produce "well-equipped" young that are capable of out-competing their conspecifics, usually referred to as "high quality" young. As resources are limiting, the production of such young means that the parents must reduce the number of young that are produced so that they can invest more resources in each individual offspring. That is, there is a trade-off between the production of many young and the production of high-quality young.

In summary, a K-selected species will be expected to have a higher competitive ability and hence a lower reproductive effort than will an r-selected species. In addition, K-selected species will be expected to produce a smaller number of young per litter so that their parental investment per offspring can be maximized, so giving the offspring increased competitive ability. A K-selected species will therefore be characterised by having a later age at first reproduction, longer development time, lower birth rate and fewer, larger young than a more r-selected species.

It can therefore be seen that r- and K-selection can be viewed as being at two ends of a spectrum of selective forces shaping life-histories. At one end there are species that are found only in colonising situations where resources are abundant and mortality is independent of population density, whereas at the other end species are at the carrying capacity of their environment and any increase in fitness is determined by an increase in competitive ability. It is obvious that many species are found in indeterminate situations where there is both density dependent and density independent mortality, where opposing selective forces will be acting to increase both competitive ability and the natural rate of increase. Here one would expect some indeterminate solution.

Bet-hedging theory

Schaffer [1974a] produced a theoretical model which considered the effect that age-specific mortality patterns would have on life-history evolution. This model differs from that of MacArthur and Wilson in that it does not assume that a fluctuating environment affects all age classes equally. Instead, Schaffer uses a simple model which assumes that a fluctuating environment will have an effect on either juvenile mortality or adult mortality and he then predicts the optimum adaptive response to these conditions. This mathematical treatment of the relation between environmental fluctuation and mortality patterns predicts that, contrary to MacArthur and Wilson's theory, a fluctuating environment will not always select for a high r_{max} and a high R.E.. The contrasting assumptions and predictions of Schaffer's theory and r/K theory can be seen in table 1.1.

As can be seen, Schaffer's model predicts the same constellation of traits as does the r/K

Table 1.1

The assumptions and predictions of adaptive theories of life-history evolution

Model	Assumptions	Predictions
r-selection	i) exponential population growth ii) stable age distribution iii) fluctuations in population density	1. early maturity 2. many small young 3. large R.E. 4. short life
K-selection	i) stable environment ii) population near K iii) logistic population growth iii) competition important	1. late maturity 2. few large young 3. small R.E. 4. long life
Bet-hedging	i) environmental fluctuation ii) population near equilibrium iii) iteroparity iv) "trade-off" between R.E. and probability of survival	
	a) juvenile mortality fluctuates, while adult mortality does not	1. late maturity 2. few young 3. small R.E.
	b) adult mortality fluctuates, while juvenile mortality does not.	1. early maturity 2. many young 3. large R.E.

model, but for different reasons. Unlike r/K theory it suggests that, if juvenile mortality is mostly effected by environmental fluctuations then selection will prefer a large, "slow" organism to a smaller "faster" one. This result has been restated by Stearns [1976] in intuitive, rather than mathematical, terms under the title "bet-hedging".

Schaffer's model assumes that there is an inverse relationship between the resources put into reproduction in one season and the probability of surviving to the next season for a further breeding attempt. The adult must therefore "choose" whether to put a large proportion of its resources into one season's litter or whether to "hold back" some of these resources so as to have a better chance of surviving to the next season. Schaffer [1974a] showed that the "choice" made depends on the age class most affected by the fluctuating environment.

If adult mortality is affected, then Schaffer's results agree with those of r- and K-selection, i.e that fluctuating environments will select for organisms with a high reproductive effort and rapid breeding. This is because an adult with a low probability of surviving to the next breeding season will be selected to put a large amount of energy into reproducing as soon as possible. Adults that save their resources run the risk of not surviving to the next season, and hence losing them completely.

However, if it is juvenile mortality that is threatened by the unpredictability of the environment a different set of traits will be favoured. In this case the adult's chance of surviving to the next season is not affected by the fluctuations of environment, but its offspring's may well be. The adult therefore runs the risk of losing some or all of its offspring from one "bad" season. However, if breeding attempts are spread over several seasons there is a higher chance that some of the offspring will be born in "good" years, and hence that more will survive. Given that the adult has a better chance of surviving to the next season if it holds back some resources from reproduction, selection will therefore operate to decrease the proportion of resources put into reproduction [or the reproductive effort] in such species. In this case, therefore, a fluctuating environment can select for a low reproductive effort, and slower rates of reproduction. Stearns [1976] has called this the "bet-hedging" model, as it predicts that, in fluctuating environments, the adults will "hedge their bets" by putting some resources into reproduction in one season, whilst holding some back in reserve for the next season.

One problem with bet-hedging theory is that it is based on a very simple mathematical model, the initial assumptions of which may not be valid. A criticism of the bet-hedging model has been made by Hastings and Caswell [1979], who suggest that the results of Schaffer's model will be different if the some of the initial assumptions of the model are changed. The choice of models is dependent on knowledge of the way in which environmental variability affects fitness, something that must be determined from empirical work. Despite this problem, Hastings and Caswell's work agrees with that of Schaffer [1974a] in that it produces models that predict that unpredictable environments may select for low reproductive effort. It is therefore possible to look for a link between an unpredictable environment and a low RE and to then investigate the causes [i.e. whether it is due to variation in juvenile or adult survivorship] if and when it is found. As bet-hedging has received more attention than has Hastings and Caswell's predictions, and has also been explained in non-mathematical terms, it is considered more fully in this work.

Variation due to age specific fecundity

Another explanation for life-history variation does not [necessarily] invoke environmental variability as a cause, but instead looks at the effects that differing fecundity levels at different ages can have on selection for reproductive parameters. The nature of this relationship has been considered, in more detail than I have included here, by several people, including Emlen [1971], Bell [1980] and Schaffer [1974b].

In many natural situations, individuals of a certain age are capable of producing more young than are individuals of another age. In most animals fecundity initially rises with age and then falls off as the animal approaches the end of its life. The initial rise is due to a variety of factors that may include the increase of body size with maturity or the attainment of a high rank in a social group that gives increased access to resources. If one assumes that there is a trade-off between survivorship and fecundity, it is not difficult to imagine that, in certain circumstances, it will be advantageous to delay the age at first reproduction until an age where fecundity is high. This can be illustrated by a very simple example.

Imagine a population where individuals have the capacity to produce a single offspring at one year old and two offspring a year from the age of 2 to 4 years old, after which they die. Assume that bearing offspring at a year old increases the probability of dying before the age of 2 years from 0% to 30% and thereafter mortality is nil until death at 4 years. On average, an adult that begins to breed at 1 year will produce $1+[0.7 \times 6] = 5.2$ offspring/lifetime. An adult that waits until it is two years old to breed will produce 6 offspring in its lifetime. Although this example does not measure the rate of increase of a population, it is not difficult to see that a similar argument could be applied to this character to show that selection could also act to increase r by delaying reproduction.

Are these theories of life-history evolution reconcilable?

The last theory discussed, that of age-specific fecundity could operate with either r/K theory or bet-hedging theory. Variation in age-specific fecundity may be caused by variation in environmental predictability or may be caused by variation in some other parameter. For example, an animal may be less successful in breeding at young age because a predictable environment allows the population to reach the carrying capacity of its habitat. In this situation younger animals might be excluded from resources by older more dominant animals and would therefore have less success in breeding. K-selection and selection to breed at the "optimum time" would therefore both operate to delay reproduction. Alternatively, a very seasonal environment could also select against young animals breeding. For example, a small mother might have problems in keeping infants warm during cold winters and might be selected to delay reproduction. Hence, selection due to variation in age-specific fecundity may operate alongside other selective mechanisms.

Both r/K theory and bet-hedging theory explain variation in life-history strategies as being due to the effect of differing amounts of environmental variability. The former predicts that the faster breeding population will be found in a more unpredictable environment where there is a larger degree of density independent mortality. On the other hand, bet-hedging theory offers two alternative explanations for the observation. The first explanation is similar to that offered by r/K theory, i.e. the faster breeding population is found in a more fluctuating environment than the slower breeding population and is being selected to breed rapidly because of periodic fluctuations in adult numbers. However, the second explanation predicts that the slower breeding population may also be found in an unpredictable environment where juvenile mortality is the main result of fluctuation.

Although the two theories predict different things, it should also be realised that they are based on different assumptions and are thus not necessarily contradictory. The decision to use one or other of the models to explain any observations must therefore rest both on the accuracy of its primary assumptions and on that of its predictions. Ideally, one would require information both on environmental predictability and on differential age-specific mortality before it could be decided whether one or either of the two models could be used. For example, if one were comparing the reproductive output of two species of annual plant one would not consider applying the bet-hedging model to explain any observed differences between them as this model explicitly applies only to populations that may breed more than once. Alternatively, if one were looking at two populations in the same environment with the same amount of fluctuation in population density, but with different life-histories, it would seem advisable to look for differences in age-specific mortality.

The non-adaptive theory of life-history evolution.

The above ideas seek to explain the observed patterns of life-histories as being due to adaptation to different levels of environmental predictability and/or age-specific variation in fecundity. An alternative viewpoint is that certain traits are linked together because a cause other than adaptation causes them to covary. I am therefore discussing these ideas together under the heading of "the non-adaptive theory".

Gould and Lewontin [1979] criticised evolutionary biologists for relying too heavily on "adaptionist" explanations for the variation seen in nature and suggest non-adaptive alternatives. They note the common tendency among modern biologists to explain all variation by adaptation, they term this tendency "the adaptationist programme". The salient point of their paper is that there can be non-adaptive causes for variation. Such causes include the effects of genetic drift, the occurrence of several adaptive solutions to the same evolutionary problem, phenotypic plasticity and variation in one feature arising as an epiphenomenon when another feature is selected.

Gould and Lewontin particularly discuss these problems in terms of the constraints on the organism that are imposed by its phylogenetic history and its developmental pathways. Any one feature of an organism is limited in its ability to adapt to the environment because the overall "design" of the organism in question will only be able to accommodate a limited change. Such design constraints may exist for a variety of reasons. These include: mechanical limitations [e.g. an elephant could not support its weight on the legs of a racehorse even if it would be adaptive for it to run faster]; energetic limitations [e.g. selection for increased energy input into young may not be possible if nutrients are limiting]; lack of genetic variability; or developmental constraints early in the individual's history preventing changes from occurring that might have deleterious effects later in life.

Even the apparent utility of some structures may not necessarily mean that they were originally brought about by adaptive means, for, as they say;

> "One must not confuse the fact that a structure is used in some way ...... with the primary evolutionary reason for its existence and conformation."
>
> [*ibid* p.587]

When looking at life histories, several people have noted that both body size and taxonomy are frequently correlated with variation in various parameters. As such correlations may well be indicative of design constraints, they are discussed in some detail below.

Evidence for design constraints: The importance of body size and taxonomy in mammals

In this section, the scaling of life-history parameters to body weight is discussed. The form of these relationships is also considered, but for a more complete discussion of the nature and derivation of these relationships the reader should turn to Chapter 2.

It has long been recognised that an animal's size is correlated with other features. These include physiological, reproductive and ecological traits. The form of this relationship is often an allometric one i.e. the ratio of the parameter: body weight does not remain constant but alters predictably with size. This type of relationship is encountered very frequently encountered in biology. It is more commonly found than an isometric relationship in which parameters increase in direct proportion to each other [isometry]. The form of the allometric equation, can be written as follows:

$$Y = bM^a$$

Where Y = a hypothetical parameter, M = body weight and a and b are constants specific to the parameter concerned, [a being known as the allometric exponent and b the allometric coefficient].

A large range of examples of allometric scaling can be found in Peters [1983] and Calder [1984]. One of the most well known of these is that of the relationship between basal metabolic rate and body size. Kleiber [1961] showed that basal metabolic rate and body weight are related by the equation:

$$BMR = kM^{0.75}$$

Where BMR = basal metabolic rate , M = body weight and k is a constant.

In this case, the value of a is positive [0.75] indicating that as body weight increases the value of P also increases. As basal metabolic rate is determined by the food supply one would expect that environmental variables that determine the food supply will also scale to $M^{0.75}$. This means that the allometric scaling of basal metabolic rate to body size could have important influences on the many features of an animal's ecology that relate to its energetic requirements. As Calder [1984, p. 290], notes, [referring to body weight as (W)] this means that:

> "......we are biased towards finding [$W^{0.75}$] patterns and quite legitimately look for them. It is exciting to find another [$W^{0.75}$], and tempting to imagine one.

The question of basal metabolic rate and its scaling to body weight is discussed further in Chapter 3. Life-history traits have also been found to correlate with body size in a wide range of organisms. For example, Fenchel [1974] described the relationship between the maximum intrinsic rate of natural increase [r_{max}] and body weight for a wide range of organisms. He showed that there is a negative correlation between r_{max} and body weight [M] and that the relationship between the two could be described by the equation: $r_{max} = bM^a$, [where a and b are constants, b depends on whether one is looking at unicellular organisms, heterothermic metazoa or homiothermic metazoa, and a about the same value for all groups].

Another study that demonstrated correlations between body weight and life-history parameters in mammals was carried out by Western [1979], who found that age at first reproduction, life expectancy at birth, life span, and gestation length were positively correlated, and birth rate negatively correlated, with body weight. As with the relationship between r_{max} and body weight, there is not a constant ratio between the parameter and body weight; the ratio alters with body size.

The above examples are only two of the many available studies which serve to illustrate that the life-history parameters of an organism can be partially predicted from its body weight. More specific examples of the way in which various life-history parameters vary with body weight can be found in Chapter 4.

The reasons for these apparently widespread correlations between life-history parameters and body size are not clear and, indeed, they probably vary with the parameter in question. The explanations fall into two categories, those that link body size with life-history parameters because of reasons of "design", and those that suggest that the link is adaptive. It is possible that the frequently observed covariance in life-history characters is not due to their being adaptive but, instead, is a result of selection for body size "carrying along" the other characters with it. In the terms of Gould and Lewontin, life-history parameters could be thought to be constrained within certain limits by the size of the organism. A large number of correlations have been explained by links of a physical [e.g. chemical, thermodynamic or mechanical] nature. For example, it has been suggested that the growth rate of an organism is determined by the maximum possible rate of growth of the slowest growing tissue, which is the the brain [Sacher and Staffeldt, 1974]. These type of explanations can be taken as examples of what Gould and Lewontin call design constraints. hence, in the example above, the growth of an animal would not be directly selected to take place at a certain rate, but would be constrained within limits imposed by the size of the animal's brain. A further discussion of such causes of correlations with body weight can be found in chapters 3 to 7.

An alternative to the "design constraint" explanation has been suggested by Pianka [1970]. Pianka demonstrated that both generation time and r_{max} vary predictably with body weight over a wide taxonomic range of animals. He suggests that this observation can be explained within the framework of r- and K-selection theory. He points out that large organisms will suffer less "environmental resistance" [e.g. from predation pressure], and are "better buffered from changes in their physical environment" than smaller species. He therefore argues that as such large species:

> "...are better buffered from environmental vicissitudes, their population sizes do not vary as much as those of smaller, shorter-lived organisms. Futhermore, presumably their competitive relationships are also more predictable and constant."
>
> [*ibid* p.596]

In other words, the body size of an organism may influence the way in which it is affected by its environment. A large bodied animal will not be as threatened by environmental fluctuations as will a smaller animal in the same situation. In this way, body size can influence life-history characters. This idea is an important one, both for its specific content and because it illustrates an often ignored general principle, i.e. the environment cannot be considered as separate from the organism, as the perception of the environment is partially determined by the organism itself. Stearns [1976] also makes this point when he says,

> "The standard organism-environment dichotomy........ dangerously oversimplifies the situation. To the population, <u>the definition of the 'environment' depends on the biological characteristics that the population has already evolved.</u> " p. 37. [my stress].

The ideas that selection for a certain r_{max} occurs <u>because</u> of the organism's body size assumes that selection acts primarily on body weight. Life-history parameters are therefore assumed to be, at least partially, determined by the animal's body weight. However, it should be remembered that correlation does not show causation and it could equally well be that selection for a life-history trait could determine an animal's body weight. In the case of "design constraint" explanations, selection could act equally well on a life-history variable or on body weight. If the two are closely linked, then selection for a change in one will bring about the corresponding change in the other. If selection acts primarily on the life-history parameters then the possible causes of variation will include those already discussed. However, if the primary selection is on an animal's body weight then one needs to ask: What determines selection for body size?

There are many factors that have been suggested to select for body size. These include factors such as predation pressure, where a prey species is either selected to be larger or [less commonly] smaller so as to escape the attentions of a predator that is only capable of dealing with prey items of a certain size. Conversely, selection may act to change the size of a predator species so that it can deal with a different size prey [or, in the case of a herbivore, different sized plant items]. A third possibility, that may be linked to one of the first two, is that size changes are selected so as to avoid competition with similarly sized species occupying an equivalent ecological niche [the competitive exclusion principle, or Gause's hypothesis]. Other possible selective forces include temperature, with a cold climate being hypothesised to select for high body weight [Bergmann's law], and a scarcity of food, being suggested to either select for small body size so as to decrease the resources required or a large body size so as to enable the organism to survive for longer on increased reserves [Zevellof and Boyce, 1986].

Although such forces may be important in determining an animal's size, this does not mean that selection of life-history parameters cannot be operating at the same time. If the environment is selecting for rapid or slow breeding it may do so either via selection for body weight [if the traits are strongly linked to body weight], or by directly acting on the life-history parameters. If the latter is occurring, and the links between body weight and the life-history parameters are very strong [or if they are weak but the effect of changing body weight is effectively neutral in terms of fitness], then selection for life-history parameters will give the concomitant change in body weight. This suggests a way in which the link between body size and life-history parameters can be accepted within the framework of adaptive life-history evolution. However, it is not effectively very different from the other types of selection for body weight discussed, as these too may be operating through another variable [e.g. in the case of selection by cold temperatures, it has been hypothesised that the primary selection is not for a large body size *per se* but for a low surface area to volume ratio].

A more complex situation will arise if there is selection for a certain set of life-history parameters at the same time as an opposing selection for body size. For example, if low temperatures do select for a large body weight and unpredictable environments select for rapid breeding, one would predict that in temperate regions selection would be simultaneously operating to increase body size and increase breeding rate. Such a combination of selective pressures would give a large, fast breeding animal, i.e. a combination of traits that is the reverse of that usually observed. It has been suggested [Western, 1979; Western and Ssemakula, 1982] that in the case of selection acting in this way the result will be to "decouple" the links between life-history parameters and body size or to give "scaling readjustments". This idea leads to the need for an evaluation of the extent to which life-history parameters are dependent on body size. It may then be possible to understand the situations in which these relationships can be altered.

Western and Ssemakula argue that the high correlations seen between life-history parameters and body size, and the fact that the scaling principles are very similar in birds and mammals, suggests that:

> ".......the life history patterns of birds and mammals are much the same in their developmental traits and suggest that they conform to a single homeotherm, allometric model."
> [Western and Ssemakula, 1982: pp. 283-4].

This, together with other evidence that within mammalian taxa the scaling principles of life-history parameters are also comparable leads them to conclude that:

> "The results of our analysis .... suggest to us that most of the diversity in homeotherm life patterns can be explained by a common design scaled up or down in size." [*ibid* p.285]

The above comments, and the examples of scaling relationships given, indicate that body size probably has a significant influence on life-history parameters, but quantifying this amount is difficult. Although Western and Ssemakula [1982] showed that the amount of variation that could be predicted from body size varied from 24% to 95% for a number of mammalian life-history traits it is impossible to tell from this how much of the variation is actually caused by body weight variation.

There is still variation in life-history parameters that is not accounted for by body weight. Another possible correlate is phylogeny. Generally, correlations are higher within smaller taxonomic groups, e.g. in Western and Ssemakula [1982] body weight is shown to account for only 24% of the variation in age at first reproduction in 39 mammal species from several taxa, but it accounts for between 74 and 90% of the variation within the mammalian orders [Western, 1979]. This type of result implies that phylogeny is also important in determining an organisms life-history. This is another example of the effect that a design constraint can have on evolution. As a result of their common ancestry, species within a phylogenetic group will tend to resemble each other more closely than they do members of other groups, and this resemblance applies to the scaling of life-history parameters as well as to more obvious similarities such as in anatomy and behaviour. One aspect of this resemblance of related species is that, when looking at the scaling of parameters with body weight, one group of related species may show a different "grade" of organization from another group, this is discussed in more detail below.

A study that looked specifically at the variation in life-history parameters and its relationship to body weight and phylogeny was carried out by Stearns [1983]. Stearns investigates the patterns of covariation between life-histories, body weight and taxonomy in mammals. A somewhat lengthy discussion of this study is included here because it illustrates possible ways of investigating life-history variation, and because the results have important implications.

Stearns [1983] begins by asking four questions, which are:

1) Is the perception of a life-history tactic a function of the taxonomic unit used?

2) Are there identifiable phylogenetic constraints on the evolution of life-histories?

3) If the constraints exist do they vary from lineage to lineage?

4) Does the removal of body weight effects change the patterns of covariation significantly?

To answer these questions, he carries out a series of bivariate and multivariate analyses that investigate the patterns of covariation between the life-history parameters and the influences that phylogeny [as measured by taxonomy] and body weight have on these patterns. The bivariate [regression] analysis shows that all of the traits are highly correlated with body weight, with body weight accounting for 29 to 76% of the variation in the other parameters. The results of the bivariate analysis are then used to "remove" body weight effects from the data [these methods are described in more detail below and in Chapter 2].

A principal component analysis on the raw data for 62 mammal species shows that there are two main patterns of covariation, the first principal component [accounting for about 70% of the variance in all traits] arranges the species from small, fast-breeding to large, slow-breeding species. The second principal component [accounting for about 12% of the variance in all traits] arranges them from altricial to precocial species. Although the figures are altered slightly when the sample size is increased for some of the parameters, and when the analyses are carried out on average values for families or orders, they are basically the same indicating that this result is robust.

When weight effects are removed from the data, the amount of variance that is explained by the first principal component [the "small, fast to large, slow" axis] is reduced, whereas that explained by the second [the altricial to precocial axis is increased]. Removal of the effects of order and the effects of family from the data give a reduction in the amount of variance explained by both of the first two principle components.

In addition, Stearns uses a nested analysis of variance [ANOVA] to "see which [taxonomic] levels accounted for most of the variation in each trait." [*ibid* p.175]. The ANOVA is done on both the raw data and the data after removing the effects of body weight. The amount of variance accounted for at the different taxonomic levels varies from parameter to parameter, but on average 70% is accounted for by order and 18% by family effects. This pattern is significantly altered by the removal of the effects of body weight, which reduces order effects to 48% and slightly increases family effects to 23%.

The use of complex multivariate analyses, and the fact that the results vary slightly between the two data sets used and from trait to trait, make the interpretation of small details of this work rather difficult. However, several fundamental facts are revealed. Firstly, there are two basic patterns that organise the life-histories of mammals the first that arranging the species from "small and fast" to "slow and large" reproductive types, and the second from altricial to precocial.

Secondly, both weight and taxonomy are important factors in this organisation and these effects are operating independently, so that:

> '..... both size and phylogeny have significant independent effects on patterns of covariation in life-history traits, and ..... both effects contribute to the ordering of mammal species onto a "slow-fast"" continuum.' [*ibid* p.186]

Another result that shows the influence of taxonomy is the finding that different taxonomic groups show different patterns of covariation between the parameters. Stearns therefore shows that the overall pattern of life-histories is strongly influenced by taxonomy, he concludes that:

> "Higher-level taxa represent major differences in morphological design. One plausible interpretation of these results is that once a major lineage splits off from its sister groups, the subsequent scope of life-history evolution is constrained within that lineage, and the nature of the constraints differs from lineage to lineage. This interpretation is in close agreement with the idea that organisms are mosaics of relatively recent adaptations contained within a framework defined by relatively old constraints." [*ibid* p.186].

Stearns [1983] does not examine the relationship of environment to life-histories, but he considers that the strong patterns of covariation seen, which remain even when taxonomic effects are removed, are indicative of adaptation, with body size possibly being the primary trait selected.

In conclusion, the work carried out on mammals by Western [1979], by Western and Ssemakula [1982] and by Stearns [1983] seems to support ideas of there being a number of constraints on the evolution of life-histories. These constraints show that body size, taxonomic group and degree of precociality are all important correlates of life-history parameters. So that;

1) Mammals vary from those that are large and slow breeding to those that are small and fast breeding, with body size being a good predictor of most life-history traits.

2) There appears to be a separation between altricial and precocial mammals.

3) Removal of body weight effects changes the patterns of covariation found.

4) Variation can also be partly explained by taxonomy, as shown by the decrease in covariance between traits when order and family effects are removed.

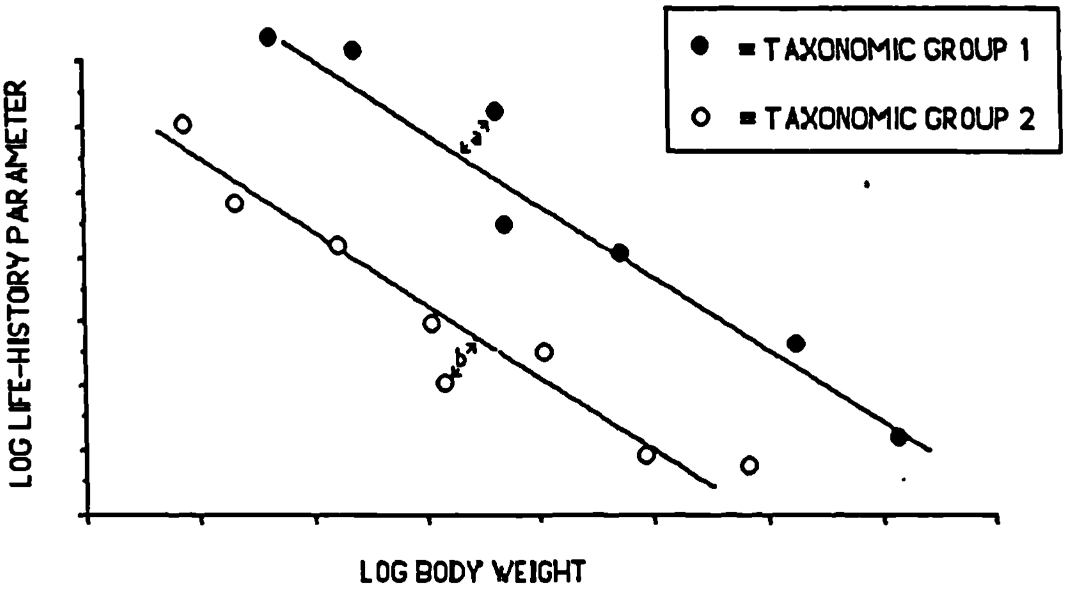
5) Species in different taxonomic groups have different patterns of covariation between reproductive traits.

The apparent importance of both body weight and phylogeny led Western [1979] to suggest that the evolution of life-histories can be usefully thought of as having two components; a "first order strategy" and a second order strategy". His approach offers a way of separating variation that can be explained by body size and taxonomy from that that can be explained by other factors. Figure 1.1 illustrates the way in which this approach can be practically used.

In figure 1.1, the two best-fit lines indicate the scaling relationship of a hypothetical character to body weight. The elevation of these lines is affected by the taxonomic group of the species, and the particular line and its elevation therefore give information about how both phylogeny and body weight affect the character. In the situation above group 2 has a smaller value for the life-history parameter, at any given body size, than does group 1. [This type of "grade" difference between taxa is discussed further in Chapter 2.] This line can therefore be thought of as representing the "average" state of an organism of a particular taxonomic group. The variation along this line is what Western [1979] refers to as the "first order strategy" of a species, i.e. the variation in strategy that can be explained by body size and phylogeny. In addition to variation <u>along</u> the best-fit line, there is also variation <u>about</u> the line, and this variation cannot be predicted from a knowledge of body size and phylogeny. In figure 1.1, examples of this variation are the distances [a] and [b], i.e. the distances from the two best-fit lines to the points. It should be remembered that there is no reason to assume that the variation of body weight and of the "designs" of different taxa are not adaptive, and possible environmental

Figure 1.1

Illustration of the scaling of a hypothetical life-history parameter to body weight, showing grade effects



correlates with these patterns should therefore be investigated. However, there is still variation that is not accounted for once effects of body weight and taxonomy have been removed. This variation may be due to the direct effects of selection on life-history parameters, and may also be important.

One possible problem with this kind of approach is that it can very easily lead to the assumption that variation that correlates with body weight and/or taxonomy cannot be adaptive. Even if one is aware of the fact that variation in a life-history parameter may be causing variation in body weight, or that the two may be varying in response to some third variable, it is often difficult to avoid the implication that variation in body weight is causing the variation in the life-history parameter. However, the use of the terms first and second order strategy represents a convenient shorthand to describe variation that may have many causes but can be described by allometric statistics of the best-fit line and the residuals from that line, and will therefore be used as such in this work.

Studies investigating links between environment and the life-histories of mammals

The above discusses some of the theories *of life-history evolution, and also looks* at the evidence for design constraints in life-history evolution. I will now concentrate on work that tries to uncover correlates between the environment and the life-history strategy of a species. This section is included for two reasons. Firstly, it shows the different approaches that can be used to understand life-history strategies in different groups and, secondly, it gives some idea of the problems that can arise when trying to interpret the results of these studies.

As a very large number of studies have looked at the relationship between life-histories and the environment, I have not attempted to give an exhaustive list. Instead I have concentrated on a small sample of studies that have looked at variation in mammalian species, and that highlight particular important points. As studies on primates are discussed later in this chapter, I have included only non-primate studies here. [For a summary of studies on groups other than mammals see Stearns (1977) who provides an extensive list of references and a review of the data.]

Relevant studies fall into two main groups. The first are analyses carried out on several species and usually examining several parameters. Such work often includes the use of bivariate and multivariate statistics to try and understand the inter-relationships between the life-history parameters and between these parameters and environmental variables. The second type of study is a more detailed one carried out on populations of a single species [or a few closely related species] at different sites. These sites usually vary in latitude or altitude, as these variables are generally believed to be positively correlated with environmental variability and therefore will be predicted by r/K theory and bet-hedging theory to give rise to populations with different life-histories.

There are several studies that look at the variation in life-history parameters over the whole mammalian group, although many [such as those by Stearns and Western discussed above] do not include a discussion of possible environmental influences. In two papers Millar [1977, 1981] looks at body size, birth weight, weight at weaning, time to weaning, gestation time and litter size. He finds the usual pattern, i.e. that there is a high correlation between body weight and reproductive parameters such that large species tend to have higher birth weights, larger weights at weaning, a longer time to weaning, a longer gestation time and a smaller litter size and small species the opposite set of traits. Although Millar [1981] did consider the possibility of this variation being linked to the environment and ecology of the species, he concludes that: "Animals with similar habits do not necessarily exhibit similar reproductive traits."

Although this conclusion may be confirmed by further research there are two basic reasons for not seeing it as a conclusive result. The first reason is that the statement is based only on a very general classification of environments. Secondly, the comparisons between related species are based on the values of their reproductive traits as compared to those one would expect to find for an "average" mammal of the same size. This type of approach does not take into account the possibility of grades of organisation and so may give misleading results [see above and Chapter 2 for a discussion of grades].

To find studies that address the predictions made by life-history theories, it is necessary to look at studies done on smaller taxonomic groups where more detailed information of the environmental conditions were available. The studies discussed in detail below are a small selection of those that discuss life-history variation in small taxonomic groups. I have chosen these works in particular because they specifically look at ecological factors that their authors consider to be important in determining environmental predictability. The important points of these and a selection of other studies are summarised in table 1.2.

Swihart [1984] looked at the patterns of reproduction in 22 lagomorph species, using correlation and principal components analysis.The results of the correlation analysis showed that body weight can explain a large proportion of the variance of the life history characters looked at. The principal components analysis indicates that the first principal component [PC1] is a size variable, whereas PC2 and PC3 are separate measures of the rapidity of development. Swihart therefore uses the principal components analysis to separate out the variation that is due to body size from that that is mainly independent of it. From this work, and from a consideration of the ecologies of the species, he concludes that rates of development, litter sizes and reproductive effort [during gestation] are characters that are directly adapted to the environment [second order strategies]. He states that;

> "In highly seasonal environments, lagomorphs opt for a big-bang reproductive strategy coupled with relatively great maternal investment in offspring ..... Long breeding seasons promote a strategy characterized by increased iteroparity and reduced investment per litter." [*ibid*p. 288]

This study illustrates the way in which multivariate analyses can be used to give one ideas about the way in which life history patterns are influenced. However, it contains no detailed examination of the precise environmental factors that might be selecting for the different life history strategies, and, does not contain the necessary information to attribute the variation to selection of the r/K type or of the bet-hedging type. For studies that address these questions more specifically, it is necessary to look at more detailed work carried out in the field.

In a single-species study Bronson [1979] looked at 5 populations of golden-mantled ground squirrels [*Spermophilus lateralis*] at different altitudes. He found that higher elevations were associated with a shorter active season, a higher adult survivorship, lower litter sizes and a later age at sexual maturity. He gives three possible explanations for these results. The first is that the higher elevations are associated with a greater variation in juvenile mortality and hence that bet-hedging is occurring. Secondly, he suggests that differential fecundity among age classes could be the explanation. If older females were relatively more fecund than younger ones [say because the shorter growing season at higher altitudes meant that younger females had not grown large enough to produce many young successfully], then evolution would favour a lower reproductive effort in these females at an early age. They would be more likely to survive to breed later when they were capable of producing more young. The third possibility considered is that the variation is not genetic but is caused by "phenotypic plasticity" which may, or may not, be adaptive.

As Bronson's study includes no information on the variation in juvenile survivorship from year to year, it is difficult to test the assumption that high altitudes will be associated with a high variability in this character. Similarly, there is no information available on age-specific fecundity. It is therefore not possible to infer whether bet-hedging is occurring or whether the other possibilities are equally likely. Bronson does not consider the possibility that selection could be r/K in type, with the higher altitudes having a more predictable environment.

The problems that can arise if one assumes, without evidence, that certain environments are unpredictable are highlighted by work on another species of ground squirrel. In two articles, Zammuto and Millar [1985a, 1985b] looked at the life-history characters of six populations of Columbian ground squirrels [*Spermophilus columbianus*] at different altitudes. They found that there was no evidence that bet-hedging was occurring, as a decrease in juvenile survival was associated with a decrease in generation length and an earlier age at first reproduction [i.e the opposite response to that predicted by bet-hedging theory]. Similarly, the correlation of a high variance in litter size with an early age at maturity and a short generation length was contrary to the predictions of bet-hedging. They next tested the predictions of r/K theory by measuring the variability and predictability of the six sites.

It is usually assumed [e.g. Bronson, 1979] that higher altitudes will be more variable and less predictable than will low altitudes, and that r/K theory therefore predicts that organisms found in higher places will be more r-selected. Zammuto and Millar [1985b] did, indeed, find that the higher altitudes had slightly more variable temperatures than did lower elevations, but that this higher variability was not linked to a lower predictability. This finding is important, as it shows that the commonly made link between variability and predictability is not always valid, and that is is possible for an area to be predictably variable. Their subsequent findings, that the low altitude populations had earlier maturity and lower adult survival than did the higher elevations, need to be considered in the light of these results. A conventional interpretation of the link between these life-history characters and elevation would have concluded that the results were opposed to r/K theory. However the measurement of predictability as well as variability allows the results to be show that an unpredictable environment is linked to some "r-selected characteristics", as would be predicted from r/K theory. Despite this support of r/K theory litter size was not found to vary with altitude and body size was found to be larger at lower sites, indicating that the life history parameters in this species at least do not have to covary in the usual way. Zammuto and Millar conclude that:

> "It is possible that some problems with r/K theory in the past may have been caused by a failure to detect the apparent paradox that a variable environment can be predictable. .... We propose that environmental predictability may be more important to the evolution of the Columbian ground squirrel than environmental variability."
>
> [Zammuto and Millar, 1985b: p.1790].

These, and the other studies listed in table 1.2, show there is no conclusive evidence for any of the life-history theories in the mammals. Stearns [1977] also notes this, and suggests that part of the reason for this is that the long generation times of most mammals prevent their use in long term experimental work on these problems. However, the comparative approach should be able to yield some useful information if it is applied. The three studies discussed above illustrate two basic problems with such work. Firstly, it is noticeable that many works [e.g Swihart, 1984; Conaway *et al.*, 1974] simply describe the patterns of variation in reproductive characters without testing any specific hypotheses. The problem with this approach is that the results are then difficult to interpret in the light of established theories, as the necessary parameters have not been measured. The work of Zammuto and Millar [1985a, 1985b] highlights the second problem, i.e. the assumption that a parameter represents a

Table 1.2

Some studies investigating relationships between life-histories and environmental variables in mammals

Study[A]	Taxa	Parameters[B]	Results and conclusions drawn.
1.	Eastern Cottontail rabbits (*Sylvilagus floridanus*)	Life-history 1. W_f 2. litter size 3. onset of breeding Environmental 1. latitude 2. longitude 3. altitude	Results of partial correlations indicate that onset of breeding is later at high latitudes and altitudes. Litter size is positively correlated with body weight, onset of breeding, and negatively with elevation. Body size positively correlated with latitude, negatively with longitude and elevation. Supports bet-hedging.
2.	lagamorphs 22 species	Life-history. 1. W_m, W_f, W 2. AFR 3. gestation 5. FGR, PGR 4. no. young/yr. 6. MRI 7. survivorship Environmental 1.breeding season length 2. general ecology	Most parameters correlated with body wt.. PCA separated spp. firstly by body wt and then by developmental rate. Variation found in different taxa. Breeding season length is an important factor in determining the life-history. Seasonal environments select for fewer, larger litters, and increased maternal investment in offspring
3.	New world rabbits.	Life-history gestation length Environmental 1. Northern limit 2. Southern limit 3. Median latitude	Both northern limit and median latitude are negatively correlated with gestation length. No correlation with southern limit.Some support for r-K theory.

Table 1.2 [continued]

4. Golden-mantled ground squirrel (*Spermophilus lateralis*) 5 populations	Life-history. 1. W_f ,W_m 2. young/litter 3. mean AFR 4.survivorship 5. age-specific fecundity Environmental 1.altitude	High latitudes linked with lower fecundity, later age 1st reproduction and greater adult female survivorship. Support for bet-hedging and/or age-specific fecundity .
5. Columbian ground squirrel (*Spermophilus columbianus*) 6 populations	Life-history. 1. W_f 2. young/litter 3. mean AFR 4. suvivorship Environmental 1. temperature variability 2. rainfall variabilty 3. growing season length 4. environmental predictabilty	Survival rates were negatively correlated with degree of iteroparity. More variable environments were associated with a comparatively high adult: juvenile survival ratio, a low degree of iteroparity, and low survival to maturity. The greater the variance in growing season length the lower the adult survival. No support of bet- hedging. High environmental predictability linked to high adult survival, late age maturity, and large body size, i.e. supports r-K theory

Table 1.2 [continued]

6. 5 spp. of mice: *Peromyscus* spp.	Life-history 1. litter size 2. energy content of litter at birth and weaning. 3. energy requirements during gestation and weaning 4. efficiency of energy use during gestation and weaning 5. W_f Ecological 1. resource availability 2. latitude 3. breeding season length 4. colonizing ability	No obvious correlations with body size, latitude or breeding season length. Species with high reproductive potentials are better colonizers, i.e. supports r-K theory. However, spp. with larger litters do not produce smaller offspring or offspring with lower energy content. Spp. with large litters and faster rates of energy expenditure do not have lower efficiencies than other spp. i.e. does not support r-K theory.

A - 1. Conaway et. al. 1974; 2. Swihart; 1984 3. Chapman 1984; 4. Bronson 1979; 5. Zammuto and Millar 1985a and b; 6. Glazier 1985.

B - W_m, W_f, W = mean body weight of adult male, adult female and average adult.

FGR = foetal growth rate

PGR = postnatal growth rate

AFR = age at first reproduction [females]

MRI = maternal reproductive investment

measure of environmental variability when it may not do so. These are problems that I hope to address in this study.

This study is an attempt to test theories of life-history evolution for the primates, the following section therefore looks at this group and the work that has already been done on its life-history evolution.

The primates

Characteristics of the order

There are about 180 species in the mammalian order Primates, a group which includes lemurs, lorises, tarsiers, monkeys, apes and humans. The following account of the order is taken from a variety of sources, including Richard [1985], Napier and Napier [1985] and Smuts *et al.* [1986].

Although they are generally considered to be adapted to an arboreal life, the basic primate design is not very specialized as compared to many mammalian orders. However, it is this lack of specialization that enables the group to be flexible and to occupy a wide variety of habitats. The group is found mainly in tropical and sub-tropical areas [macaques, langurs and people being the only species to be found in temperate zones], where they inhabit habitats varying from primary and secondary forest to grassland and savannah. In the New World all species are arboreal, but in the Old World there is a wide range in the degree of arboreality found, with some species [e.g. the gelada baboon] being exclusively terrestrial. Primates are generally omnivorous, eating a varying proportion of insects and other invertebrates, small vertebrates, leaves, fruit and seeds. The characteristics of each primate family are briefly summarised in table 1.3. The variation found in primate ecology makes them a particularly interesting group for this type of study.

Taxonomy and general characteristics of groups within the primate order

The taxonomy followed in this work follows that of Jolly [1972] except where stated in Appendix II. It should be realized that taxonomic classification is debatable for most of the groups at one or several taxonomic levels [varying from debate over the correct splitting of infraorders and families in the strepsirhines to discussion as to whether the various subspecies of *Galago senegalensis* and *Gorilla gorilla* should be viewed as separate species]. I will not attempt to review all of the arguments regarding taxonomy, as such a work could be a thesis in itself, but instead concentrate on describing the major groups as listed in Jolly [1972]. The

Table 1.3

Characteristics of the primate families

Suborder: Strepsirhini

Family	Common names	Distribution	Other information
Lemuridae	lemurs & dwarf lemurs	Madagascar	Nocturnal, diurnal, variety of diets
Indriidae	indriids	Madagascar	Diurnal, variety of diets & habitats
Daubentonia	aye-aye	Madagascar	Nocturnal, arboreal, insectivorous
Lorisidae	lorises & bushbabies	Africa & Asia	Nocturnal & arboreal, diet mainly insects, gums and fruit

Suborder: Haplorhines

Family	Common names	Distribution	Other information
Tarsiidae	tarsiers	Asia	Nocturnal, arboreal, insectivorous
Callitrichidae	marmosets & tamarins	South & Central America	Diurnal and arboreal, Diet mainly insects, gums and fruit
Cebidae	cebid monkeys	South & Central America	Diurnal, arboreal, variety of diets
Cercopithecinae	cercopithecine monkeys	Africa & Asia	Diurnal, mainly frugivorous. Both arboreal & terrestrial species.
Colobinae	colobine monkeys	Africa & Asia	Diurnal, folivorous. Both arboreal & terrestrial species.
Hylobatidae	gibbons or lesser apes	Asia	Diurnal, arboreal, mostly frugivorous
Pongidae	great apes	Africa & Asia	Diurnal, folivorous & frugivorous. Both arboreal &terrestrial species

description of each group is brief and therefore necessarily simplified, for example the description of a group as "frugivorous" is not meant to imply that all species of this group are solely fruit eaters but only that most species in the group have a diet that mainly consists of fruit.

Traditionally, mainly following Simpson, [1945], primates have been split into two groups, the Prosimii [lemurs, lorises, and tarsiers] and the Anthropoidea [New World and Old World monkeys, apes, and humans], but the grouping of the tarsiers with the more "primitive" lemurs and lorises is questionable as tarsiers share features of both groups. Recent evidence suggests that the characters that tarsiers share with the lemurs and lorises are primitive in nature and therefore not indicative of a shared common ancestor. However, tarsiers share several derived characters with the members of the Anthropoidea [for example, see Luckett [1975] on foetal and placental morphology, Szalay [1975] on basicranial evidence, Noback [1975] on the visual system]. The presence of shared derived characters suggests that tarsiers and the members of the Anthropoidea share a common ancestor and from an evolutionary point of view tarsiers are more usefully considered as being a part of this group. For this reason the split made in this work is between the Strepsirhini [lemurs, lorises and bushbabies] and the Haplorhini [tarsiers, monkeys, apes and humans].

In the classification employed here the strepsirhines consist of two groups - Lemuriformes and Lorisiformes. The former are found only in Madagascar and include the true lemurs [lemurs, gentle lemurs and sportive lemur], the dwarf lemurs [dwarf lemurs and mouse lemurs] and the three species of the Indriidae. In addition, the single species of aye-aye [*Daubentonia madagascariensis*] has been included in this group, although it is so different from other strepsirhines that it has been suggested that it should be placed in an infraorder of its own [Groves, 1974]. The Lemuriformes group has a considerable diversity of forms and habitats, with both nocturnal and diurnal species. Their social structure is similarly diverse, with the small nocturnal species being solitary, but the diurnal societies having a variety of gregarious structures. The isolation of the Malagasy species from the other primate species found in mainland Africa is thought to be a major factor in its success and a reason for the wide diversity of forms found. From the point of view of this study, a particularly salient point that must be made is that, until recently [about 2000 years ago], there were many more species found in Madagascar than are alive today. The arrival of humans on the island was most probably the cause of the extinction of several species of lemur in a wide variety of habitats. It may well be the case that the present habitat of species has been affected both by these extinctions which could have left niches empty for them to invade.

The other strepsirhine group, the Lorisiformes, includes the four genera of the slow-moving loris family [lorises and pottos] and the faster-moving bushbabies. These species are found widely distributed over Africa and Asia and have tended to retain more primitive characteristics than have many of the Malagasy strepsirhines [e.g. they are all nocturnal and most are primarily insectivorous]. All of the lorisiforms are solitary species, the usual pattern seeming to be that mothers forage and sleep with their young while other adults do so alone [although several bushbaby females may share the same nest].

The haplorhines are separated geographically and taxonomically into New World species [the Ceboidea] and Old World species [Tarsioidea, Cercopithecoidea and Hominoidea]. The New World species are found only in South and Central America [there are no living primate species native to North America] and consist of two families, the Callitrichidae [Geoldi's monkey, marmosets and tamarins] and the Cebidae. All of the New World monkeys are arboreal and, with the single exception of the owl monkey [*Aotus trivirgatus*], diurnal.

Several characteristics [small body size, production of twins, dental features and claws] of the Callitrichidae have been suggested to indicate that they are more primitive in form than the Cebidae. However, more recent work [e.g. Ford, 1980] suggests that these characteristics are not primitive retentions but have been derived, probably because of selection for small size and/or rapid breeding potential. The social structure of callitrichids is not well understood but seems to vary both between and within species. They are found in groups varying in size from 2 to 15 or more with only one reproductive female, which appears to be either monogamous or polyandrous [Goldizen, 1986]. Geoldi's monkey [*Callimico geoldii*] is included in the family Callitrichidae, as recent chromosomal evidence [Dutrillaux *et al.*, 1988] suggests that it is more closely related to marmosets and tamarins than it is to cebids. However, it is retained in a separate subfamily as the same evidence also indicates that it represents an early split from the group.

The cebid family is a group with a wide variety of forms and diets, a diversity reflected in its subdivision into five subfamilies. Their evolutionary relationships are not clear [for example, see Rosenberger, 1981] and the taxonomy used here may not accurately reflect phylogeny. Several cebid species [*Aotus, Callicebus* spp. *Pithecia* spp. and possibly *Chiropotes spp.*] are monogamous [Robinson *et al.*, 1986] but others [*Alouatta* spp., *Saimiri, Cebus* spp. and the Atelinae] are found polygamous groups [Robinson and Janson, 1986].

In the Old World, haplorhine primates [tarsiers, monkeys and apes] are found in Africa and Asia [the small population of Barbary macaques in Gibraltar are thought to have been introduced]. With the exception of the tarsiers, all of the Old World haplorhines are diurnal.

As already noted, the tarsiers have retained many characteristics thought to be typical of ancestral primates, and they share some of these "primitive" characters with the strepsirhines. The three extant tarsier species are all found on Asian islands. They are very similar in appearance and ecology being small, nocturnal and feeding almost entirely on invertebrates and small vertebrates. Their small size and nocturnal habits mean that little is known of their social structure in the wild, but there are suggestions that one species *Tarsius spectrum* may be monogamous whereas the other two species *T. bancanus* and *T. syrichta* are probably solitary.

It is generally considered that the Old World monkeys and apes have evolved to be more different from the ancestral haplorhine stock than have the New World monkeys, which have retained an essentially conservative "design". The Old World monkeys are all members of the family Cercopithecidae and can be split into two subfamilies, the Cercopithecinae and the Colobinae. The subfamily Cercopithecinae includes macaques, baboons, mandrills, mangabeys and the guenons. This subfamily has more species and covers a wider range than does any other primate subfamily and includes several terrestrial and semi-terrestrial species. The group contains several species that are particularly adaptable and appear to be able to occupy a wide range of habitats, including several [e.g. savannah, temperate zones and areas of human habitation] that other primate groups have been unable to survive in. The subfamily Colobinae [leaf monkeys] consists of langurs, colobus monkeys and the proboscis monkey. Although their diets vary less, [they are predominantly folivorous] than do those of the Cercopithecinae, the langurs are also very adaptable species being found in temperate zones and are often semi-terrestrial. Most Old World monkeys live in multi-male/multi-female groups or in single-male harem groups, although the structure and size of these groups is highly variable.

The apes, or Hominoidea, can be split into three families, the Hylobatidae [the gibbons and the siamang], the Pongidae [chimpanzees, gorilla and orangutan] and Hominidae [humans]. The Hylobatidae, or lesser apes, include the gibbon [*Hylobates*] species which are all very similar arboreal frugivores and the larger folivorous siamang [*Symphalangus syndactylus*]. All of the Hylobatidae studied to date are monogamous and live in family groups of 2 parents and their offspring. The Pongidae, or great apes, are the group most closely related to humans, with the orangutan being an arboreal frugivore, the gorilla a terrestrial folivore and the chimpanzee species ranging widely in habitat but being semi-terrestrial and frugivorous/omnivorous. Gorillas are harem-living animals whereas chimps live in multi-male/ multi-female groups. The social structure of the orangutan is less well understood, but it appears that females travel with their offspring and males are solitary.

Life-Histories of primates: a review of the literature.

Several studies [e.g. Western, 1979; Robinson and Redford, 1986, Case, 1978] have noted that primates generally tend to have a life-history strategy that is notably different from those of other mammalian groups. Compared to an "average" mammal of the same size, primates are slow-breeding, slow to mature, and have a large amount of parental care. The individual life-history characters of primates as compared to other mammals are discussed in more detail in Chapter 4.

There have been several studies of variation within the primate order that have looked at the relationship between life-history parameters and body weight. The most extensive of these are three studies that have looked at a wide range of life-history parameters, Rudder [1979], Harvey and Clutton-Brock [1985] and Harvey *et al* [1986]. In addition, there have been studies looking at variation in a particular variable, [e.g. Leutenegger [1973] on litter weight, Rasmussen [1985] on variation in litter size] in varying numbers of species. There are also some studies that have looked at the variation in overall life-history strategies of species in relation to their environment [e.g. Nash, 1983; Rowell and Richards, 1979].

Rudder [1979] studied the scaling of various life-history parameters to body weight and made an attempt to explain variation in terms of environmental selection, with particular reference to broad differences between the haplorhine and the strepsirhine species. Rudder also compared the r_{max} values of "forest" and "non-forest" species, and found no obvious separation of the two. However, there are several reasons for not taking this result as being definitive. Firstly, his sample size was small [31 species], secondly, there are several calculations of r_{max} that are based on poor data [as shown in this study] and thirdly, the division into these two categories meant that all forest species, whether they were found only in primary forest or in a wide range of forest habitats were classified as being forest species. In addition, some of his habitat classifications are questionable e.g. *Lemur fulvus* is classified as being a non-forest species and *Macaca fuscata* is classified as a forest species.

Harvey and Clutton-Brock [1985] also looked at the allometry of primate life-history characters and their relationship to some ecological and behavioural variables. They found no relationship between the life-history parameters and the ecological variables, but did not look at any measure of environmental predictability or mortality.

To find studies that directly address the question of whether primate life-history parameters fit in with theories such as r/K selection one must look at studies of smaller taxonomic groups. Rowell and Richards [1979] compared the maturation and breeding rates of captive African monkeys and concluded that open grassland species were faster-developing and faster-breeding than forest species. This result was backed up by later work [Chism *et al*, 1984; Cords and Rowell, 1986; Cords, 1987] on wild populations.

The work on African monkeys seems to support r/K theory, or at least not to refute it, but studies on other groups give more ambiguous results. Nash [1983] looked at breeding rates in bushbabies [*Galago* species] as related to the climatic variability in the areas in which they are found. She concluded that, although breeding rate did increase with increasing variability in temperature, the relationship with rainfall variability and the probability of drought was less clear. However, Nash does not consider the allometry of these characteristics or the variation in age at first reproduction.

Another study that casts doubt on the application of r/K selection theory to primates is Rasmussen's [1985] comparison of litter sizes in lemurs. He notes that of the 11 taxa [species and subspecies] of lemurs that were examined:

> "The lemurs with the highest mean litter sizes [the two ruffed lemurs, the crowned lemur, Sanford's lemur, and the white-fronted lemur] are all from the moist dense tropical forest of Madagascar's northern and eastern coastal regions. Those with the lowest mean litter sizes [red-fronted, brown and mongoose lemurs] are from the drier deciduous woodlands of the western side of the island ..."
> [*ibid*p.511]

As one would predict that tropical forest would be more stable than the deciduous forest, this result is the opposite to that that would be predicted from r/K theory. If the mortality rates of infants are high in deciduous forest, the result could support bet-hedging theory or, alternatively other factors may explain the result [e.g. the deciduous species may compensate for their low litter sizes by having shorter inter-birth intervals, or the differences may be an effect of selection for body weight]. Implications of this study, and that by Nash [1983], are discussed further in later chapters.

These studies are an indication of the generally found dichotomy between comparative scaling studies that discuss the primate group as a whole and the more ecologically based studies that look more closely at a smaller taxonomic group within the primates. The results of the two types of studies do not give either a clear refutation, or any definite support of any of the life-history evolution theories. This study is an attempt to fill this gap.

Aims of this study

In this introduction I have outlined the ideas and theories that are commonly used to explain life-history evolution and some of the more important studies that have attempted to test these theories. Although evolution in primates is of particular interest, as the group contains ourselves, there has been no comprehensive study carried out on primates in order to find out the possible determinants of life-history evolution in this group.

There were two ways in which I could have investigated life-history evolution in the primates. Firstly, I could have chosen two, or more, closely related species [or sub-species] and carried out field research to investigate their reproductive and ecological characteristics. The second possibility was to carry out a theoretical survey which compared the life-histories and ecologies of a large sample of primate species. My reasons for choosing the latter option were based on two considerations.

1) There was no coherent and comprehensive theory of life-history evolution in primates. Results of any field study would therefore be interesting in that they would reveal facts about the species being studied, but would not necessarily be applicable to any general theory that tried to

explain the evolution of the group as a whole.

2) There was a large body of data available in the literature that had not been systematically extracted and analysed. This fact means that the primate order is an ideal one for such a study because there is a broad range of data available on a wide range of species.

Given these considerations, my general aims were as follows. Firstly, to compile a good data base for primate life-history characteristics that could be used for my study and for future investigations. Secondly, to investigate [using comparative methods] the relationships between life-history characters, body size and environmental variables in primates. And finally, to review the results of the analyses in the light of the current theories that have been used to explain life-history evolution. More specific aims were also formulated.

As primates are a long-lived and slow-breeding group my study is limited to the comparison of species and could not include experimental work. With this restriction and with the above theoretical and practical literature in mind, I formulated the following specific questions that seemed to be of importance if one is to understand the way in which primate life-histories have evolved.

1) How much of the variation in primate life-history parameters can be explained by body size?

2) Do primate life-history parameters vary with body weight, and with each other, in the same way as in other mammals? If not, what is the pattern [if any] of their covariation?

3. Can the variation in primate life-history parameters be explained by environmental predictability and/or variation and, if so, how?

4. Do patterns in life-history variation vary within and between primate groups? Similarly, do the apparent causes of variation vary from group to group?

5. Is there any difference in the pattern of variation seen at different taxonomic levels?

6. What are the implications of these results, as regards theories of life-history evolution?

Chapter 1

Summary

There is a wide diversity in the life-history parameters of organisms. These parameters are frequently found to vary together, so that large animals tend to be slow breeding and slow developing whereas small animals are fast breeding and fast developing. One of the most commonly quoted explanations for these patterns in variation is that of r- and K selection. This theory proposes that unpredictable environments [where populations suffer mainly density independent mortality] will select for fast breeding and development [r-selection]. However, in more predictable environments most mortality will be due to the effect of competition for limited resources and here selection for competitive ability will give slower breeding, slower developing organisms [K-selection].

Alternatively, the theory of bet-hedging argues that, in some situations, an unpredictable environment may select for "slow" individuals. This is predicted from a mathematical model, where the major effect of unpredictable environmental fluctuation is to increase juvenile mortality. In such cases it is argued that a parent will be better off if it spreads its breeding resources over several seasons and thus lessens the chance of all its young dying in a bad season. Other work has not supported the predictions of bet-hedging but shows that its conclusions can be altered depending if other mathematical models are used.

Variation in life-history parameters may not necessarily be linked to environmental predictability. If fecundity varies with age and survivorship varies with reproductive effort, one would predict that there will be a certain optimum spread of reproductive effort over a lifetime. In cases where breeding at an early age means that the animal will be unlikely to survive to breed later at an age, when it will be capable of producing more young, selection will act to delay the age of first reproduction. Similarly, selection may act to decrease fecundity at a certain age if this means that more young can be produced later. The similarities and contradictions of these ideas are considered.

The relationship of life-history parameters to body size and phylogeny is discussed, with particular reference to the ideas of design constraints. It is noted that the values of many life-history parameters can be predicted quite accurately from a knowledge of the animals size and taxonomic group. Ideas of allometric scaling and first and second order strategies are introduced.

Previous studies carried out on mammals generally and on primates in particular give no clear support for any of the adaptive theories of life-history evolution. It is considered that, to a certain extent, this lack of clarity may be due to a lack of integration of the comparative method [including allometry] and the ecological approach. With this in mind, the aims of this study are set out.

Chapter 2

Data used and methods of analyses

This chapter describes the statistical methods of analyses used throughout this thesis. This study is based on the analyses of data collected from the literature, and from personal communications. As such, it relies on a vast body of knowledge that has been amassed by primatologists, zoos and research institutions over the years. By collecting the data together in this thesis it was hoped that patterns and relationships previously overlooked would be discovered. I begin by discussing the reasons for choosing certain parameters and describing the data finally used. The parameters that will be referred to throughout this work are defined and problems associated with specific variables are mentioned. In particular the problems associated with the use of data from a variety of sources is addressed. There follows a discussion of the comparative method [including the application of scaling analyses] and a brief description of the various statistical techniques that have been employed.

The Data

The data used in this study comes from a range of sources, these are discussed below. The data is given in appendices III-VI. The life-history data is described first, followed by a description of the metabolic rate data and of the data relating to the ecology and environment.

Life-history data

There are many parameters that could have been included under the general heading of "life-history parameters". The choice of which life-history parameters to examine was determined by two things. Firstly, by their relevance to the commonly discussed theories of life-history evolution [outlined in the introductory chapter] and, secondly, by the availability of data. The two life-history parameters that are most significant in terms of the evolutionary history of an organism are its rate of reproduction and the proportion of its resources that it puts into reproduction. This study therefore concentrates on the variables that go to make up these two parameters, and on measures of the variables themselves.

The rate of reproduction can be most conveniently measured by the maximum rate of intrinsic increase, or r_{max}. The methods of calculation and the potential problems that may be encountered when using r_{max} are discussed in more detail below. The calculation of r_{max} requires information on the number of young born per year, the age at first reproduction of females and the female age at last reproduction. Data relating to these variables are widely available for a reasonable number of primates and analysis has therefore been carried out on these parameters separately and on r_{max} itself.

The proportion of its resources that an animal puts into reproduction is synonymous with its reproductive effort [RE]. The calculation of a measure of reproductive effort was more difficult than that of r_{max}. As discussed in the introduction, reproductive effort [RE] is a measure of the total energy spent on reproduction and is therefore made up of the energy expended before conception in courtship, mating etc., and during the gestation period [the pre-natal RE], and that expended post-natally in raising the young to maturity. Factors that are thought to be important in determining the average RE of a species include neonatal weight, gestation period, age at weaning, weaning weight and growth rates and these parameters are therefore discussed. Unlike the relatively simple data that are used to calculate r_{max}, those needed to calculate total RE require the measurement of many variables. As data on many of these variables are not available a single measure of RE could not be devised and, instead, a number of measures have had to be used, these are discussed in more detail below.

In addition, the body size of the species was felt to be important. As discussed in Chapter 1, the body size of an animal may have an important influence on its life-history strategy and therefore needs to be considered.

It would have been interesting to look at patterns of mortality in different primate species, as variation in mortality rates and/or age-specific mortality has been suggested to be a major determinant in the evolution of life-history strategies. Unfortunately this was only possible for a very limited number of species, as such information is not available for most primate species. This is mainly due to the long generation time of primate species which means that very long term studies are necessary for adequate information on mortality to be collected. The consideration of mortality patterns is therefore left out of the bulk of this work, although there is a consideration of those that are available for the Cercopithecine monkeys in Chapter 7.

The starting point for the data set used was a large data base compiled by Ann MacLarnon, Bob Martin, and B. Rudder at University College London. This extensive body of information contains average values for several parameters, of which I used data for the parameters listed.

1) Adult female body weight [M_f].

2) Adult male body weight [M_m].

3) Average adult body weight [M], i.e. [M_f+M_m]/2, or an average figure reported from the literature when no separate data for M_f and M_m were available.

4) Mean neonatal body weight [N].

5) Mean gestation length [G].

6) Mean litter size [L].

In addition to these data further information was collected for the following parameters. This was done using primary sources, with many of the references being provided by Ann MacLarnon, Bob Martin, and B. Rudder.

1) Female age at first reproduction [A].

2) Interbirth interval [IBI].

3) Maximum recorded longevity [L].

4) Age at weaning [AW].

5) Weight at weaning [W].

6) Postnatal growth rate [PNGR].

Every effort was made to use accurate information, although in some cases provisional data have been used in preference to no data at all. The criteria used when deciding whether or not to include measurements were to prefer data for which the following conditions were met:

i) The sample size was large.

ii) Measurements were made under "natural" conditions, or conditions as close as possible to those found in the wild state.

iii) Measurements were taken from wild populations over several seasons.

iv) The data related to known individuals, rather than being estimates made from the changing state of a population over time.

Unfortunately such criteria could rarely be met in full. For a few species [e.g. see, Goodall (1986) on chimpanzees; Dunbar (1984) on the gelada baboon; Altmann (1980) on the yellow baboon] reasonably long term field studies have provided good life-history data that are probably a reasonable reflection of the life-histories of wild populations. Even in such work the period of study usually covers only a few years. As noted by Dunbar [1986], this means that the life-history data from the period of study may not be representative of the data that would be found if the population were to be observed for a longer period of time. In such cases short term anomalies in fecundity or mortality patterns may be taken as the norm, with a corresponding bias thus being introduced into the data used. However, this was generally the best data available and was therefore used. In many cases information from long term field studies was not available and an even less rigorous selection procedure had to be followed.

Generally, data from wild populations was preferred to that from free-ranging provisioned colonies which, in turn, was preferred to that of captive animals in zoos or laboratories. In some cases however, data from provisioned or caged animals was used preferentially when it was felt to be much more accurate than alternative sources of information from wild studies. This was usually because the wild study was for a very short term, or because the estimation of variables relied on a very small sample size compared to that of a captive study. The majority of data for all of the life-history variables is from captive animals, and this will have different implications for different parameters.

Body weight

The body weight data used in this thesis is described by Rudder [1979]. Wherever possible the data is from animals that were captured or killed in the wild but some data is from captive animals. Data from captive animals tends to give heavier weights than does that from wild animals, mainly because captive animals are better fed and undertake less exercise than their wild conspecifics.

In many works of this type [e.g. Harvey and Clutton-Brock, 1985] average female body weight has been used in the analyses. This is because it is felt that female body weight is more likely to be directly related to reproductive parameters such as neonatal weight and gestation length. However, average adult body weight is used throughout this work unless otherwise stated. This is done as many of the variables being discussed might be linked as much to the individuals own sex as to that of its mother. For example, infant growth rates might be related to the mothers size or to the eventual adult size of the infant. As many of data [particularly basal metabolic rate data, growth rate data and weaning age data] used are taken from only a very small number of individuals it is not possible to test for differences between the sexes in these parameters, hence average measures were used in such cases and it was felt that the corresponding average body weights should also be used. In addition, the ecological parameters used are usually taken from studies including both male and female adults amd the two are not generally separated. For example, data on diet is often presented as a a table listing the proportions of food types eaten. These proportions are averages for the population and it was felt that average body weights should be paired with such data. There is a very high correlation between male and female body weights [r=0.99, 2 sig. fig.] and repeating the allometric analyses found in chapters 3-7 gave no essentially identical results when female body weights were used in place of average adult body weights. Hence, when comparing this study to other similar studies that have used female body weight, the use of average body weight used in this study is not thought to give rise to any of the differences in results.

Gestation length

Gestation length is a particularly difficult parameter to measure as the date of conception is not usually known precisely. As this is particularly true of wild animals virtually all of the data on gestation comes from captive females. The effect that using captive data will have on the gestation lengths recorded is not clear. An indication that primates may vary their gestation length in response to food supply comes from Riopelle and Hale [1975]. This work demonstrates that rhesus monkeys that are fed on protein deficient diets have gestation lengths that are significantly longer [by an average of 9 days] than do those fed on "normal" diets, although the neonatal weights of the two groups are the same. The animals on the restricted protein diet therefore manage to produce a normally developed infant but cannot manage to sustain the higher foetal growth rate of the better fed mothers.

It is by no means unlikely that species other than the rhesus monkey may lengthen their gestation periods in times of protein, or other nutrient, shortage and hence that the gestation periods of wild animals may be longer than those used in this study.

Neonatal weight

Mean values of the weight of young at birth are reported quite widely in the literature from zoos and laboratories. However such data is, for obvious reason, not generally available for wild animals. Due to the lack of data available for wild young it is not possible to assess the extent to which captive conditions may effect this parameter. It is possible that the nutritive state of the mother may have an effect on the weight of her young although this may only become important in conditions where food is particularly scarce. As indicated by the work of Riopelle and Hale [1975], discussed above, neonatal weights appear to remain constant when food is restricted in rhesus macaques with the monkeys compensating by increasing the gestation length, it therefore seems likely that the neonatal weights used in this study will be representative of those found in the wild.

Litter size

Together with interbirth interval, the size of the litter determines an animal's birth rate. In primates the variability in this parameter is small [i.e there are generally 1 or 2 young per litter] but it may still have an important effect on overall birth rate.

Data on number of young per litter was taken mostly from captive animals. It is possible that higher levels of nutrition can also effect litter sizes with captive species producing larger average litters, although this is probably only true for those species that regularly produce litter sizes that are greater than one. For example, Kirkwood [1983] found that alterations in the diet of cotton-top tamarins increased the incidence of triplet births. Kirkwood suggests two possible reasons for the production of triplets in captivity.

> ".....It is possible that they [marmosets and tamarins] have evolved a reproductive strategy to produce triplets when food is abundant, so that in the event of the perinatal death of one baby, twins can still be reared. Since the gestation period is long the effect on the lifetime reproductive output of the failure to rear twins may be large enough to offset the costs of a triplet pregnancy. Alternatively, twins may only occur rarely in the natural habitat but may result from the over-stimulation in captivity of a mechanism by which the female normally adjusts litter-size from one to two according to food abundance."

The second mechanism may be the more likely explanation. As the production of triplets would be associated not only with increased costs during pregnancy but would probably mean that the neonatal weight of each baby was decreased, thus increasing the chances of perinatal mortality. However, if the first explanation were true and tamarins were being selected to produce triplets their only being capable of rearing two babies at a time would mean that the effective litter size would still be two. [Such species are therefore not recorded as having a litter size of greater than two in this study].

With the exception of the marmosets and tamarins all of the haplorhine species, for which data was available, had a litter size of one. As this appears to be a parameter that does not vary among related haplorhine species a value of one infant per litter was used for any haplorhine species, except marmosets and tamarins, for which litter size data were not available.

Female age at first reproduction

Age at first reproduction, i.e. age at which the first young is born, has been used in this study both because it is a measure of the attainment of maturity and because it is one of the determinants of r_{max}. Other studies [e.g. Harvey and Clutton-Brock, 1985; Rowell, 1977] have used additional measures for age at maturity such as age at first menarche, age at attainment of adult body weight and age at first conception. In this study age at first reproduction is used as the measure of sexual maturity, although age at attainment of adult weight is also discussed briefly as a measure of rate of development.

Age at first menarche is not considered because of the uncertainty over its biological relevance. As noted by Rowell [1977] age at first menarche is not a good measure of the age at which primates reach fertility. In some species [e.g. some macaques] young females can begin cycling a year before they conceive for the first time whereas in other species [e.g. the olive baboon] conception can occur before any signs of menstruation have been observed. Age at attainment of adult weight has a similarly uncertain relationship to sexual maturity, with some species conceiving well before they reach adult weight and others not becoming pregnant until after the adult size is gained [this study, see Chapters 6 and 7]. Age at first conception and age at first reproduction are both clear indications of an animal's sexual maturity and are therefore to be preferred over the other measures discussed. When discussing life-history strategies their relevance is obvious as they give an indication of the rate of development and the age at which an animal starts to produce its own progeny. The age at first reproduction is preferred in this study because it is easier to measure accurately, because, unlike impregnation, the birth of an infant is a directly observable event.

Female age at first reproduction can be accurately measured in wild populations where the ages of primaparous females are known, i.e populations that have been studied for a number of years. However, if a species is well known, it is also possible to estimate ages of animals with reasonable accuracy, particularly in the case of species that reproduce seasonally. The use of such estimates has increased the number of species for which age at first reproduction is from wild animals, but despite this there is still a predominance of data from captive animals.

Primates in captivity tend to breed at a younger age than do members of the same species in the wild. This is for several reasons. Animals in captivity are often better fed, and therefore grow faster than do their free-living conspecifics [for example see Altmann and Alberts (1987) for a comparison of the growth rate of wild and captive baboons]. For several species it appears that attainment of a certain body weight is necessary before a female can breed [Goodall, 1986; Rowell, 1977; Frisch, 1978] and, if this is the case, the increase of developmental rates in captivity will allow a female to breed at an earlier age than she could have done in the wild. Evidence of this is found in data from chimpanzees where captive data shows an age of first reproduction of 11.5 years [Rudder, 1979] whereas wild animals at Gombe, Tanzania do not breed until they are 12-13 years old [Goodall, 1986]. Similarly wild savannah baboons [*Papio cynocephalus*] reach menarche two years later than do those in captivity [Altmann *et al.*, 1978]. However, this type of reduction of age at first reproduction in captivity is not observed in all species. For example, both wild and captive female patas monkeys are found to produce their first infant at about three years of age [Chism *et al*, 1984].

Another factor that may delay reproduction in free-living populations is the restriction of breeding only in certain seasons. This restriction may be removed, or reduced in effect, in captivity, where fluctuations of climate and food resources do not place restrictions on the animals.

Social mechanisms may also operate to prevent young females from breeding in wild populations. For example, almost all field studies on marmosets and tamarins have recorded that young females remain in their natal groups without breeding even when they are apparently old enough to be able to breed [Dawson, 1978; Stevenson and Rylands, in press; Ferrari, pers. comm.]. However, the removal of a young female from the restrictive influence of others allows her to breed at an earlier age in captivity [Sussman and Kinzey, 1984].

Interbirth interval

Interbirth interval is defined as the time which elapses between one birth event and the next. It is a parameter that is important in determining the birth rate of an animal [particularly in primates where the capacity for producing and raising large litters seems to be either lost or not selected for] and therefore is important in determining r_{max}.

Wild data is quite widely available for this parameter, as it is relatively easy to collect, and has been used as much as possible. However, it should be realized that the use of data from short term studies will mean that interbirth interval may be underestimated as only those intervals that are shorter than the length of the study will be observed [Cords and Rowell, 1987].

Data was also taken from captive animals. Like age at first reproduction, interbirth interval is likely to be effected by captivity. Increased levels of nutrition found in captivity may allow the mother to regain breeding condition after a birth more rapidly than she would in the wild. In addition, the disruption of normal social groups may mean that weaning is effected earlier thus removing the contraceptive effect of lactation, and allowing conception to occur earlier than it would in the natural state. In species that breed seasonally the lifting of the effects of a fluctuating food supply may also mean that an animal can give birth at any time in the year. Evidence of such effects have been found in several species. For example, increased levels of nutrition have been implicated in the reduction of interbirth intervals in women [May, 1978], and in captivity *Theropithecus gelada* has been found to have an interbirth interval of 1.4 years whereas this is increased to 2.14 years in the wild [Hadidian and Bernstein, 1979; Dunbar, 1984]. There is also evidence [Goldikas, 1981] that in wild orangutans the interbirth interval may be as much as 6 years longer than is found in captive animals [9 years in the wild as opposed to 3 to 4 years in captivity].

Maximum recorded longevity

Of all the parameters discussed so far longevity is the most difficult to find wild data for and in fact the data used here is, without exception, from captive animals. The measure of longevity used is the maximum recorded longevity for a species rather than an average value. This is because an average value would be greatly biased by those individuals dying at a young age through accident or disease. It has been argued that the maximum recorded longevity is the best measure of a species lifespan as it is primarily determined by the genetics of the organism and is not effected by environmental factors [Sacher, 1959]. The use of this measure is therefore appropriate for this study, which is concerned with the ways in which life-history characters have responded to natural selection. As is discussed below the use of this parameter for the calculation of r_{max}, in place of age at last reproduction, is also considered to be appropriate.

It could be argued that the actual maximum lifespan is probably genetically determined and therefore this value will be the same for wild and captive animals, but there is no reason to suppose that the maximum recorded lifespan is equivalent to the maximum value that could be obtained. Animals that do not adapt well to captivity will tend to have low values recorded, as will those who are not well represented in captivity for other reasons, as the probability of one of these rarer creatures surviving to the maximum possible age will be less than for one in a larger population.

The intrinsic rate of natural increase: r_{max}

As has been discussed in the introductory chapter of this thesis, the evolution of an "optimum" value of the intrinsic rate of natural increase [r_{max}] is a central feature of life-history theories.

The value of r_{max} is a theoretical figure that can be taken as an indication of a species potential for "filling up" an available habitat, i.e. it is a measure of the species maximum rate of population growth that is possible when resources are not limiting. The equation is generally used for calculating r_{max} is from a 1954 paper by L.C. Cole and is based on two assumptions which are that:

1) The birth rate is constant, at least for the first few litters.

2) There is no mortality until the age of last reproduction is reached.

Of these, the first is probably a reasonable assumption to make for mammals, whereas the second is not. The calculation of r_{max} using this method requires knowledge of only three parameters, the earliest age at first reproduction in females [a], the maximum birth rate of female offspring, i.e. number of female offspring born per year [b], and the maximum age at last reproduction [w]. From these r_{max} can be found by iteratively solving Cole's [1954] equation:

$$1 = e^{-r} + be^{-ra} - be^{-r[w+1]}$$

It should be realized that the value of r_{max} differs from that of r, the latter being an empirical value that is a measure of a population's actual growth rate. The latter value will therefore include the effects of mortality before the age at last reproduction is reached and also effects of the birth rate varying with age. It will also include the effects of immigration and emigration from the population under study. It has been argued [Hayssen, 1984] that the value of r is a more relevant one than is r_{max} for studies on the interaction between life-histories and evolution. Her argument is that the assumptions that are made before r_{max} is calculated are frequently not valid for natural populations, and that r_{max} is not therefore a suitable measure of a populations capacity for growth. In addition Hayssen points out that:

> "......Cole's equation was not intended as a method for the estimation of *r* from field-gathered life history data but rather as a tool for the exploration of the populational consequences of certain life history phenomena." [Hayssen, 1984: p. 420, stress in original.]

[N.B. The value of "*r*" that is mentioned above is the value commonly known as r_{max}].

Both of these points are important ones and raise valid objections to the use of r_{max} in studies of this sort. As already stated, the assumption of 100% survivorship to age at last reproduction could be given as a serious objection to the use of r_{max}. However the lack of data on age-specific mortality rates and their effect on a population's growth means that it is virtually impossible to remedy this situation and either estimate a value for r or measure it in natural populations. It is partly the simplicity of its calculation that has meant that r_{max} is generally used instead of r, although there are other reasons for preferring its use.

An advantage of using r_{max} is that it is a value that can be compared between species, without confounding effects of the local environment's influence. Values of r for wild populations are rarely reported and even when available their relevance to the evolutionary potential of the population is often obscured by the fact that r can easily be altered by short-term climatic changes or by human interference. For example, both the yellow baboon and the vervet monkey populations in Amboseli national park, Kenya have been declining over recent years, because of habitat changes leading to a decrease in the food supply [Struhsaker, 1973; Altmann, 1980]. The population data from either of these populations would therefore give a negative value for r [i.e. they would show a negative growth rate for the population], whereas the mere existence of these two species shows that they have a potential for a positive growth rate. The critical value for r that is needed for these populations, i.e. that which represents their capacity for expansion after population decline, is not available. As problems such as these are found for most of the published values of r, I have not used these figures in analyses.

Another advantage of using r_{max} is that, as a physiological extreme, it is determined more by the genetics of the organism than by variation in the ecological and nutritive condition of the species, and as such can be thought of as being subject to selection pressure. However, it is phenotypes, and not genotypes, that are selected. This means that an organism that may be genetically capable of reaching some theoretically optimum rate of increase, but that cannot do so because of environmental [or other] reasons, will not be selected for this characteristic. For example, the capacity for some callitrichids to produce triplets in captivity is not one that is likely to be selected for in the wild as they can rarely raise more than two infants [Kirkwood, 1983].

As has already been noted, age at first reproduction and interbirth interval can also be affected by conditions in captivity. Because of such problems, the value for r_{max} that is used should ideally be one that could found in the wild state, and hence be subject to natural selection, rather than a figure derived from captive colonies. As has already been noted much of the data in this study has come from captive studies. For these reasons I have followed Robinson and Redford [1986] in using average values [or sometimes median values when distributions were skewed], rather than extreme values for these parameters, in the hope that these will be closer to those found naturally.

The parameters used to calculate r_{max} were; the mean age at first reproduction [years], the female birth rate [number of females born per year] and maximum recorded longevity in years [in place of age at last reproduction]. The female birth rate was calculated from the mean number of young per litter and the interbirth interval. A 50:50 male: female sex ratio was assumed in these calculations. [Although there is some evidence that in some species the sex ratios may be biased [e.g. Silk *et al*, 1981] it is not known if these observations are representative of the species sex ratio or anomalous effect induced by stress in captivity or sampling procedures on the wild.]

Data on female age at last reproduction [w] is rarely reported in the literature, and the maximum recorded lifespan has therefore been substituted for this variable. Fortunately the age at last reproduction has very little influence on the value of r_{max} and this substitution can therefore be made without greatly affecting the r_{max} obtained. For example, in humans using either w= 50, [i.e the maximum age at last reproduction for women], gives an r_{max} of 0.055, whereas using w=100, i.e. the maximum lifespan, gives a figure for r_{max} of 0.059 [assuming age at first reproduction is 15 years and interbirth interval interval is 3.5 years]. The longevity of closely related and similar sized species was used to calculate r_{max} for those species where no value for longevity was available. Given the relatively small effect of large variations in w on r_{max}, the close correlation of maximum longevity with body size [see Chapter 4] and the observation that closely related species have similar lifespans this substitution seemed reasonable. These values for longevity were not used in any calculation other than that to determine the r_{max} of the species concerned.

Age and weight at weaning

The major problem in determining the age at weaning is that of deciding when the suckling period terminated. In some species e.g. *Microcebus murinus* the young are suckled until a certain age and then are weaned in a few days (R. D. Martin pers. comm.). For such species the determination of when weaning occurs is more fairly straightforward.

In other species there is a long period during which the suckling time is being gradually decreased as the young become decreasingly dependant on their mother's milk. In these species it is not always clear were the cut-off age should be. Another problem with such species is that the fact that the young are in contact with the nipple may not mean that it is still obtaining milk from the mother, as such behaviour may be simply reassuring the infant. It was hoped that a survey of the literature would enable a definition of weaning to be drawn up [perhaps as a percentage of time spent suckling or a proportion of nutrients gained from milk] and thus to standardize the data for different species. However, the type of data obtained was very variable and it was found that it was impossible to give a satisfactory definition that would enable a reasonable sample size to be collated.

Generally speaking an infant was said to be weaned when it had stopped suckling, although some data has been included where the author of the original paper has not given any definition of weaning but has simply stated that "at age X the infants were weaned". In addition, length of lactation has been assumed to be synonymous with weaning age. The data on weaning age comes from both wild and captive animals, the majority being from the latter. It is possible that increased levels of nutrition may effect age at weaning, as a better fed mother may put more resources per day into her young and therefore the infants would grow faster and gain independence more rapidly.

Data on the weight at weaning is not always from the same source as is that from age at weaning. In some cases a weight at weaning was given without the age of the animal being stated and this data was also used. Nearly all of the data from weight at weaning comes from captive animals.

Postnatal growth rate

Postnatal growth rate was collected from the literature for the period between birth and weaning. The criteria used to select data on postnatal growth rate is described in detail in Chapter 6 and the data itself can be found in Appendix III.

Chapter 2

Basal metabolic rate data

The metabolic rate of an animal is a measure of the rate at which it expends energy in order to maintain itself, grow and support its activities. The metabolic rate will therefore vary depending on whether the animal is active, whether it is growing, whether it is a homeotherm and needs to expend energy on keeping its body temperature constant and on how large it is. Hence the comparison of the metabolic rates of different species is not an easy task. Ideally one would like to measure the energy requirements of animals in their natural state over a long period of time but this is not presently possible and we must be content with measurements obtained under laboratory conditions.

In order to make such measurements comparable between different species certain standard conditions of measurement have been set out. These conditions are devised in to measure the minimal metabolic rate needed to maintain homeostasis and require that the animal be in the following conditions:

1) Experiencing no heat or cold stress ["thermoneutral"].

2) Resting and calm.

3) Postabsorbative, i.e. not digesting or absorbing a meal.

Metabolic rates measured under these conditions are known as standard or basal metabolic rates. It has been noted [Schimdt-Nielsen, 1986] that the term "basal" implies a level of metabolic rate below which it is impossible to fall whereas some sleeping mammals and poikilotherms at low temperatures will have metabolic rates below this "basal" level, and he therefore suggests that the terms "resting" or "maintenance" metabolic rates are more appropriate. Despite this problem metabolic rates measured under the conditions above are usually referred to as being "basal" and this is the terminology used in this thesis.

It is recognized that young animals frequently have a higher basal metabolic rate [BMR] for their body size than do adults of the same species [e.g. Dobler, 1980] and it is therefore important to know the ages of the animals from which data is obtained. In addition to the three criteria listed above it is therefore preferable that the animals be adult.

Data on metabolic rate were extracted from the literature, by Ann MacLarnon and Bob Martin and by myself. Data were collected for as many species as possible, these are listed in Appendix IV, together with some details of the experimental procedure. As can be seen from this appendix much of the data did not meet the four criteria needed [i.e. the three listed and being adult] to ensure strictly comparable data. Several of the data come from immature animals and analyses were therefore carried out both with and without these data. Another major problem was that, for the larger species especially, several experiments were done with the animals restrained in "chairs". This method involves restraining the animal [sometimes by first anesthetizing it and then leaving it strapped in a "chair" until the anesthetic has worn of] and measuring oxygen consumption by means of a perspex "bubble" being placed over its head. It is difficult to believe that an animal in these conditions can be described as "resting" or "calm", and indeed several studies report problems with the animals struggling. The usefulness of such work is therefore debatable, and the data from these studies has not been used in the analyses although, for reference, it has been listed in Appendix IV and the data points are plotted on some graphs.

Better data generally came from the smaller species as these are presumably easier to handle and the animals oxygen consumption could be measured by placing than in a chamber. This was usually done at the time the animal would naturally be sleeping and most studies report that the animals were calm and resting and/or sleeping while the measurements were being done.

As the quality of data was variable, the data was classified in two sets, with only the better data being used for analyses [the classifications can be found in Appendix IV]. Data was classified as being "good" if the animal was adult, was resting or sleeping, had not eaten immediately prior to the experiment, and was at a temperature of at least 20°C. Although these criteria mean that some species in the "good data" set may have metabolic rate measures that are above the BMR [either because they are not totally inactive or because the temperature is not in the thermoneutral zone] it did mean that a reasonable sample size of metabolic rate data was ensured. Cases where metabolic rates may be above basal are mentioned in the text where appropriate.

Ecological and sociobiological data

The relationship of the various life-history parameters to ecological variables was investigated with a view to testing various theories relating life-histories to ecology and environment. As with the choice of life-histories parameters, choice of ecological parameters were chosen both because it was felt that they were of relevance to theories of life-history evolution and because data were available on them. The ecological variables used were:

1) Diet.
2) Habitat type.
3) Degree of arboreality.
3) Geographical range.
4) Climate found in range.

The effects of social structure were also looked at as it was considered that the social structure of a species might be related to its apportioning of resources between reproduction and maintenance.

Chapter 2

Diet

Primates are generally omnivorous and diet may vary considerably within a species depending on the season and the area. It is therefore difficult to put a species into a "frugivore class" or a "folivore class", or to some other dietary classification, without some qualifying comments. Because of this problem I have followed two courses when looking at the effect of diet on life-histories. Firstly each species, for which dietary data was available, was classified as belonging to one of the following categories:

1) Frugivore, feeding on fruit and/or seeds
2) Folivore, feeding on leaves and other structural plant materials [e.g. stems]
3) Animal eating, i.e. feeding on invertebrates and/or vertebrates, [in practice, animal eating non-human primates can generally be considered as insectivores]
4) Gum eating [including eating of any exudates].

The inclusion in a category was based on the food stuff that was predominant in the species diet regardless of the amount of other food that was eaten. This classification was therefore a very rough one and could be misleading, particularly in cases where the proportion of the main food eaten was much higher than the second most important food. For example, when one averages the results of two studies [Milton, 1980; Estrada, 1984] the mantled howler monkey, *Alouatta palliata*, is recorded as eating an average of about 47% fruit and 49% leaves and would therefore be classified as a folivore, despite its only eating very slightly more leaves than fruits. This difference could easily be due to sampling error and, in fact, in the study by Estrada the proportion of fruit eaten [51%] was very slightly higher than the proportion of leaves eaten [49%], a second type of analysis was therefore employed in order to avoid problems of this type.

The second approach was to take each food type separately and to investigate the way in which differing proportions of a food type in the diet related to the life-history parameters. Here an additional food category was employed -flower eating. This method meant that it was possible to investigate the effect of minor dietary components on life-histories.

In the collation of the dietary data only wild studies were used Whenever possible these were studies that included the collection of data over at least 12 months so as to minimize the effects of seasonal food availability on the overall diet. One problem that is particularly relevant to the data on diet, but that also occurs in the comparison of other ecological variables, is that of using data from field studies whose methodologies are not consistent with each other. When collecting dietary data several methods are used in the field and these may give very different results. For example a food item may be recorded only when it is actually eaten or the records may be of time spent foraging for a particular food. If the latter method is used food that is difficult to find or to capture, such as insects, will have a higher score than when the former method is employed. The following types of records were found to be used in the literature:

1. The time spent feeding on different items.
2. The frequency with which different items were taken.
3. The number of items eaten.
4. The time spent foraging for different items.
5. Stomach contents.

It is thought [Robinson and Janson, 1986] that the use of record types 1-3 give comparable results, whereas the use of type 4 records means that the importance of animal foods are over-estimated. For this reason I preferred firstly records of types 1-3, secondly those of type 5 [assuming these to be roughly equivalent to type 3] and only used foraging time records where no others were available.

All dietary data used, including the dietary categories, can be found in Appendix V.

Habitat type

The habitat of an animal is determined mainly by the climate and its geographical location, and the measurement of these factors will give some information on habitat. However, within an area there can be several types of habitat, due to factors other than climate and location e.g. the soil-type, the proximity of rivers or seas, human activity. In addition, two species living in the same general area can be utilising quite different habitats. For these reasons, it was felt that there should be a measure of habitat type in addition to the data on latitude and climate [discussed below].

A habitat classification was made for each of the species for which data on body weight were available. In the majority of cases information on habitat was taken from Wolfheim [1983], although some additional sources were used when it was felt that more precise information was available [see Appendix V]. There were several problems with this method, the main one being that confusion of classifications could easily occur due to different sources giving different names to the same type of habitat. For example it was difficult to know whether an area described as "forest edge" was synonymous with those described as "thicket", "clearing", or "scrub". In addition the listings for some species stated quite clearly that they had a preference for one type of habitat but also listed other habitats that they were found in, whereas for other species there was simply a list of habitat types where they occurred. The problem here being whether to include all the habitat types or whether, in cases where a preference was stated, to list the preferred habitat only. In an attempt to avoid confusion, and to simplify the analysis the following approach was taken.

The number of habitat classifications was reduced to 6 for the first analysis. The six classifications were:

1) "Primary forest species", species found only in or preferring primary and wet forest habitats.

2) "General forest species", species found in several types of forest, including some secondary forest.

3) "Forest and edge species", species that include large amounts of secondary forest and forest edge in their habitat, but that are also found in less disturbed areas.

4) "Disturbed and edge forest species", species that are restricted to or that prefer secondary forest and forest edge. Some species that are found in temperate forests were also included in this category.

5) "Savannah and woodland species", species that are restricted to or that prefer open woodland and savannah.

6) "Savannah and open grassland species", species found only on or preferring savannah and open country.

Due to the problems already mentioned it was not always easy to be certain which one a particular species should be in. In particular, categories [2] and [3] became rather "catch-all" classifications owing to there being a large number of species that were mentioned as being "forest living" or as "also being found in" secondary forest and/or forest edge. It is therefore quite possible that someone else could assign different categories to some of the species. However I think that no species would move up or down more than one category and that the results are therefore quite robust. The classifications made can be seen in Appendix V.

To simplify the results further a second analysis was done using combinations of these categories. It was hoped that using this approach would compensate for the possible mis-classification of some species. The three broader categories were:

i) Forest species [1 and 2 above].

ii) Edge and secondary forest species [3 and 4 above].

iii) Woodland and open country species [5 and 6 above].

It was thought that there could be a problem with taxonomic bias [discussed later]. The problems of assigning a habitat type to a genus were even greater than those encountered when trying to classify species. For many of the taxonomic groups species fell under several habitat types and it was therefore difficult to label the entire group with one classification. It was therefore decided to follow the procedure used by Clutton-Brock and Harvey [1977a] and to take average values for genera found in the same type of habitat but to treat members of the same group found in other habitats as separate entries. e.g. for the macaques the data for *Macaca fuscata, M. mulatta* and *M. nemestrima* were averaged to give a single "forest and edge" macaque value whereas that for *Macaca silenus* was used as the macaque value for "primary forest". The same procedure was used when classifying subfamilies, with the averaged generic values being used to obtain the average subfamily values.

Degree of arboreality

Species were classified as being arboreal, semi-terrestrial or terrestrial. As the length of time spent on the ground is rarely reported the assigning of each species to a category was done on rather subjective criteria. Generally speaking species that were reported to spend all or most of their time in trees were classified as arboreal whereas those that spend all or most of their time on the ground were classified as terrestrial. Species that spend time feeding on the ground but that travel in trees or *vice versa* were classified as semi-terrestrial.

Species latitude

Two measures of latitude were taken. The first was an extreme measure and was the species northerly or southerly range limit. This was an indication of the species' ability to survive in high latitudes and hence in variable climates. The latitudes to North and South were taken as equivalent and were converted to radians for analysis, i.e. 4°30'N and 4°30'S would both be considered simply as 4.5. In cases where species were found on both sides of the equator the greater of the two measures was taken. The second latitudinal variable was the "centre" of the species range. This was measured by taking the northerly and southerly limits of the range for each species and then taking the average of these two measures. As for the range limit data, northern and southern measures were taken as being the same. This second variable was taken as a measure of the "typical" latitude of the species.

The range of most species was taken from Wolfheim [1983], although in the few cases where it was felt that her information was not precise enough [as when several species were included under one combined reference] other sources were used.

The analyses were repeated using average generic and subfamily values of the life-history parameters. To calculate the range limit for a genus the most extreme latitudinal value for that genus was taken, and to calculate the range centre the mid-point between the most northerly and the most southerly point for the genus was used. Subfamily values were calculated in a similar manner.

Climate variables

The climate an animal experiences will have a very large influence on its total environment, as it will both effect the animal directly and also its ecological niche via the effect on other life forms. Ideally the climate records used for each species would have been taken from a site where the animals concerned were studied, and thus life-history and climate records would have been directly related. Needless to say, such records are only available for a minute number of species and hence less direct matching of the two sets of parameters was necessary. The methodology used and the climatic parameters that were calculated are described below.

To measure the effect of climate on the life-histories of primates two parameters have been examined, average precipitation and average temperature. The choice of these variables was almost mandatory, as they are the only two measures of water availability and temperature available for the majority of areas. Fortunately they are also a reasonable indication of the overall climatic conditions found. Measures of these two parameters have been calculated using standard weather tables from "World Weather Records", for the years 1940-1960 [Environmental Science Services Administration, 1955-1968].

A weather station was chosen for each species in the following way. Using Wolfheim [1983] the northern, southern, eastern and western limits of each species' range was determined [and in addition any information on the altitude that the species were found at was noted]. The "centre" of each range was then calculated by taking the average of the two latitudinal points [as for the latitude parameter above], and the average of the two longitudinal points [see figure 2.1]. These co-ordinates were then used to represent the typical position of each species. In the majority of cases this method gave a position for the centre of the range that appeared to be reasonably placed, as in the example of figure 2.1a. However in a few cases the "centre" of the species range fell outside the actual range of the animal concerned, e.g. as in *Cercopithecus aethiops* [figure 2.1b]. When this happened the range was split into two, or more, parts and a "centre" was found for each one, the climate variables being averaged to give a single value for each parameter.

Using "World Weather Records" a weather station was then taken for each species. The station closest to the species centre range point was preferred unless it was excluded for one, or both, of the following reasons:

1) Its altitude was out of the range of altitudes that the species was said to occur. This was done as altitude it has an important influence on climate.

2) It had very poor records of either rainfall or temperature [i.e. of less than 10 years].

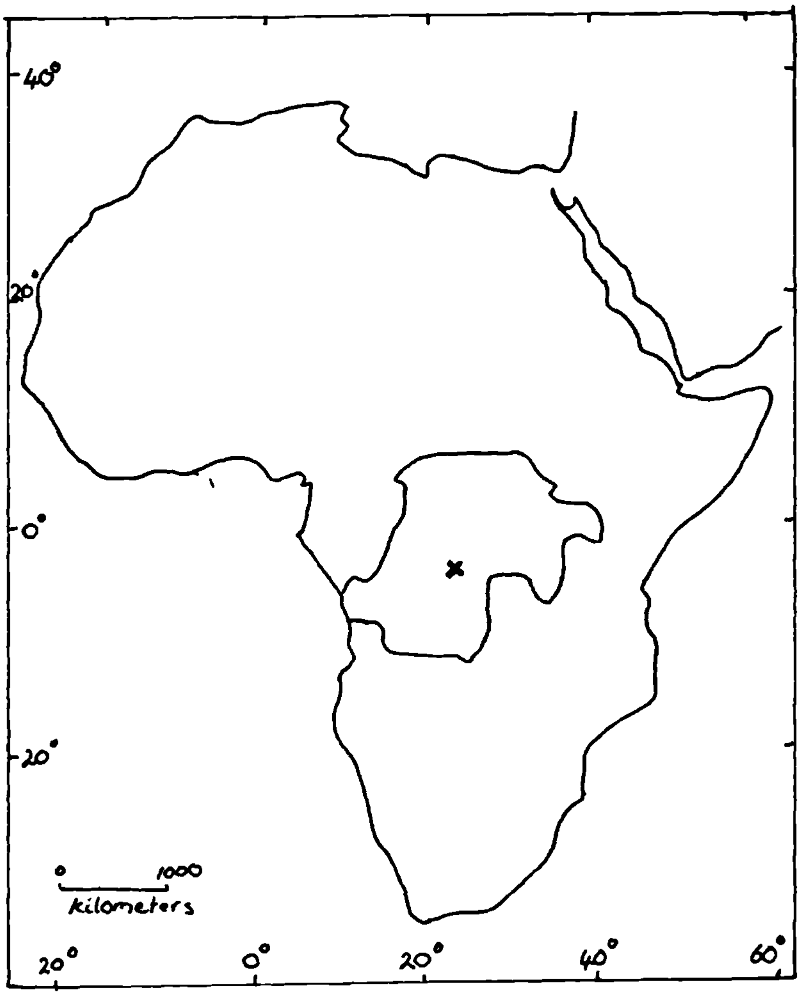
When either of these conditions occurred the next nearest station was examined to see whether it would give better records. In all but a few cases a station with good records was found that fell near to the species centre and within its altitude range [the correlation between the actual latitude of the weather station and the species range centres is high, $r = 0.95$]. The details of the stations used for each species can be seen in Appendix VI. A total of 64 weather stations were used, with an average of 14 years of records [range 8 - 20 years] from each.

I originally intended to repeat this method to obtain a second set of records for each species,

Figure 2.1

Diagram to illustrate the method of determining the position of weather stations

a) Where "range centre" is simple to determine; example showing the range of the redtailed monkey, Cercopithecus ascanius *(from Wolfheim, 1983)*

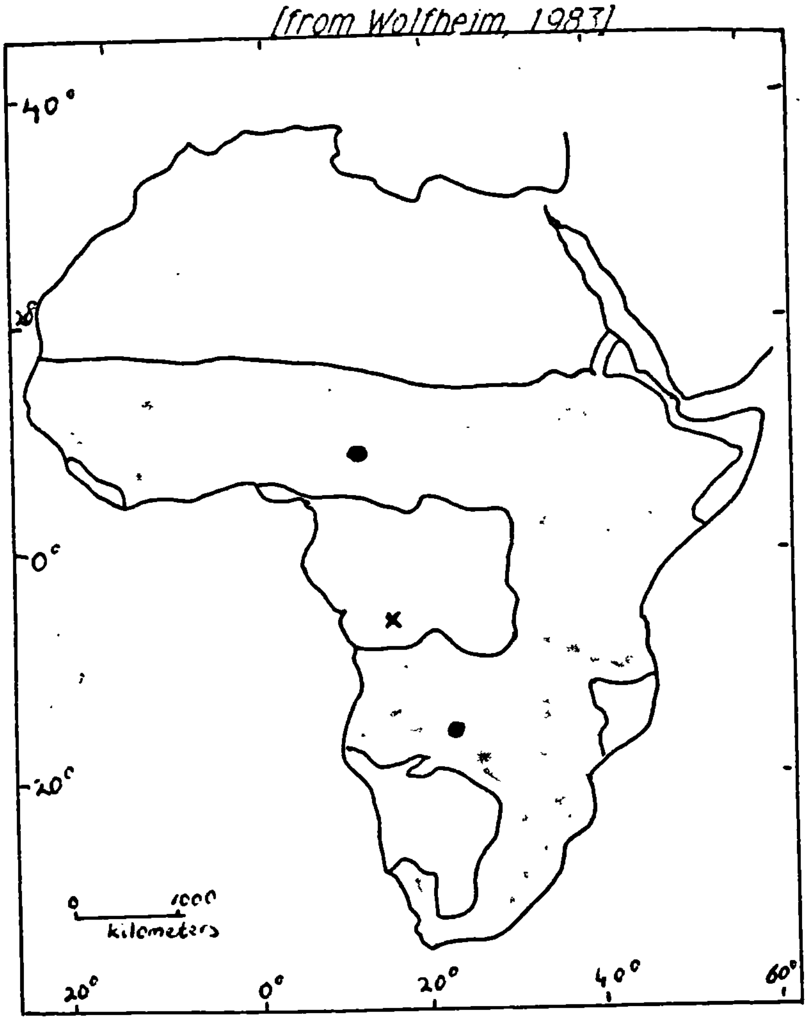


X indicates the approximate position of the "range centre" [2°38'S, 24°18'W], calculated as discussed in the text. As can be seen, this position falls within the actual range of this species and appears to be a good approximation of the actual range centre. The nearest suitable weather station to this point was therefore used to determine the "average" climate experienced by this species.

Figure 2.1 [Continued]

b) Where "range centre" is more difficult to determine; example showing the range of the vervet monkey, Cercopithecus aethiops

[from Wolfheim, 1983]



X indicates the approximate position of the "range centre" [7°30'S, 14°46'E], calculated as discussed in the text. As can be seen this position falls outside the actual range of this species. The weather stations were therefore chosen by taking the range in two parts and finding the centre of each part, these positions are marked ● above. The nearest suitable weather station to these points were therefore used to determine the "average" climate experienced by this species.

Table 2.1

Measures of climate used

	Measures of "average" climate	Symbol
1)	Annual mean temperature	AN.AV.$_t$
2)	Mean temperature in the hottest month	HI.AV.$_t$
3)	Mean temperature in the coldest month	LO.AV.$_t$
4)	Annual mean precipitation	AN.AV.$_{ppt}$
5)	Mean precipitation in the wettest month	LO.AV.$_{ppt}$
6)	Mean precipitation in the driest month	LO.AV.$_{ppt}$
	Measures of inter-year variability	
7)	CV* of mean temperature in hottest month	HI.CV.$_t$
8)	CV of mean temperature in coldest month	LO.CV.$_t$
9)	CV of total annual precipitation	AN.CV.$_t$
10)	CV of mean precipitation inwettest month	HI.CV.$_{ppt}$
11)	CV of mean precipitation in driest month	LO.CV.$_{ppt}$
	Measures of intra-year variability.	
12)	CV of temperature within the year [= CV mean monthly temps].	MNTH.CV.$_t$
13)	CV of ppt. within the year [= CV mean monthly precipitation].	MNTH.CV.$_{ppt}$

* CV = coefficient of variation

representing the climate at its most northerly or southerly point. However, in many cases the information given for the limits of the species' ranges were not accurate and it was very difficult to determine the best point to represent the range limit. In addition there was a high correlation between the range centre and range latitude measures indicating that the results obtained would be similar for both sets of data. It was therefore decided to use only the one set of climatic data for each species.

Having chosen a weather station to represent each species a decision then had to be made as to which climatic variables were to be used. The data given in "World weather Records" has temperature records showing the average temperature per month throughout the year, and the mean temperature during the whole year. The precipitation records show the mean precipitation per month, and the total rainfall during each year.

Following the practice of Zeveloff and Boyce [1986], measures were chosen that described the "average" climate and the extremes of climate for each weather station [variables 1-6 in table 2.1]. In addition to needing measures of the average conditions found in each area some indication of climatic variability was also required. Measures of the variability of these parameters were calculated to give an indication of both the inter-year and intra-year variability of the area [variables 7-11 and 12 &13, respectively, in table 2.1]. As can be seen, the measure of variability used is *the coefficient of variation, rather than the standard* deviation. This was done to remove the effects of the mean temperature on the measure of variation. The measure of inter-year variation can be taken as measure of the predictability of the climate from one year to the next whereas the intra-year variability is a measure of the seasonality of the climate.

Although these measure of climate are, by no means, exhaustive they do measure the broad differences of climate found by species in different areas. They do not take into account the differences in habitat of the different species, which could mean that two species with the same geographical range could be experiencing different microclimates because of their different habitats or behaviours. However, until a method of measuring such microclimates becomes available this type of climatic data will have to be used.

Relationships between environmental variables

It was considered that there would be correlations between latitude, climate and habitat type and that these might effect correlations found between these parameters and the life-history variables. This was tested using correlation analyses and analyses of variance, methods that are described later in this chapter.

Latitude and climate

The two measures of latitudinal position are strongly positively correlated with each other at all taxonomic levels [$p<0.001$ in all cases]. This demonstrates that those species that have a range limit with a high latitude will similarly have the "centres" of their ranges further from the equator.

Both of the latitude variables used correlates with several of the climatic variables. As might be expected, from the high positive correlation between these two variables, the climatic variables that correlate with the species range limit correlate in the same way with the species range centre, in the majority of cases. Both latitudinal parameters have positive correlations with several of the measures of environmental variability [the coefficient of variation (CV) of rainfall in the driest month, CV of total annual rainfall, CV of monthly rainfall, CV of temperature in the coldest month, and CV of monthly temperature]. They have negative correlations with average rainfall in the driest month, total annual rainfall, temperature in the coldest month and mean annual temperature. The general picture that therefore emerges is that high latitudes are associated with low average temperatures, low average rainfalls and high variation in both rainfall and temperature.

Latitude and habitat type

To determine whether there were any differences between the latitudes of species found in the various habitat types an analysis of variance was carried out. This was done by treating each species as a separate data point and testing for differences between the means of each latitude parameters in each habitat. These tests gave virtually no significant results. In only three cases did any two pairs of habitat types have mean latitudes that were significantly different at the 10% level. These all involved "savannah and edge" species, which tend to have a latitude limit that is higher than either "primary forest" species, "general forest" species, or "forest and edge" species.

Climate and habitat type

As with latitude and habitat, an analysis of variance was used to find whether species in a particular habitat type are more likely to experience certain types of climate than others in different habitats. The relationship between habitat type and climate is more clear cut than that between latitude and climate. One clear result is that the species found in the savannah habitats are experiencing a different climate than are species in forest and in edge habitats. The majority of the significant differences in rainfall patterns between any pair of habitat types involve those species found either in "savannah and edge" or in "savannah only" habitats. Both "savannah and edge" and "savannah only" species tend to be in areas with a comparatively low average rainfall in the driest month and throughout the year, and a high variability in rainfall during the year.

"Savannah only" species are also found in areas where the variability in rainfall in the driest month is high as compared to that in all other habitats. In addition to these patterns there is also an indication that the "primary forest" species are found in habitats that have a high rainfall (both in the driest month and in total over the year) and a low variation in rainfall within the year. "General forest" species are also found to have a higher rainfall in the driest month and a lower variation in rainfall throughout the year than do "forest and edge" species.

Differences in temperature variables mainly involve "savannah only" species, which are found in colder and more variable inter-year temperature regimes than are other species. In addition, "forest and edge" species have a higher variation in temperature in the coldest month than do "primary forest" species. There is also some indication [$p<0.1$, generic level only] that "savannah only" species are found in a climate that is hotter in the warmest month than are "primary forest" species.

Conclusions regarding relationships between environmental variables

The results of these analyses are a mixture of the expected and the surprising. The clear relationship between latitude and climate was not at all unexpected. As mentioned above, the relationships found between the climate and the latitude of the weather station and those found between the climate and the estimated latitude of the species' centres are very similar, which is an indication that the climatic data used is representative of the climate that would be found by the species concerned. Furthermore, the relationships of climate to range limit are very similar, indicating that, despite there not being a direct link between these two measures [unlike that found between range centre and climate, where the climate data was deliberately chosen to be the best possible for that position], the close correlation between species range centre and species range limit means that there is no need to calculate a second set of climate data to give an estimation of the weather conditions at the species' range limit.

As predicted, high latitudes are correlated with lower rainfalls and lower temperatures than are areas nearer to the equator. The negative correlation between rainfall and latitude is due to the species concerned being virtually all in tropical and sub-tropical zones so that as one moves away from the equator one is moving from tropical areas with a high rainfall into areas of savannah and desert. If temperate zones were included the precipitation level would presumably start to rise again after the desert zones. The other correlation with latitude is a positive correlation between latitude and variability in both inter- and intra-year variation in temperature and rainfall, as was also be predicted.

Somewhat surprisingly, in the light of these relationships, there is no clear connection found between the latitude of the species and their habitat. Although there is some indication that savannah species are found at higher latitudes than are other species the results are only weakly significant and the expected correlations between a "primary forest" habitat and a low latitude are not found. The explanation for this is, presumably, the previously mentioned fact that habitats can vary considerably within a small geographical area. This can be for many reasons and means that two species found in the same area can in fact be experiencing quite different environments. In addition to this, animals select their own niche within a ecosystem so that even within the same ecosystem different species will have a different habitat type [and indeed Gausse's theorem predicts that no two species can inhabit the same niche]. For example, in South America the range of the marmoset and tamarin species overlaps with that of spider monkeys in many areas, however the former are mainly found in edge habitats whereas the latter are animals of primary forest [Wolfheim, 1983]. In this case one would expect that the latitudes these species are found in to be basically the same, despite their very different ecologies.

I suspect that the lack of an obvious link between the latitude and habitat variables is further obscured by the primates being found almost exclusively in tropical and sub-tropical areas, and nearly all in some kind of forest or woodland. The gross changes in habitat that would be found if one were looking at organisms that spanned wider latitudes would more probably be found to be linked to latitude, and indeed the one correlation that was obtained from the primate data involved the savannah species which are found in the most "extreme" environments and latitudes of any primate species [with the possible exception of the temperate zone macaques and langurs].

The link between habitat type and climate is an indication that, despite the lack of correlation with latitude the habitat types do have a discernible link with other geographical variables. However, for the narrow categories the majority of the significant differences involve differences between the "primary forest" and "savannah" habitats with the others being difficult to distinguish from each other in terms of climate. The same pattern is repeated in the broader habitat categories with the majority of differences being between the climates of the savannah species and those in the other two groups. It seems clear that savannah species are experiencing a climate that is significantly different from the other habitat groups. These differences are found at all taxonomic levels (i.e. when species climates are taken as independent points or when the data are averaged to genus or subfamily level) which indicates that this link is not simply due to to the propensity for some taxonomic groups to all be found in a similar habitat and climate.

The lack of correlation between the geographical position and the habitat of a species shows the importance of looking at both of these variables when investigating relationships with the environment. Although climate is, to some degree, linked to both latitude and habitat it is clear that no single measure adequately describes the environment of the primate species being investigated. In terms of selection for body size and life-history traits, a population that is in an area that has an apparently stable and predictable climate may well be experiencing unpredictable fluctuation in its resources for some other reason. For example it may be living predominantly in areas of secondary growth and thus its resources may be unpredictable spatially even if constant temporally.

Methods used

In the past order two basic lines of inquiry have been used to explain variation in life-histories. The ecological, comparative approach has been based on the comparison of different groups in different environments with the aim of discovering regular, and hence predictable, variation of life-history strategies with the environment. In addition to this comparative approach there have also been attempts to manipulate life-histories in the laboratory by artificial selection, thus hopefully isolating the forces that give rise to the selection of a certain trait. As discussed extensively by Stearns [1977] both of these approaches have their shortcomings and ideally should be used together to obtain a complete picture.

Because of the problems associated with the comparative method, hypotheses generated by comparing species should ideally be tested with artificial selection experiments under controlled conditions. However, although such tests have been carried out on species with short generation times, [for example, those of Barclay and Gregory (1981) on *Drosophila melanogaster* and Luckinbill, (1978, 1979) on bacteria and protozoa], they are of little use for the slower breeding, larger species, e.g. trees, larger birds and mammals. To a certain extent it may be possible to use available data on the selective breeding of domestic plants and animals to find patterns that support or refute theories generated from the study of wild populations. For most mammal species, though, it would be impossible to rigorously test theories in the laboratory without an enormous allocation of space and time. For this reason this work is based entirely on the comparative method and I will therefore discuss its problems at some length.

The comparative method

The comparative method is usually undertaken in the following way. Firstly data on the characteristics of a number of species [or populations of the same species] are compiled together with information on the environments of the different groups. The data is then examined in order to see if there is any correlation between the variables under investigation and the environment. If any such correlation is discovered an attempt is made to explain the variation as being due to the results of natural selection. For example, the observation that mammals with prehensile hands and feet tend to forage in the terminal branches of trees and bushes led Cartmill [1972] to suggest that grasping hands and feet evolved in primates as a result of their being selected for this type of foraging ability. Comparing species is this manner is most usefully done when they are closely related, as such species will be likely to differ in fewer parameters, thus facilitating comparison of those traits which do differ.

One problem with this type of approach is that it assumes that a species is adapted to the environment in which it now found. If a species has only entered a particular habitat recently in evolutionary terms it is very probable that it may have characteristics that have been selected for a different habitat and the linking of those characters to the new environment will give rise to spurious conclusions. A good knowledge of the evolutionary history of the species concerned is the only way of avoiding this problem.

Another problem with the use of the comparative method is that it is assumed that a correlation between phenotype and environment is indicative of a causal relationship i.e. that a certain type of environment gives rise to a particular trait. However, the presence of a correlation cannot be taken to imply causality and it should be realised that there may be other reasons that can explain the linkage of two variables. In the case of a connection between environment and phenotype there may be several other reasons why a connection would be observed.

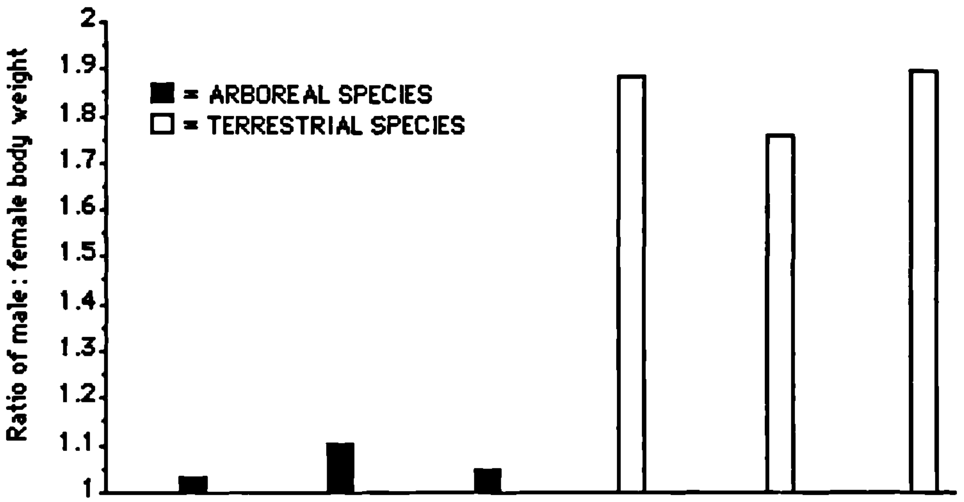
For example, if one was looking at the prevalence of sexual dimorphism in primates it could be proposed that there might be some relationship between this character and the degree of arboreality found. For the sake of illustration let us assume that data is available for only six species, three are members of the gibbon group and three are baboon species. As can be seen in figure 2.2, such a data set indicates that arboreal species have a low degree of sexual dimorphism whereas terrestrial species have a high a degree of sexual dimorphism.

One might therefore conclude that arboreality selects for a low sexual dimorphism [say, because the arboreal environment lends itself less readily to visual displays of size that have led to the sexual selection of large males by females in more terrestrial species]. However, when one realizes that, of the species examined, all of the gibbon species are arboreal whereas all baboon species are terrestrial it becomes clear that the link between these two characters may have other explanations.

Assuming that these traits are linked does not take in to account the possibility that gibbons may all be descended from an arboreal, monomorphic ancestor and do not have sufficient variation in whatever genes determine arboreality and sexual dimorphism to become arboreal and dimorphic [or terrestrial and monomorphic], with the converse situation possibly occurring in baboons. If this is the case the apparent link between the traits could, in fact, be

Figure 2.2

Histogram of sexual dimorphism for six primate species, showing arboreality



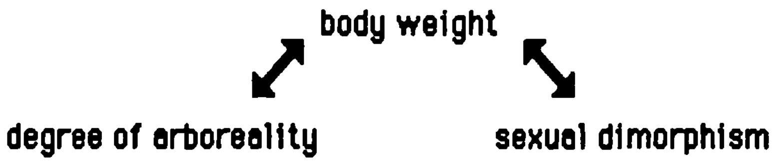
Species

due to a taxonomic relationship rather than any adaptive reason. [Although it is still possible that the links between habitat and sexual dimorphism may have had an adaptive explanation in the ancestors of the two groups.]

A second problem with the assumption of causation from correlation is that two traits may be linked via a third trait. To again use the example of a links between arboreality and sexual dimorphism figure 2.2 may seem to indicate that in the primates as a whole arboreality leads to a low degree of sexual dimorphism. However, both terrestriality and a high level of sexual dimorphism are linked to a high body size in primates [Clutton-Brock and Harvey, 1977a] and the link between habitat and sexual dimorphism could be due to both traits being independently effected by body size. i.e. the relationship is not:

degree of arboreality ⟷ sexual dimorphism

<u>but:</u>



To some extent the confusion caused by the action of intervening variables can be unravelled by the use of statistical methods such as allometric analysis and partial correlations discussed later in this chapter. However, these methods rely on one being able to identify the parameters that are effecting the variables under scrutiny and then remove their effects and this is not always possible.

The following describes the statistical techniques used to identify the relationships between the life-history variables and between the life-history variables and the ecological parameters.

Statistical methods

Correlation analysis

Correlation analysis is a way of measuring the degree of association between two variables. The measure of correlation is the <u>correlation coefficient</u>. To calculate a correlation coefficient the data should have a bivariate normal distribution, so that if variable (x) is plotted against variable (y) the data points will form an ellipse with the highest density of points in the centre. This type of distribution is obtained when the two data sets being compared have a normal distribution, a condition that is met by the log-transformed life-history data used in this study.

The correlation coefficient (r) varies from 1, a perfect positive correlation, so that an increase in x is totally predictable from an increase in y, and *vice versa*, to -1 where there is a perfect negative correlation so that an increase in x is totally predictable from an decrease in y. If there is no correlation at all between the two variables, i.e. so that x is cannot be predicted y or *vice versa*, r is equal to 0. The value r^2 is a measure of the proportion of x accounted for by y or *vice versa*. E.g. if the correlation coefficient between x and y is 0.80 then $r^2=0.64$, so that 64% of the variation in x can be accounted for by the variation y and 64% of the variation in y can be accounted for by the variation x. The significance of r is dependent on the sample size, with smaller sample sizes requiring larger values to be significant.

It should be stressed here that a significant correlation can only be said to indicate that two parameters are <u>associated</u> and cannot be used to establish whether variation in one parameter is the <u>cause</u> of variation in another.

Partial correlations

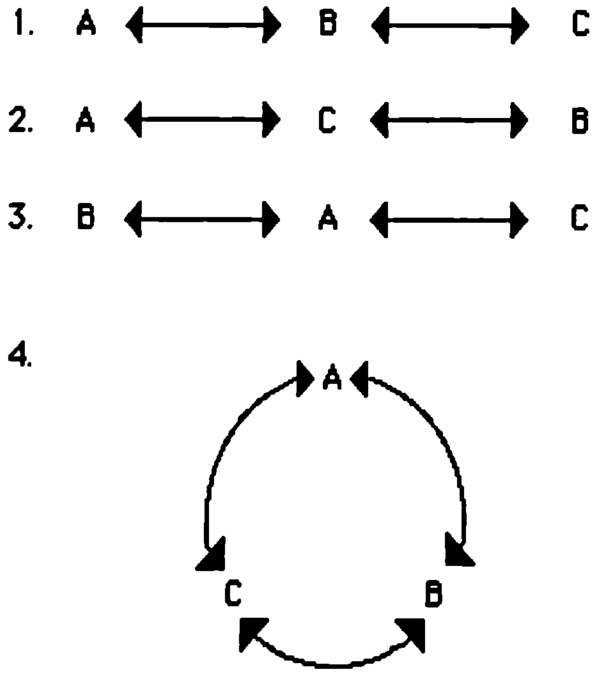
A partial correlation analysis is used to measure the correlation between two variables when one, or more, other variable[s] have been held constant. This is the kind of analysis that is needed when faced with the type of problem discussed above, that of determining whether there is a direct link between arboreality and sexual dimorphism. The use of this technique is best explained by means of a simple, hypothetical example. The following correlation matrix was obtained for a dummy set of data representing data on three variables; A, B, and C. for 20 "species":

	A	B	C
A	-		
B	0.85	-	
C	0.97	0.78	-

This table shows that all three variables are highly correlated with the other two but this knowledge does not explain the way in which the variables are inter-acting. Any of the four links shown in diagram 2.1 could account for the results. By using partial correlations one can distinguish between these different scenarios. Three possible partial correlations are possible; A correlated with B holding C constant [$r_{AB.C}$], A correlated with C holding B constant [$r_{AC.B}$],

Diagram 2.1

Possible interpretations of a correlation matrix
[see text for explanation]



and B correlated with C holding A constant [$r_{BC.A}$]. These partial correlation coefficients can be calculated, using a simple formula, from the correlation coefficients of A & B, A & C and B & C.

If the results showed that $r_{AB.C}$ and $r_{AC.B}$ were significant positive correlations but that $r_{BC.A}$ was insignificant then scenario [3] above is supported. i.e. the results suggest that the reason for a correlation between B and C is due to B and C being independently correlated correlated with A. Similarly, the removal of the effects of B from the correlation between A and C would give an insignificant correlation if scenario [1] was correct, and the removal of the effects of C from the correlation between A and B would give an insignificant correlation if scenario [2] was correct.

The situation in [4] is more complex. In this case one would expect that all three partial correlations would show a decrease when compared to their equivalent full correlations, but that some correlation would still remain. For example, the removal of C from the correlation between A and B would remove the correlation in the later parameters that is due to their both being correlated with C and thus lower the correlation. However some correlation would remain between A and B because they are also acting directly on each other.

For example, using the figures in the correlation matrix above the following partial correlation coefficients can be calculated:

$r_{AB.C} = 0.61$; $r_{AC.B} = 0.93$ and $r_{BC.A} = -0.35$.

The first two of these are significant positive correlations but the last figure is not significant, indicating that parameter A is linked to both B and C but that B and C are not directly linked, i.e. that scenario (3) above best explains the data.

Calculation of the allometric equation

The use of correlation and partial correlations can reveal the quality of relationships between parameters, i.e. whether the parameters are linked and whether their association is a such that as one increases the other decreases, or if an increase in one is associated with an increase in the other. Correlation analyses can also indicate the strength of a relationship, i.e. the value of the correlation coefficient indicates the percentage of X that can be predicted by Y, and *vice versa*. However, correlation analyses do not show the form of the relationship, i.e. if one knows the value of one parameter one cannot predict the value of the other by knowing the correlation coefficient. To find these details one can use the techniques of scaling or allometric analyses.

The importance of scaling effects has already been discussed in Chapter 1, where examples of life-history parameters that have been found to scale to body weight were given. Here I will discuss the different methods of allometric analysis that are commonly used and their possible applications to this work. As the allometry in this work is confined to the study of the scaling of parameters to body weight the discussion will be limited to a discussion of scaling as it relates to body weight.

In the case of some parameters there is an isometric relationship with body size, so that an increase in body size [M] by [say] 30% will correspond with an increase in the parameter [P] of 30%. i.e..

$$P = kM, \text{ where } k \text{ is a constant.}$$

In cases where isometry is found the ratio of the parameter to body size is, therefore, the same for all organisms of all body sizes. However, the more general situation is that the parameter will vary in an allometric fashion with body size, so that the equation relating the parameter [P] to body size [M] is of the form:

$$P = aM^b, \text{ where a and b are constants.}$$

If this formula is expressed logarithmically it describes a straight line, i.e.:

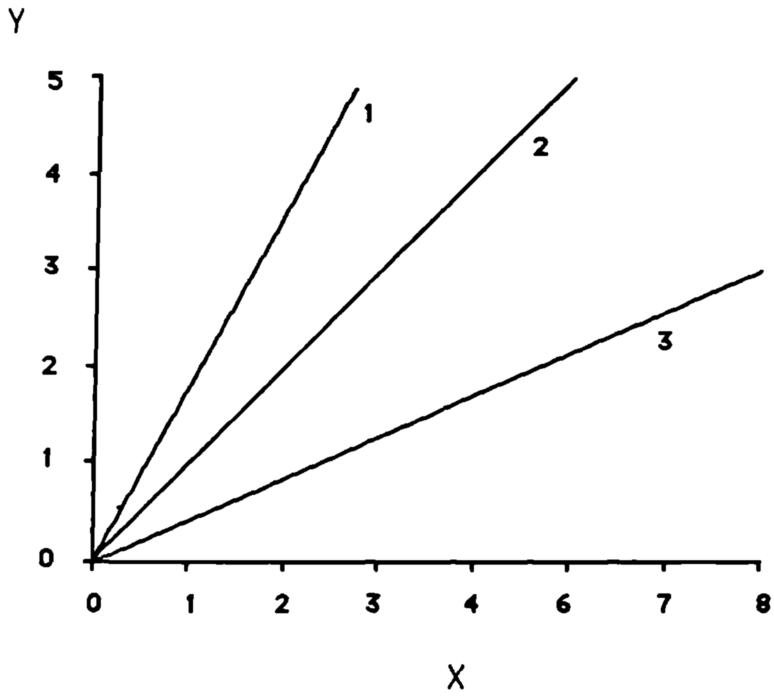
$$\log_{10}P = b(\log_{10}M) + c, \text{ where } c = \log_{10} a.$$

When this is shown as a graph of $\log_{10}P$ against $\log_{10}M$ one obtains a straight line with a slope of b that intercepts the Y axis at c. Figure 2.3 shows relationships of this type. Line (2) of this diagram shows an isometric relationship i.e. as body weight increases the parameter increases in direct proportion to it. Line (1) is an example of positive allometry, a slope that is steeper than that for an isometric relationship [i.e. when $b>1$], this means that the value of the parameter changes at a faster rate than does the body size. In the last line (line 3) the slope value is less than 1, this is negative allometry, this means that the value of the parameter changes at a slower rate than does the body size. A similar diagram could be drawn for for examples of inverse allometry, where the correlation between X and Y is negative, i.e. the slopes have negative values.

If the relationship between a parameter and body size was perfect the form of the allometric equation would be discovered simply by drawing a straight line through the points and thus measuring the values of b and c. However, in the real world perfect relationships are hard to find and one must therefore make an estimate of the the position of the line. The following description of the statistical methods available to do this is taken from Sokal and Rolf [1981] and from Harvey and Mace [1982].

Figure 2.3

Examples of isometry, positive allometry and negative allometry for parameter (Y) versus *parameter (X)*



There are three line-fitting methods that are frequently used, these are regression analysis, reduced major axis analysis and major axis analysis. Which method one uses depends on the type of data that is being analysed, as the different methods have different underlying assumptions. One assumption that all three methods share is that the data is normally distributed. This means that in some cases data must be transformed so that it more nearly approximates to a normal distribution. For the type of data used in this study [i.e. body weight and life-history data] the data needs to be logarithmically transformed to bring it closer to a normal distribution.

Intuitively, one can say that the main aim in fitting a best-fit line to data is to draw a line through a number of points so that the mean deviation of the points from the line is minimized. However, when one wants to calculate the precise position of the best-fit line a decision must be made as to which measure of deviation from the line should be minimized. It is this measure that varies in the three line-fitting techniques discussed here, this is illustrated in figure 2.4.

Regression analysis assumes that the values on the X axis have been measured without error and that those on the the Y axis are dependent on the X axis values [i.e. any that correlation between X and Y values is due to the variation of Y with X, and not caused by a third confounding variable]. As the X values are presumed to be correct the value that must be minimized is the distance of the point from the line perpendicular to the X axis, i.e. distances A-B and A*-B* in figure 2.4. To calculate the position of the line the sum of the squared distances of the points from the line is therefore minimized.

Neither reduced major axis analysis [RMA] or major axis analysis [MA] assume that the points are without error along the X axis, but instead assume that the error is equal along both axes. The two methods therefore minimize different values than does regression. RMA minimizes the sums of the areas of the triangles. As illustrated in figure 2.4 the triangles [ABC and A*B*C*] are made up of sides from the best-fit line and the lines that can be drawn from the best-fit line to the data points parallel to the X and Y axes.

Like regression MA minimizes the distances of the points from the line but, it does so perpendicular to the best-fit line rather than perpendicular to the X axis, distances BD and B*D* in figure 2.4. As Harvey and Mace [1982] note:

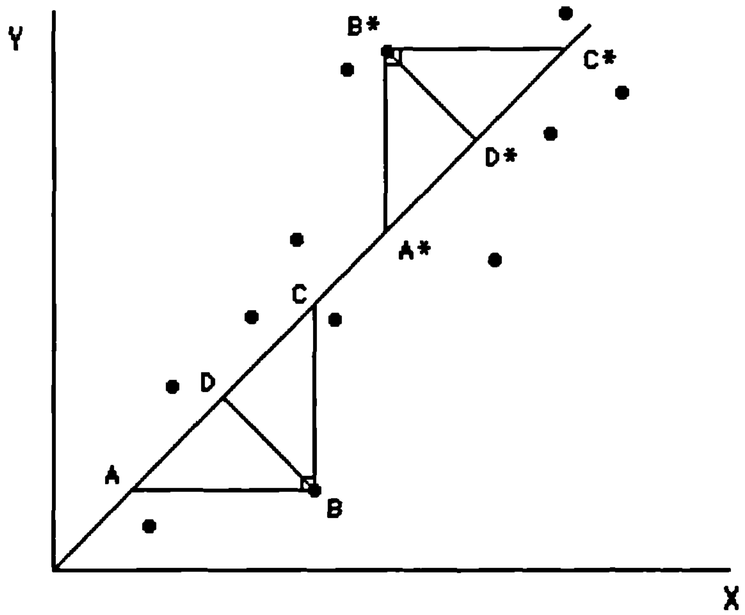
> "This line of best fit, therefore, is that which has the maximum variance of points about itself and consequently accounts for the maximum amount of variance in the data."

The choice of which method to use is also discussed by Harvey and Mace using dummy data sets with "error" deliberately introduced into either the X axis and/or the Y axis. They demonstrate that regression will give the slope nearest to the correct slope only when the co-ordinates for the X axis are measured without error. When the variance is equal for both the

Figure 2.4

Diagram to demonstrate calculation of best-fit lines

[drawn from figure 16.1 in Harvey and Mace, 1982]



See text for explanation

ordinate and the abscissa co-ordinates regression does not give the best slope value, and RMA and MA should therefore be preferred.

One problem that may arise with MA is that the slopes that it gives are altered by changing the scale of the data. For example, if the data set is multiplied by 10 for the Y co-ordinates the slope value for both regression and RMA is also increased by a factor of 10. However, that for MA does not increase in such a regular fashion. This may preclude the use of MA in some analyses, however, when the data is logarithmically transformed these problems of scaling no longer apply and MA can be used without fear of confusion.

For the type of life-history data that is being looked at in this study assumptions can rarely be made that any parameter is measured without error. For this reason regression analysis is not appropriate and either RMA or MA must be used. In cases where the correlation coefficient is high these two methods will give similar results and the choice of which to use will only matter if the data is not logarithmically transformed. As the data in this study is logarithmically transformed the use of MA does not pose a problem and it is this method that is used throughout this study. MA is used in preference to RMA mainly because it allows comparison with the more of the previous studies on this topic [e.g. Martin and MacLarnon, 1985; Wootton, 1987]. MA also allows the use of the test for heterogeneity of slope given in Harvey and Mace [1985] and, although this test is not employed in this study the use of MA statistics will enable others to use this test on these results.

Residual variation

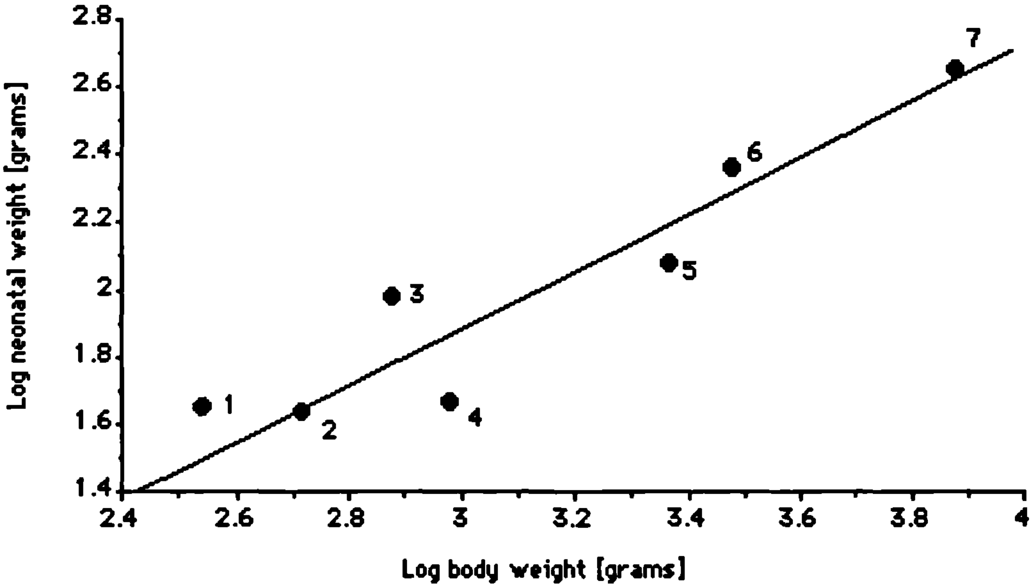
The calculation of the best fit line determines the basic form of the relationship between the parameter and body weight. Unless the correlation between the two parameters is perfect there will be a certain degree of scatter about the best fit line. For some species the degree of deviation from the best fit line will be negligible and these species can therefore be thought of as being "normal", in that they have the expected relationship between body weight and the parameter in question. Other species, however, will be found to deviate further from the best fit line. For example, figure 2.5 shows a plot of log neonatal weight against log body weight for a small sample of primate species. Species 2 and 7 can be seen to have an an neonatal weight that is as would be expected for primates of their size, but species 1, 3 and 6 both have a higher neonatal weight than is expected and species 4 and 5 have a lower neonatal weight than is expected.

As discussed in Chapter 1, it has been suggested that the deviation from the line of best fit can be taken as an indication that the species concerned has been selected to have an unusual relationship between the parameter in question and body weight, this deviation possibly being due to a specific adaptation or alternatively because of error in measuring the parameter or the body weight of the species in question. If one wishes to compare species a measure of the degree

Figure 2.5

Diagram to demonstrate measurement of residuals

[Diagram shows log neonatal weight vs. log body weight for seven primate species, with major-axis best-fit line calculated in Chapter 4 for larger sample]



of deviation from the expected relationship is needed. In this study the measure of deviation used is the logarithmic distance from the major axis best-fit line to the data point measured parallel to the Y axis. This distance represents a measure of the difference between the observed and expected values of the parameter given a certain body weight. On logarithmic plots, such as will be used in this study, these distances will be logarithmic values. Although the distances could have been measured by taking the anti-logs of these distances, logarithmic values were preferred to the anti-logged figures because they give the same weight to positive and negative deviations from the line.

These measures of deviation are used throughout this thesis and are referred to as the residual values or simply residuals. It should be noted that the correlation coefficient of two sets of residual values, produced from the scaling of A and B to body weight, is essentially the same as carrying out a partial correlation of A and B removing the effects of body weight, and these two procedures therefore produce almost identical results.

The problem of grades

The idea of grades of organization was introduced in Chapter 1. The example given in figure 1.1 shows a log-log plot of a parameter versus body weight for two groups of animals. In this case, there is a fairly clear cut distinction between the two groups of animals but in other situations the distinction between two groups may be less clear cut. In some cases there are other good reasons for treating the data as two sets, even if it is not clear if grade differences exist. For example, if one wanted to carry out correlations between the residuals of two scaling analyses and one showed a clear grade difference whereas the other did not it would be advisable to treat the data of both parameters as being made up of two subsets. Problems arise when there is a possibility of a grade effect operating but when the evidence is not clear and there is no other reason for wishing to treat the data as two sets. In such situations a test for a difference between the lines is needed.

As previously explained, differences in allometric relation- ships may be reflected by differences in the slope of the line, or in its elevation. If the former is occurring the difference may be detected by comparing the confidence limits of the lines' slopes to see if they overlap. If the confidence limits are overlapping one can treat the slopes of the lines as equivalent, if not it is likely that they should be treated as having separate slopes. If two lines are found to have the same slope it is still possible that their elevations may be different, and it is this type of difference that seems to occur most frequently in biological systems. The procedure used here to test for different elevations of line in two groups is as follows:

1) The complete data set is split into the two groups - A and B.

2) Group A is taken separately and the slope of its major axis line [b_A] is calculated. Similarly

the slope b_B of group B if found.

3) If the slopes are not found to be different a common slope $b_{AV.}$ is calculated from: [b_A + b_B]/2.

4) Using $b_{AV.}$ a single line is drawn through the whole data set [i.e. a line that passes through the the means of X and Y of the total data] and residuals are calculated from this line.

5) An analysis of variance is then used to test for any differences in the values for the residuals of group A and group B.

6) If there is no difference between the two groups the data set is treated as a single group, if there is a significant difference the data set is treated as two separate groups.

Choice of taxonomic level

One problem with determining the relationships between parameters is that of deciding which taxonomic level the analysis should be carried out at. Most previous studies have taken average values for individual species as the points from which to calculate best-fit lines [e.g. Hennemann, 1983; Wootton, 1987; Martin and MacLarnon, 1985]. However, it has been pointed out that closely related species may resemble each other because of their recent common ancestry, and hence cannot be thought of as independent [Harvey and Mace, 1985]. It may therefore be preferable to use an average value for a genus, or higher taxonomic group, for analysis.

The decision of which taxonomic group to use depends on several factors, not least the type of information one is interested in. To average data to [say] the family level may mean that much of the variation in parameters is lost, and/or that the sample size is reduced so far as to make the analysis worthless. Alternatively, using the species as the unit of analysis may mean that one genus with a large number of species will dominate the sample, causing the results to be biased towards reflecting the characteristics of that genus rather than the whole sample. A compromise must therefore be reached between the taxonomic level that allows one to remove a large element of bias due to the influence of any one group of species, and that level which gives a useful amount of information.

In their 1985 paper, Harvey and Clutton-Brock argue that the correct level of analysis for primates is that of the subfamily. This is based on a nested analysis of variance [nested ANOVA] conducted on the logarithmic values of life-history data, where it was found that an average of about 85% of the variance of the tested parameters could be accounted for at the subfamily level or above. A similar pattern was found when the same analysis was carried out on the data in this study, with about 80% of the variance of the tested parameters being at the subfamily level or above [table 2.2]. However, the high correlation between body weight and life-history parameters means that any variation in the former will be reflected in the variation of the latter. To examine variance in life-history parameters without the interference of the effects of body weight requires that the variance of the residuals rather than of the raw data are examined.

Because of the potential problem of taxonomic bias, the residuals were calculated using the best-fit lines from species values, average genus values, average subfamily values and average family values. It was found that these residuals were all very highly correlated with each other [average r= 0.98]. The results given here from the nested analysis of variance are from the species best-fit line [table 2.3], but the results found using the residuals calculated from either the generic, or the subfamily best-fit line were essentially the same [average difference between any two equivalent figures = 0.67%, maximum difference less than 3%].

The analysis of the residuals shows that a large amount of the residual variation occurs at the generic and species levels [table 2.3]. This means that by taking average subfamily levels over 60% of the variance is lost on average, and even using the average genus values over 35% of the variation is ignored. These results support Harvey and Clutton-Brock's use of average subfamily levels when looking at the relationships between the parameters and body weight, i.e. when using the original data. For this reason the bivariate analyses were carried out firstly on the species values, then on the average genus values and then on the subfamily values. The average genus values were calculated by taking the average of the logged species data for each genus. When average genus body weight were calculated the average used included only those species for which data on the second parameter was available. Similarly, average subfamily values were calculated from the logged average genus data.

To facilitate comparison with other studies on similar topics some of which have examined individual species [e.g. Western, 1979; Hennemann, 1983; 1984], some average genus values [e.g. Clutton-Brock and Harvey, 1977a] and some average subfamily values [e.g. Harvey and Clutton-Brock, 1985] the results of the bivariate analyses have been given for all three taxonomic levels. The results of the ANOVA on the residuals indicate that a considerable amount of variance in the residual values is found below the subfamily level. Although some of this variance may be due to error it is also possible that some is due to the adaptations of species to particular environments. It was therefore decided that the analyses of the variation of the residuals should be carried out at the species level so as to increase the percentage of residual variance examined. As with the bivariate analyses the examinations were also carried out using the genus and subfamily data, this was done in order to check for the possibility of taxonomic bias effecting the results.

Table 2.2

Results of the nested analysis of variance for logarmithic values of life-history parameters[1]

Variable	% variation among:					
	Families	Subfamilies		Genera		Species
Average adult body weight	74.3	11.6	[85.9]	9.1	[95.0]	5.0
Female weight	69.2	18.7	[87.9]	7.1	[95.0]	5.0
Neonatal weight	81.2	10.8	[92.0]	4.3	[96.3]	3.7
Litter weight	81.9	7.5	[89.4]	5.4	[94.8]	5.2
Gestation length	26.1	64.7	[90.8]	3.7	[94.5]	5.5
Interbirth interval	68.9	5.1	[74.0]	1.2	[75.2]	24.8
Birth rate	76.1	6.4	[82.5]	2.4	[84.9]	15.1
Age 1st reproduction	78.3	12.5	[90.8]	0.7	[91.5]	8.5
Age reaching adult wt.	78.7	9.6	[88.3]	4.7	[93.0]	6.9
Longevity	37.9	20.4	[58.3]	27.2	[85.5]	14.5
Foetal growth rate	83.6	0.9	[84.5]	6.9	[91.4]	8.6
Postnatal growth rate	26.5	25.1	[51.6]	26.5	[78.1]	21.9
Litter postnatal growth rate	34.4	0.0	[34.4]	34.8	[69.2]	30.8
Growth rate to adult wt.	26.0	33.4	[59.4]	26.8	[86.2]	13.8
r_{max}	79.8	9.4	[89.2]	2.3	[91.5]	8.5
Basal metabolic rate	82.0	6.6	[88.6]	0.0	[88.6]	11.6
Weaning age	61.7	24.8	[86.5]	8.0	[94.5]	5.5
Young per litter	55.8	32.7	[88.5]	5.2	[93.7]	6.3
Average	**63.3**	**16.7**	**[79.0]**	**9.8**	**[88.8]**	**11.2**
Average for all parameters except body weight	61.2	16.9	[78.1]	10.0	[88.1]	11.9

[1] Figures in brackets represent the total amount of variance accounted for up to, and including, the taxonomic level concerned.

Table 2.3

Results of the nested analysis of variance for residual values of life-history parameters[1]

[i.e. once body size affects have been removed]

Variable	% variation among:			
	Families	Subfamilies	Genera	Species
Neonatal weight	53.9	3.7 [57.6]	16.4 [74.0]	26.0
Litter weight	42.3	23.1 [65.4]	14.8 [80.2]	19.8
Gestation length	36.0	42.3 [78.3]	14.4 [92.7]	7.3
Interbirth interval	24.2	1.3 [25.5]	0.0 [25.5]	74.5
Birth rate	32.4	0.0 [32.4]	2.9 [35.3]	64.7
Age 1st. reproduction	18.2	0.0 [18.2]	42.2 [60.4]	39.6
Age reaching adult wt.	0.0	0.0 [0.0]	50.3 [50.3]	49.7
Longevity	0.0	29.0 [29.0]	39.2 [68.2]	31.7
Foetal growth rate	0.0	65.6 [65.6]	19.5 [85.1]	14.9
Postnatal growth rate	8.9	23.1 [32.0]	31.1 [63.1]	36.9
Litter postnatal growth rate	29.9	0.0 [29.9]	35.2 [65.1]	34.9
Growth rate to adult wt.	0.0	3.9 [3.9]	39.7 [43.6]	56.4
r_{max}	17.0	0.0 [17.0]	23.0 [40.0]	60.0
Basal metabolic rate	0.0	72.2 [72.2]	4.0 [76.2]	23.8
Weaning age	7.4	4.9 [12.3]	51.2 [63.5]	36.5
Average	**18.0**	**17.9 [35.9]**	**25.6 [61.5]**	**38.5**

[1] Figures in brackets as for table 2.2 (p 92)

Computing: hardware and software

The processing of data was carried out on two computer systems, in London I used the University College mainframe "GEC" computer for all analyses and in Zürich I used an "Apple Macintosh" microcomputer. On both systems a variety of programs and packages were available, these are briefly listed here.

University College London

Much of the analysis was carried out using a statistical package called "Minitab". I used this package in two ways; firstly, by carrying out simple direct manipulations on the data and, secondly, by running programs written for "Minitab" by Fred Brett, Ann MacLarnon and myself. Further analyses were carried out using several Fortran programs written by Fred Brett, Ann MacLarnon and myself. In addition, the nested analysis of variance was done using a Basic program written by Paul H. Harvey.

Zürich University

Analyses using the "Macintosh" microcomputer were done using the statistics package "Statview 512" and with Basic programs written by myself.

Summary

This chapter describes the data and method used throughout this thesis. The life-history parameters are listed and defined, this includes discussion of the differences expected between data from wild and captive animals. The environmental and ecological parameters are also listed and described and correlations between some of them are mentioned.

The statistical methods used are described in some detail and there is a discussion on the comparative method and some problems associated with its use. Allometric techniques are described and some problems with their use are dealt with. It is found that although the majority of variation in most life-history parameters can be accounted for by using mean subfamily values, much of the variation of the relative values of life-history parameters [i.e. variation that is left after body weight effects are accounted for] is lost if mean genus or subfamily values are used. The chapter concludes with a brief description of the computer facilities used.

Chapter 3

Body weight & metabolic rate

Both body weight and metabolic rate have been widely suggested to either cause, or at least constrain the evolution of, other physiological and life-history characteristics of animals. It was therefore decided that the variation in these two characters should be examined before the variation in life-histories was looked at. The importance of the effects of body weight on an animal's physiology and ecology, and its high correlation with several life-history parameters, were mentioned in the introductory chapter. The metabolic rate of animals has also been suggested to be linked to several aspects of ecology and life-history [e.g. see Calder, 1984] and this parameter is therefore investigated along with body weight.

This chapter starts with a discussion of the correlates of body size and environmental variables in the primate group. There then follows the analyses of basal metabolic rate. As noted by Kleiber [1961], and many subsequent workers [e.g. Stahl, 1967], basal metabolic rate [BMR] is highly correlated with body size in a wide range of organisms. The relation of BMR to body size in primates is therefore discussed here before looking at the variation of BMR with other factors.

Body weight

As discussed in the previous chapters, an animal's size is one of its most important characteristics. A number of ecological variables have been shown to be associated with body weight in mammals, those discussed here are diet, habitat, latitude and climate. Each species was assigned a diet and habitat category, one of four categories for diet and one of five categories for habitat, these are shown in Appendix V. Habitat was also divided into three broader categories, as described in Chapter 2. In addition, more detailed data on the proportions of different food types in the diet were also used, these data are also listed in Appendix V. The data for latitude and climate were collected on the basis of each species' geographical range. Details on all of these data, how they were collected and possible problems associated with their use can be found in Chapter 2.

The question of taxonomic bias, raised in Chapter 2, is considered to be particularly relevant to these analyses as the ecological variables being discussed frequently show a close correlation with taxonomy. For example, all species of Cercopithecinae [except *Theropithecus* *gelada* are mainly frugivorous, whereas the colobine monkeys are basically folivorous. As the nested analysis of variance for body weight and taxonomy shows that the majority of variation in body weight is accounted for at the subfamily level [Harvey and Clutton-Brock 1985, this study Chapter 2] the average subfamily values were used for the following analyses, although all analyses were also carried out at the genus and species levels. Following the method of Clutton-Brock and Harvey [1977a], species that are in the same taxonomic group but in different ecological categories are placed in separate groups for averaging. For example, when calculating the average body weight of the subfamily Lemurinae which has both folivorous and frugivorous species, there will be two figures used, an average body weight for the folivorous Lemurinae and an average body weight for the frugivorous Lemurinae. A nested analysis of variance showed that the majority of the variance in the climate data was at the species level [an average of 85%] and correlations with these parameters were therefore carried out only with species data.

Activity period

Clutton-Brock and Harvey [1977a] investigated the correlations between ecology and body weight for a large sample of primate species [100 species are represented in total, but this number was usually considerably reduced when data were needed for more than one variable]. The analysis was carried out using average genus values, with only those species that fell in the same ecological category being averaged together. Classifying each species' activity patterns as nocturnal or diurnal they found that "all nocturnal species are small". They suggest that the linking of nocturnal activity to small body size is associated with the strata of forest occupied by these species [middle and lower] and their reliance on crypsis, rather than flight or defense, to avoid predators. The results of this study agree with those of Clutton-Brock and Harvey [1977a] and no further comment is required here.

It is perhaps worth noting that the combination of small size, the occupation of low-level strata and the use of crypsis is also found in the marmosets and tamarins, which are diurnal. This is one of the several interesting features of this group that will be discussed later in this work.

Degree of terrestriality

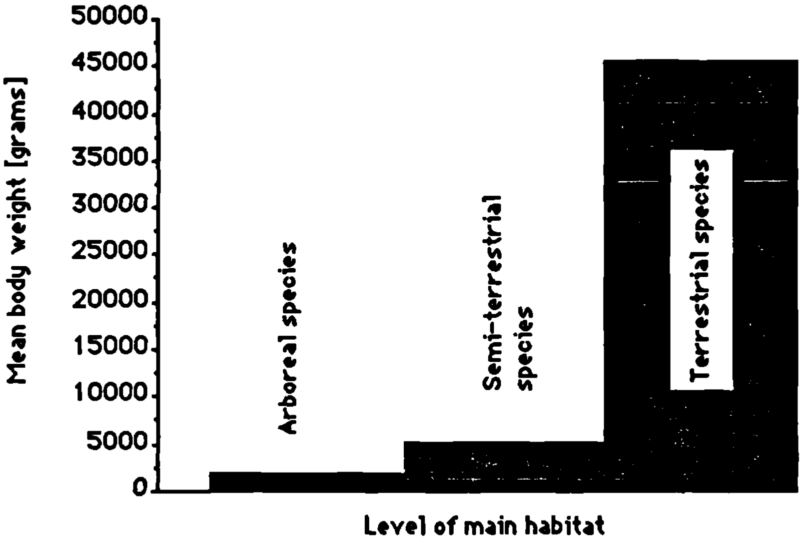
In the study discussed above, Clutton-Brock and Harvey [1977a] also look at the differences between the body weight of species that are mainly arboreal or mainly terrestrial. Their results can be briefly summarized by the following statement: "Among diurnal primates, there is a tendency for terrestrial species to be heavier than arboreal ones..".

A similar analysis by Pitchford [1986] showed that, if a third category of semi-terrestrial

Figure 3.1

Mean body weights for arboreal, semi-terrestrial and terrestrial primate species

[calculated using mean logged subfamily values]



species was used these species were found to be intermediate in size between strictly arboreal and strictly terrestrial species. This study has virtually identical data to that used by Pitchford, although additional data was used, and the results found are in complete agreement with hers [see figure 3.1]. The analysis of variance showed that the differences between arboreal and terrestrial species were significant [$p<0.05$] whether species, genus or subfamily values were used. For genera within subfamilies and for species within genera the same pattern was observed. As noted by Clutton-Brock and Harvey [1977a] there are some exceptions to this rule, with the ring-tailed lemur, *Lemur catta*, being about the same size as the more arboreal lemur species, the strictly arboreal grey-cheeked mangabey *Cercocebus albigena* being no smaller than the species of mangabey that come down to the ground more often and the arboreal orangutan, *Pongo pygmaeus*, being larger than the more terrestrial great apes.

The large size of terrestrial species is considered by Clutton-Brock and Harvey [1977a] to be related to the removal of constraints on body size imposed by the arboreal environment. As very large species cannot reach the terminal branches of trees, arboreal species are selected to be small. They also suggest that because many terrestrial species live in savannah they may be subject to increased predation pressure, which could select for larger body size.

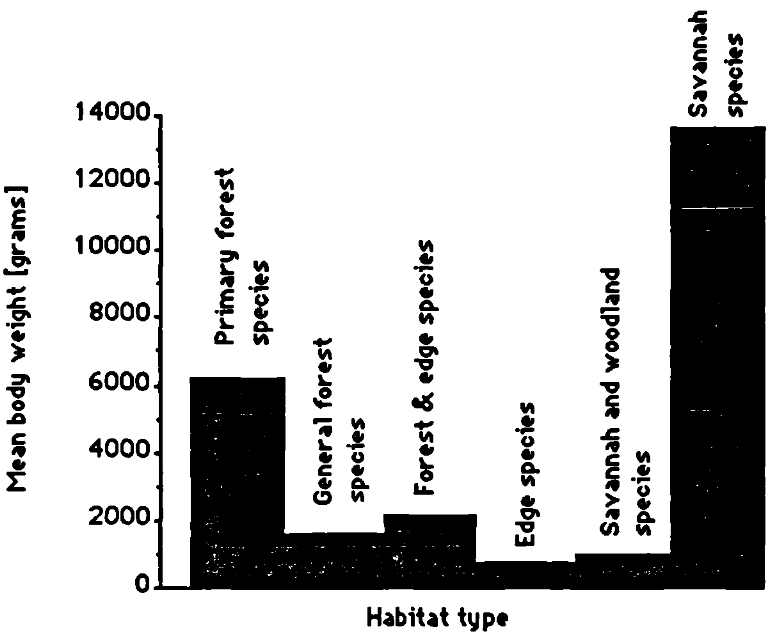
Another possible explanation for the size difference is that terrestrial species tend to be found in areas where environmental conditions are harsher and more unpredictable than for arboreal species, e.g savannah and mountainous areas. It has been suggested by Lindstedt and Boyce [1985] that such conditions may select for a large body size as larger animals are better buffered against environmental fluctuations than are smaller ones, and a large size allows for fasting in periods of food shortage.

One indication that the reason for the differences in size of terrestrial and arboreal primates is not due to the effect of habitat differences is found when one compares species found in the same habitats. The species were split into the habitat categories described in Chapter 2 and body sizes of terrestrial, semi-terrestrial and arboreal species were compared for species within each habitat where species differed in their degree of terrestriality. The results were the same as those found for the whole data set, i.e. terrestrial species are larger than semi-terrestrial species and arboreal species are the smallest, <u>even for species within a certain habitat.</u> This was found at the species, genus and subfamily levels and for both the narrow and broad habitat categories.

Habitat

Figure 3.2 shows the variation in mean body size with habitat. The data shown are for average subfamily values, but a similar pattern is seen at lower taxonomic levels. Although

Figure 3.2
Mean body weight for primate species in different habitats
[calculated using mean logged subfamily values]



these data clearly indicate that species found in forest areas and in savannah tend to be larger than those in edge habitats there is no significant difference between the groups when an analysis of variance test is carried out at the subfamily level [although some significant differences are found at lower taxonomic levels].

It was considered that a part of the reason for the differences in body weight between the habitats not being significant could be due to the strong effect of the degree of terrestriality on body size. The data were therefore split into two groups, arboreal species in group 1 and semi-terrestrial species and terrestrial species in group 2. The differences between habitat categories were then tested within these two groups, using data averaged to the subfamily level. An analysis of variance found that, within group 1, arboreal primates found in primary forest were larger than those in all other types of forest and woodland. Within group 2 it was found that the woodland and savannah primates were significantly smaller than the forest species, the forest and edge species and the savannah species.

It appears then that habitat is linked to body size with the primary forest species and savannah species both being particularly large and the species in edge habitats being small. This finding partially supports the ideas of Clutton-Brock and Harvey [1977a] who suggested that the savannah habitat could select for large body size because of increased predation in open areas. However, given the finding that arboreal species are generally smaller than more terrestrial species, it was surprising to find that the primary forest species were significantly larger than species in other forest habitats, as all these primary forest animals are arboreal. This result arises because nearly all small arboreal primates [e.g. the marmosets and tamarins, the bushbabies] are typical of secondary forest and edge habitats, a feature reflected in the small mean size of edge forest primates [figure 3.2].

Diet

Previous studies on diet and size

The size of an animal dictates both its food requirements and the range of possible strategies it can use to obtain food. A large animal requires more food than does a smaller animal; a small carnivore, such as a mongoose, cannot hunt gazelle to eat; a large gorilla cannot climb to the ends of tree branches to obtain its food. An additional complication in the relationship between feeding and size is the scaling relationship between metabolic rate and body weight, a relationship introduced in Chapter 1 and discussed later in this chapter.

The fact that metabolic rate does not increase linearly with increasing body weight, but instead scales to the three-quarters power of body weight, means that larger animals require less energy per unit weight than do smaller animals. This means that a doubling of body size is not accompanied by a 100% increase in calorific requirements but only by a 68% increase [$2^{0.75} = 1.68$]. Increase in body size therefore influences ecological parameters that are linked to calorific intake in a more complex way than if metabolic rate was isometrically related to size.

It has been suggested that the scaling relationship between metabolic rate and body weight will result in a link between body size and the proportions of different types of food eaten. Food stuffs vary both in their availability and in their "quality"., and foods therefore vary from those that are very common to those that are rare, and from "high quality" to "low quality". Although it is difficult to rigorously measure food quality, the term "high quality" is used to refer to foods that are easily assimilated so that their nutrients are readily available. The opposite term "low quality" is used for foods from which the nutrients are less readily extracted. This applies both to those foods that are difficult to digest, and hence need a relatively long time in the gut before the nutrients can be used by the animal, or to those foods that are low in nutrients.

Large animals need a higher absolute calorific intake than do smaller animals and, because of this, they must eat foods that are available in large quantities. The main problem for a large animal is therefore that of finding enough food to sustain it. For a smaller animal, its lower absolute energy needs mean that it can specialize on food that is relatively rare or patchy in distribution and still be guaranteed of a large enough food supply. However, the high energy needs per unit weight of a small animal mean that it must ensure that the food that it is eating is high in rapidly obtainable nutritive content. Eating food that is low in nutritive content, or where the nutrients are only obtainable after a long period of digestion, will mean that the animal will not be able to supply food at a fast enough rate to maintain its high [per unit weight] metabolic rate. The problem for a small animal is therefore that of finding enough high quality foods.

This difference between the requirements of large and small animals has led to the formulation of a theory that predicts the dietary quality of animals of different sizes. The basic premise of this idea is that there will be a correlation between an animal's size and its diet, this being caused by the the scaling relation of metabolic rate and body size. Small animals are predicted to mainly specialize in rare, or patchy, high quality foods whereas larger animals will tend to specialize in more common lower quality foods [Bell, 1971; Jarman, 1974; Sailer *et al*, 1985]. Obviously this relationship between food and size [referred to as the "Jarman-Bell principle"] will not be expected to result in a dichotomy between "large" and "small" species but will represent a continuum of changing dietary type with body size. The linking of low quality food with abundance and high quality food with rarity is a result of the former being mainly represented by primary production [i.e. plants] and the latter with secondary production [i.e. animals]. There is hence no theoretical reason why large animals should not eat high quality food if it is abundant enough [the large carnivores being an example of a group that does this], or why small animals should not feed on widely available high quality food. The correlation arises simply because animal prey tends to be less available than does plant fodder.

Some support for this idea is found in Clutton-Brock and Harvey [1977b], who look at the relation between the percentage of foliage in the diet to body weight and find that larger species tend to eat a higher proportion of leaves than do smaller species. Although this relation is that that would be predicted from the Jarman-Bell principle, the correlation between size and foliage content of the diet is low [r=0.48]. Further evidence that diet is linked to body size is also found by Clutton-Brock and Harvey [1977b], who note that insectivorous species are smaller than frugivorous species which are, in turn, smaller than folivorous species.

Sailer *et al.* [1985] carry out a more complex analysis of the relationship between dietary quality and size by also taking food other than foliage into account. Splitting foods into three types [structural plant, reproductive plant and animal] Sailer *et al.* use a simple weighting system for foods of a different quality. Each primate is then given a dietary quality score [DQ] by using the equation; DQ= 1s + 2r + 3a [Where s= % structural plant parts in diet, r= % reproductive plant parts in diet, and a= % animal prey in diet.] The degree of weighting for each food-type is based on the assumption that leaves are a low quality food, animal prey are a high quality food and fruit and flowers are a medium quality food.

It is found that this weighted index gives a far higher correlation between diet and log body size than does Clutton-Brock and Harvey's [1977b] measure of percentage foliage only [with the former explaining 42% of the variance but the latter explaining only 28%]. If the weightings are reversed, so that foliage has a high weighting and animal food a low weighting the correlation drops considerably. The high negative correlation found when using the DQ score from the above equation indicates that body size is inversely related to dietary quality, thus confirming the predictions of the Jarman-Bell theory. [Sailer *et al.* suggest that the weighting for animal food should be 3.5 rather than 3 because it gives a very slightly higher correlation of DQ to body weight [r=0.66 rather than r=0.65], but, as the difference is so small, the more simple formula above has been used to calculate DQ in this study].

Analyses of dietary data from this study

This study contains data on more species than do the studies of Clutton-Brock and Harvey [1977a, 1977b] and of Sailer *et al.* [1985]. In addition, the data used here include the percentage of flowers and gum eaten, information on neither being utilized by Clutton-Brock and Harvey [1977b], and gum-eating being apparently ignored by Sailer *et al.* [1985]. It was therefore decided to extend the analyses discussed above. All analyses were carried out at the species, genera and subfamily levels but, as the results for all levels were essentially the same, only those for the subfamily level are shown here. There were 86 species for which good dietary data was available, but only 70 of these had body weight data comparable to the other data used in this study. The other 16 species had a poor measure of body weight that has not been used elsewhere in this thesis, being either data from an untraceable source or from a rough estimate. The analyses were therefore carried out on all 86 species first, and then on the 70 species that had good body weight data. As the results of the two data sets were virtually identical, only those from the smaller data set are reported here. The smaller data set was chosen because it contains only species that are represented elsewhere in this thesis and the results can therefore be directly compared with other results reported here. Data for all 86 species are listed in Appendix V. Three basic procedures were carried out to test the the theories developed by Clutton-Brock and Harvey [1977b] and Sailer *et al.* [1985].

1) An analysis of variance was used to compare the average body weights in each of the four different dietary categories. The four categories were frugivores, folivores, gum-eaters and animal-eaters. The last category includes species whose main food includes both invertebrates and vertebrates in many cases but, as the main animal food is always invertebrates, these species will be referred to as insectivores. In a few cases species could be included in either of two categories [e.g. in *Galago garnettii* where the diet consists of 50% fruit and 50% insects.] Such species were included in both categories, i.e they were represented twice in the data set. This test was carried out using species values, average genus values and average subfamily values.

2) The percentages of each food type eaten [foliage, fruit, flowers, gum and animal food] were correlated with $\log_{10}$ body weight. This was done using species values, average genus values and subfamily values.

3) A "dietary quality score" was calculated for each species and the correlation of this score with $\log_{10}$ body weight. The score was calculated using a similar procedure to that used by Sailer *et al.* [1985], as described above. However, gum was also included, and given the same weighting as fruit and flowers. The "dietary quality score" [DQ] for each species was thus calculated by:

$$DQ = 1(FO) + 2(FR+FL+G) + 3(A)$$

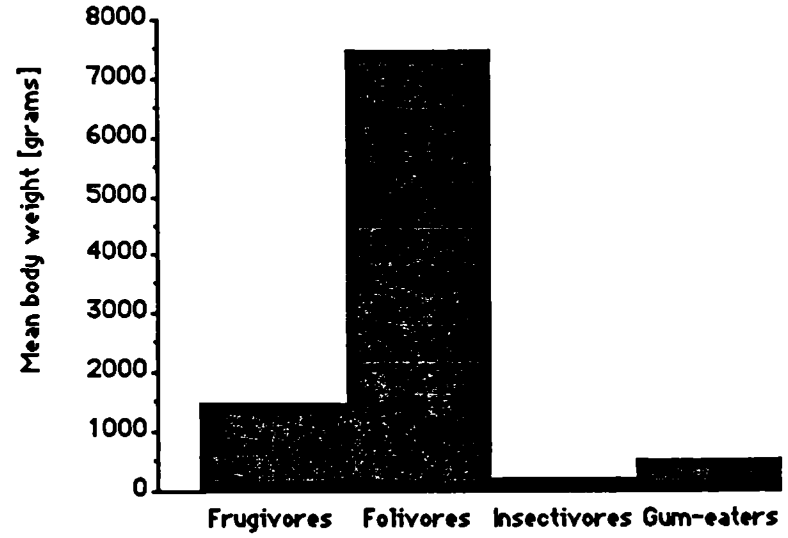
Where, FO= % foliage in diet, FR= % fruit in diet, FL= % flowers in diet, G= % gum in diet, A= % animal food in diet. This test was carried out using species values, average genus values and subfamily values.

The analysis of variance of the average body weights for each dietary category gave results that were basically in agreement with those found previously [Clutton-Brock and Harvey

Figure 3.3

Mean body weights for primate species with different diets

[calculated using mean logged subfamily values]



1977a, 1977b]. However, the inclusion of some extra species and the addition of a "gum eating" category means that there are some different results. Mean body weights of species in each category are illustrated in figure 3.3.

The observation of Clutton-Brock and Harvey [1977a, 1977b], that folivores are larger than other primates is supported by this study. Whether species, average genera or average subfamily data were used folivorous primates were found to be larger than frugivorous and insectivorous primates [$p<0.05$]. Although this pattern was found over the whole primate order, there was no such distinction between folivores and frugivores within the strepsirhines. The folivorous strepsirhine species are Malagasy species, which do not seem to be consistently larger than their frugivorous relations. For example, the brown lemur, *Lemur fulvus*, feeds extensively on leaves but is slightly smaller than the ring-tailed lemur, *L. catta*, which eats a considerable amount of fruit. Similarly, the sportive lemur, *Lepilemur mustelinus*, is mainly folivorous but weighs only about 600 grams, being one of the smallest lemur species.

Insectivorous primates have a smaller average size than folivorous and frugivorous primates, and gum-eaters are smaller than folivores. Although there is no statistical difference between the mean body weights of frugivores and insectivores within the strepsirhine species, this is due to the large size differences found between the different strepsirhine groups which obscures the size differences found within the groups. Within the two subfamilies that contain both insectivorous and frugivorous species, the insectivores are the smaller species. Insectivorous lorises [*Loris tardigradus* and *Nycticebus coucang*] are smaller than the more frugivorous pottos [*Arctocebus calabarensis* and *Perodicticus potto*], and the three smallest galagos are all insectivores. Strepsirhines that eat a lot of gum seem to have a size range that overlaps with both the mainly insectivorous and the more frugivorous species.

The haplorhine species followed the same basic pattern as did the whole primate group. As with strepsirhines, insectivorous haplorhines tend to be smaller than folivorous and frugivorous haplorhines and folivorous haplorhines tend to be larger than members of any other dietary group [ANOVA of mean body weights for each group, $p<0.05$ for all comparisons]. [Only the small-bodied marmoset (*Callithrix jacchus flaviceps*) could be classified as a gum-eater in the haplorhine data set.] Although the proportions of food eaten by species often varied considerably, the main food eaten, and hence the dietary category assigned, tended to be the same within the haplorhine subfamilies [e.g. all Colobinae are classified as folivores, Cercopithecinae are nearly all frugivores, the cebid monkeys are nearly all frugivores]. The variation within these subfamilies is therefore better examined by looking at the way body size correlates with the proportion of each food type eaten.

Table 3.1 shows the results of the correlations between the percentage of each food type given, and that found for the DQ score. Both the percentage of animal food eaten and the percentage of foliage eaten give a highly significant correlation with $\log_{10}$ body weight, and the percentage of gum eaten also correlated with $\log_{10}$ body weight [although not as strongly as do the percentage of foliage and percentage of animal food].

Table 3.1

Correlations of various measures of diet with $\log_{10}$ body weight

[using mean subfamily values]

Dietary measure	r	r^2	N	Significance level
% Fruit & seeds	0.407	0.166	15	ns[1]
% Foliage	0.637	0.406	15	0.02
% Flowers	0.215	0.046	15	ns
% Gum	-0.555	0.308	15	0.05
% Animal	-0.711	0.506	15	0.005
DQ	-0.732	0.534	15	0.005

1. ns= not significant [$p>0.05$]

The correlations shown above were also found in the strepsirhine and haplorhine species when these were looked at separately. However virtually no significant correlations were found within smaller taxonomic groups, when looking at species within genera, species within subfamilies or genera within subfamilies. The only correlations in these smaller groups that were found were within the Lorisinae, where log body size correlated with both percentage of animal food and fruit eaten [r=-1.0 and r=.99, p< .01], and in the Cercopithecinae where there was a correlation with the percentage of animal food eaten. Although this last correlation was found both when looking at both the species values [r=-.70, p<0.002] and the genus averages [r=0.95, p<0.001] within the Cercopithecinae, the high correlations seem to be due largely to the talapoin monkey, *Miopithecus talapoin*, being both very small and eating a large proportion of insects in its diet. Removal of the talapoin from the data drops the correlation coefficients considerably, to the point of insignificance for the average genus values.

As found by Sailer *et al.* [1985], dietary quality [DQ] proved a good predictor of body size [r= 0.73], and *vice versa*. However, the percentages of foliage or animal food in the diet were nearly as good separately [r= 0.64 and r= 0.71, respectively] and better when used together in a multiple regression [r=0.75]. DQ was also a good predictor of body size within the strepsirhine and haplorhine groups, with correlation coefficients similar to those for the whole primate group being found. As when looking at the dietary components separately, there was very little correlation found between DQ and body weight for species within genera, species within subfamilies or genera within subfamilies.

These results suggest that the proportion of fruit eaten is not indicative of a primate's size, but that both the proportion of foliage eaten and the proportion of animal food eaten are correlated with body size. Although the use of a dietary quality score does predict body weight better than does the use of one dietary component, it seems that this is mainly due to the DQ score combining information about foliage and animal food eaten. Given that the assignation of a weighting to any particular food type is difficult and often subjective, it would seem better to use the proportion of foliage and animal food eaten to predict body size than to use DQ. However, any such predictions can only be made on a gross scale and knowledge that one species has a different diet than does another closely related species does not allow one to predict a difference in body size between the two.

Interaction between diet and degree of arboreality

As arboreal species tend to be small and terrestrial species large, it was considered that the links between diet and body size could be partially accounted for by certain diets being linked to arboreality or terrestriality. To test for this possibility, the analysis of variance and correlation of body weight with the proportion of each food type eaten were repeated for arboreal species, semi-terrestrial species and terrestrial species separately.

All the insectivorous species were classified as being arboreal and when compared to arboreal folivores and arboreal frugivores they were found to be significantly smaller than these species [ANOVA, $p<0.01$]. Arboreal gum eaters were also found to be significantly smaller than arboreal folivores and arboreal frugivores [ANOVA, $p<0.01$]. However, the size difference found between folivores and frugivores when the whole sample was looked at, was not found to be significant when the groups were taken separately. It therefore appears that at least some of the difference in size between folivores and frugivores can be accounted for by their tending to have different degrees of arboreality.

The correlations between the proportion of each food type eaten and log body weight that were found to be significant for the whole group [i.e. with % foliage, %animal food and % gum] were also found for the arboreal species alone. However, very few correlations were found for the terrestrial or the semi-terrestrial species, with only the correlation between % animal food eaten and log body weight for semi-terrestrial and terrestrial species taken together being significant. It was considered that the lack of correlations could be due to the very small sample size that is left for these groups once the data are averaged to the subfamily level. However, even when species values were used only one extra correlation was found [between % animal food eaten and log body weight for semi-terrestrial species]. As might be expected from these results, the only correlation between the DQ value and log body size within groups was found with the arboreal species.

These results therefore seem to indicate that body size is linked to diet in arboreal species but not in semi-terrestrial or terrestrial species.

Interaction between diet and habitat

Body size has been shown to be linked to habitat type and it was therefore considered that the correlations between habitat and size could be confounding the correlations between diet and body size. The analyses of diet and body weight were therefore repeated for species within each habitat category separately. There were not enough subfamilies represented in habitat categories 5 [woodland and savannah] or 6 [savannah and grassland] to carry out the analyses and these two categories were therefore treated together. Average subfamily data was used throughout.

Generally speaking, the results obtained for species within each habitat group were the same as those obtained for the whole sample. The analyses of variance showed that insectivorous and gum-eating species, for each habitat category that they were found in, were generally smaller than folivorous and frugivorous species and that folivorous species were larger than any other dietary group in every habitat that they are found in except in savannah and woodland species [$p<0.05$ for all comparisons].

The correlations of log body weight with the proportion of each food type eaten were repeated for species in each habitat category. In habitat categories 2 [general forest] and 3 [forest and edge] there were significant positive correlations between % foliage eaten and log body weight, and significant negative correlations between % animal food eaten and log body weight. The combined sample of all woodland, savannah and grassland species gave a significant negative correlation between % animal food eaten and log body weight. In habitat category 4 [edge species] there were only two subfamilies represented, but when the five species were taken as independent points there were significant negative correlations between % animal food eaten and log body weight, and % gum eaten and log body weight. No significant correlations were found with the primary forest species. The correlations between DQ values and log body weight reflect these results, with only those in habitat categories 2 and 3 being significant.

It therefore seems that the correlations between size and diet are found even when the habitat is controlled for, with strong correlations between insectivory and size being observed in most habitat groups. It is interesting to observe that, in the two groups containing the largest species, there is no correlation found between the degree of folivory and body size. This is similar to the result found when species are split by their degree of terrestriality, with the larger semi-terrestrial and terrestrial species showing no correlations between size and folivory.

Latitude and climate

A relationship between body weight and latitude was first noted by Bergmann in 1847 [in Mayr, 1963, p.319], who stated that homiothermic species are larger in colder parts of their ranges than in warmer parts. The most generally cited cause of this is that larger species have a smaller surface area-to-volume ratio and can therefore conserve heat better than smaller species. As temperature is very closely correlated with latitude it follows that, if Bergmann's rule is correct, populations of a species near to the equator will tend to be smaller than those found at higher latitudes. Several studies, including Bergmann's own, have reported that this is generally the case [Mayr, 1963].

There has recently been a great deal of criticism of both the empirical finding, that body size correlates with latitude, and of the theory that is proposed to explain it [i.e. that larger animals are selected for their smaller relative surface area]. McNab [1981] points out that although a larger animal may lose less heat relative to body size it will still be losing more heat in absolute terms, and will therefore need to increase its food intake accordingly. Thus, he sees no reason why large animals should be selected for energetic reasons in cold areas. In addition to the theoretical objections to Bergmann's rule, McNab's 1971 study of North American mammal species did not find the expected variation of body size with latitude for the majority of species. Of the 47 species that he examined only 15 [32%] were found to be larger in higher latitudes, with 10 species showing a significant decrease in size with increasing latitude and the remainder having a body size that was independent of latitude. McNab considers that those positive correlations that are found can be explained by competition between related species leading to character displacement [i.e. the selection for a species to have a niche different from those of a close competitor].

Another strong criticism of Bergmann's rule has been made by Geist [1987] in a paper straightforwardly entitled "Bergmann's rule is invalid". Geist looks at the variation in body size of the wolf [*Canis lupus*] over its range which is from 19° to 82°. He finds that up to about 65° the body size does indeed increase with latitude, but thereafter it decreases. He explains this pattern by suggesting that the body weight is correlated with the "duration of the productivity pulse.... [which].... first increases and then decreases with latitude" [*ibid* p.1035]. This idea is also backed up by data on several species of New World deer, which show an increase in body size up to about 60° and thereafter show a decrease in size.

It is generally considered [e.g. Mayr, 1963] that Bergmann's law should only be applied to intraspecific comparisons, as members of different species may have other adaptations for different temperatures and therefore cannot be compared. Despite this, it seems reasonable to suppose that, if large body sizes are advantageous in cold climates, species found in cold areas will have a tendency to be larger than closely related species in warmer climates. This would be particularly true if the species concerned have diverged fairly recently in evolutionary time and have not evolved very different physiological adaptions to their respective climates.

It has been claimed that interspecific body size varies with latitude. Taking 102 randomly selected points in the North American continent Zeveloff and Boyce [1986], determined the average body length for mammal species at each site. Their results indicate that mammals in the North have a bigger mean body length than those found in the South of the continent [r= 0.72]. However, they suggest that the major determinant of this correlation is not that it is colder in the North, but instead that it is due to the high climatic variability of the more northerly climates. Their argument is that the high density-independent mortality of variable environments will give rise to less competition and hence more opportunities for the surviving individuals to assimilate nutrients, thus allowing them to grow larger. They also point out that in seasonal environments large animals may have a better chance of surviving periods of drought or food shortage as they have relatively larger energy reserves. [This latter point can be compared to Pianka's [1970] suggestion that a large body size gives an organism more stability rendering it less affected by its environment.] By calculating several climatic variables for each area Zeveloff and Boyce, attempt to test this hypothesis.

As would have been predicted by the positive correlation between body length and latitude, there is a negative correlation found between body length and average annual temperature and between body length and the mean minimum temperature, i.e. as they say, " Clearly, mammals are typically larger in colder places....". In addition to this correlation, there are also several correlations that show that both intra-year and inter-year variability in climate are positively correlated with body size, i.e. that a variable climate is associated with a large body size.

On the basis of these results, and those from a variety of multivariate analyses, they suggest that:

> "Attempts to explain climatic influences on body size patterns solely by discussing adaptations to cold are incomplete. Since such efforts only focus on one type of climatic parameter, they ignore the potentially powerful influences of both within and between year climatic variability."

Although it does indeed seem likely that climatic variability may influence body size directly it is not entirely clear from Zeveloff and Boyce's [1986] study that it does so. There are several flaws in their study that make it difficult to determine whether the results are valid.

One problem is that one cannot rule out the possibility that body weight and climatic variability are independently associated with temperature and hence not directly linked. A multiple regression equation is given that includes two measures of climatic variability [inter-year variation in annual precipitation and intra-year variation in AE], latitude and AE. This is said to account for "a large proportion [62%] of the variation in mean North American mammal size". However, there are no analogous equations offered for comparison that include temperature and latitude. In addition, there are no results of partial correlations that remove temperature effects from the correlations between climatic variables and body weight.

As there does not seem to be a consensus view about the validity of Bergmann's law, it was decided to investigate latitude and body size in the primates. As primates are not found beyond about 45° North and 35° South, both Bergmann's rule and the work of Geist [1987] would predict that size would increase with latitude. As there is also disagreement about whether one should expect the trend of increasing body weight with latitude only intra-specifically, between closely related species or inter-specifically for a wide range of species, the investigation was carried out at several taxonomic levels. Unfortunately, no body weight data were available for a single species at several latitudes and the lowest level of analysis is therefore for species within genera.

Analyses of latitude and climate from this study

To investigate possible correlations with latitude, the range centre and range limit of each species was found as detailed in Chapter 2. The correlation between body weight and both measures of latitude was then determined. This was carried out for the total sample [using species values, average genus values and average subfamily values], for species, genera and subfamilies within families, species and genera within subfamilies, and species within genera. The relationship between climate and body size was also investigated. The "typical climate" experienced by each species was found as detailed in Chapter 2. The correlation between body weight and the various climatic variables was examined at the species level only. As explained above, this was because a nested analysis of variance shows that virtually all of the variation in weather conditions occurs between species.

Results of analyses of latitude

Table 3.2 shows the results of correlating latitude and body size. In several cases there is evidence that Bergmann's rule is operating i.e. a positive correlation is found between the species body weight and latitude. For the larger groupings of species [i.e. all primates together, all strepsirhines, all haplorhines, families], the evidence for Bergmann's rule is negligible. Although strepsirhine species and genera show a positive correlation between range centre and

Table 3.2

Results of correlation analyses showing cases where evidence of a positive correlation between latitude and body weight was found

Level of analysis	Groups tested	Groups with significant correlations	N	r(1)	Significance level(2)
Species	All primates together	none	-	-	-
Genera	" " "	none	-	-	-
Subfamilies	" " "	none	-	-	-
Species in suborders	2 suborders	Strepsirhines*	26	0.44	0.025
Genera in suborders	" "	Strepsirhines*	15	0.43	0.050
Species in families	5 families	none	-	-	-
Genera in families	" "	none	-	-	-
Subfamilies in families	1 family	none	-	-	-
Species in subfamilies	14 subfamilies	Atelinae †	4	0.91	0.050
		Pithecinae†	3	0.95	0.025
		Cercopithecinae†	35	0.33	0.050
		Colobinae *† (without *Nasalis larvatus*)	8	0.78	0.025
Genera in subfamilies	7 subfamilies(3)	none	-	-	-
Species in genera	13 genera	*Colobus* spp.†	3	0.99	0.025
		Presbytis spp.*†	4	0.93	0.050
		Macaca spp.*†	10	0.66	0.025
		Macaques*† (4)	11	0.66	0.025

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† = range centre; * = range limit; (1) where there is a correlation with both range centre and range limit the average of the two is given; (2) where there is a correlation with both range centre and range limit the lower significance value is given; (3) includes some subfamilies with all genera represented by only one species i.e. some groups will also be included under "species in subfamilies"; (4) including *Macaca* spp. and *Cynopithecus nigra*.

body weight, the correlation is low, with only about 19% of the variation in body weight being accounted for by variation in latitude, or *vice versa.* The reason for this correlation is mainly due to the fact that the large bodied strepsirhine species are nearly all Malagasy species and are therefore found only South of the equator, whereas the smaller bodied species are to be found on both sides of the equator in tropical Africa and Asia. The range centres of the Malagasy species therefore tend to fall at a higher latitude than that of the mainland species, whose range centres tend to fall around 0°, despite the fact that both groups are found equally far from the equator. This view is supported by the fact that the correlations between range limit and body weight are not significant.

Within smaller taxonomic groups there are several significant positive correlations, for species within three genera [*Colobus, Macaca* and *Presbytis*] and species within three subfamilies [Cercopithecinae, Atelinae and Pitheciinae]. In addition, there is a significant correlation within the Colobinae subfamily when *Nasalis larvatus* was removed, this species being very large but occurring near to the equator.

It was thought that those taxa that were found in more temperate areas might be more likely to exhibit an increase in size with latitude, as variation in latitude within the tropics would be accompanied by only small alterations in climatic extremes and variability. Of the three genera that show increasing body weight with latitude, two [*Macaca* and *Presbytis*] are found beyond the tropical zone [i.e. beyond about 25° North or South]. However, the third, *Colobus*, is only found up to 14° from the equator. Within the subfamilies, where there is an increase of body size with latitude, the Cercopithecinae and the Colobinae are found beyond the tropics, but neither the Atelinae nor the Pitheciinae are found beyond 25°. It was also noted that not all groups that are found in more temperate zones exhibit a correlation of range latitude with body weight. The bushbabies, the Lorisinae and the howler monkeys all have one or more species that are found outside of 25° but do not exhibit a significant positive correlation of body weight to latitude [and in fact the three species of howler monkey show a significant negative correlation of body weight to latitude].

If one considers that the correlations found have not arisen simply by chance, i.e. that, in a few groups at least, there is an increase in body weight with latitude, the next question to be asked is; what is the cause of these correlations? Various possibilities were considered including the following:

1) That there is a change in habitat type, degree of terrestriality or diet with changing latitude, and that this change in ecology selects for changing body size.

2) The explanation given by Bergmann's rule, i.e. that size is inversely related to temperature.

3) That there is an increase in seasonality and environmental unpredictability with increasing latitude, which selects for increasing body size.

It has already been noted [Chapter 2] that there is a link between habitat and latitude, with the primates at higher latitudes tending to live in savannah habitats. There is also a link between savannah living and terrestriality. However, most groups that show an increase in size with increasing latitude have similar ecologies throughout their range. The *Colobus* species are all arboreal folivores living in forest habitat, the macaques are nearly all semi-terrestrial frugivores and live in forest and edge habitats, and the ateline and pithecine species are all arboreal frugivores living in undisturbed forest. The change in habitat and the increasing terrestriality of the more temperate cercopithecine and colobine species could account for their increase in size with increasing latitude. If one looks only at the cercopithecine species within a single habitat type and/or at only arboreal, semi-terrestrial or terrestrial species, the majority of correlations between log body weight and latitude are insignificant [$p>0.05$]. However, a significant correlation is found between body weight and range centre for savannah living, terrestrial cercopithecines [$r=0.774$, $n=6$, $p<0.05$]. Most of the colobine species in the data set are forest living and arboreal [all are folivorous], with only *Presbytis entellus* being found in more open country and spending some time on the ground. If *Presbytis entellus* is excluded from the colobine species [as well as *Nasalis larvatus*], the correlation between both measures of latitude and log body weight remains positive but becomes insignificant [$p>0.05$]. Similarly, the correlation between latitude and log body weight is lost for the *Presbytis* species if *Presbytis entellus* is excluded.

It therefore appears that the correlations between latitude and log body weight in the Cercopithecinae and Colobinae may be partially accounted for by changes in habitat accompanying changes in latitude. However, some correlations cannot be accounted for in this way and may therefore be due to climatic changes with habitat.

Results of analyses of climate

The significant correlations found between the climatic variables and body weight are listed in table 3.3. Nearly all the significant correlations are for species within genera, the only exceptions being two correlations with temperature variables found for species of the subfamily Indriinae. No correlations could be found for the suborders or the primate group as a whole.

For a variety of reasons, it is difficult to draw general conclusions from these results. Of the groups showing correlations, five consist of only three species and these small sample sizes could result in anomalous results. In particular, the climate data on the New World species may not be from a very representative area, as there are comparatively few weather stations in South America, and the stations used are not always very close to the species centres. Correlations, found with the gibbon species are also suspect as several of the weather stations

Table 3.3
Significant correlations between body size and climatic variables

Climatic variables[1]	Groups with significant correlations	N	r	Significance level
1. Precipitation Variables				
i) HI.AV$_{ppt}$	*Hylobates* spp.	6	0.98	0.001
ii) HI.CV.$_{ppt}$	*Cercopithecus* spp.	10	0.72	0.010
	Hylobates spp.	6	0.95	0.005
iii) LO.CV.$_{ppt}$	*Cebus* spp.	3	1.00	0.001
iv) AN.AV.$_{ppt}$	*Alouatta* spp.	3	-1.00	0.001
	Ateles spp.	3	-1.00	0.001
v) MNTH.CV.$_{ppt}$	*Colobus* spp.	3	1.00	0.001
2. Temperature variables				
i) HI.AV.$_{t}$	*Colobus* spp.	3	0.99	0.050
	Macaca spp.	10	-0.81	0.005
ii) HI.CV.$_{t}$	*Alouatta* spp.	3	1.00	0.001
iii) LO.AV.$_{t}$	*Cebus* spp.	3	0.99	0.050
	Hylobates spp.	6	-0.95	0.005
	Macaca spp.	10	-0.67	0.050
	Presbytis spp.	4	-0.97	0.050
	Indriinae species	3	-0.99	0.050
iv) LO.CV.$_{t}$	*Macaca* spp.	10	0.66	0.050
v) AN.AV.$_{t}$	*Colobus* spp.	3	0.99	0.050
	Hylobates spp.	6	-0.91	0.020
	Macaca spp.	10	-0.70	0.050
vi) MNTH.CV.$_{t}$	*Colobus* spp.	3	0.99	0.050
	Indriinae species	3	1.00	0.001

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(1) Symbols as in table 2.1

used for these species are not in an ideal position, particularly with respect to the altitude that they are found at. Because of these problems I have not attempted to discuss most of the results in any great detail, but instead have simply looked at some general trends that appear to be present.

Firstly, all the correlations with measures of climatic variation are positive, i.e. showing that body weight increases with increasing climate variability in all these groups. Secondly, the majority of the correlations of body weight with temperature indicate that body weight increases with decreasing temperature. The only exceptions to the negative correlation of body weight and temperature are with the capuchin monkeys [*Cebus* species], which show an increasing body weight as the average temperature in the coldest month increases and *Colobus* species which show a positive correlation between body weight and both temperature in the hottest month and the annual average temperature.

Given these results for correlations with both climate and latitude, what conclusions can be drawn regarding the theories previously discussed? That there is no simple explanation is indicated by the ways in which some primate groups show correlations between climatic parameters and body weight, others between latitude and body weight, others between both and still others show no correlations at all. It could be argued that this confusion is partly due to the limitations of the data. In particular there is a potential problem with the data for latitude not matching precisely with the data for climate, as the former used were for the centres and limits of the species' ranges whereas the latter were for a point as near to the centre of the range as possible. However, when the latitudes of the weather stations used were substituted for the species range centres the results were virtually identical, indicating that this was not the major problem.

In an attempt to unravel the chain of cause and effect partial correlations were carried out with latitude, climate and body weight for those groups that showed significant correlations of body weight with both climate and latitude. Unfortunately, no firm conclusions could be drawn from this data. For some groups the small sample sizes made partial correlations impossible, as the number of degrees of freedom for such tests are [n-3] and it is therefore necessary to have at least four data points to carry out a significance test. If one ignores those groups where there are only three species, there are four groups of species where there is a correlation between body size and a measure of climate. These are the macaques [*Macaca* species], the guenons [*Cercopithecus* species], the gibbons [*Hylobates* species] and the leaf monkeys [*Presbytis* species].

The macaques and the leaf monkeys both become larger further North and as the temperature becomes colder. In the macaques, increasing body size is also linked to increasing inter-year variability in temperature. These two groups therefore fit the predictions of Bergmann's law, i.e. that decreasing temperature is linked to increasing body size. However, in the case of the macaques the results also fit the prediction of Zeveloff and Boyce [1986], i.e. that increased climatic variability leads to increased body size.

Partial correlations were carried out on the data for both the macaques and the leaf monkeys, but the small sample sizes tended to mean that any small drop in correlations meant that the correlation became insignificant. In all cases, the significant correlations between body size and a climatic variable were lost when the effect of another climatic variable was removed. Similarly the link between latitude and body weight was removed by a partial correlation removing the effects of temperature or temperature variation. This evidence appears to suggest that it is a combination of factors acting on body weight in the macaques and leaf monkeys that is selecting for a high body weight in Northerly latitudes.

A similar situation is found with the gibbons, which are generally larger in wetter, colder and more variable climates. As with the macaques, all these climatic variables seem to be acting together and removal of any one variable causes the correlations between another pair of variables to become insignificant. In the cercopithecine monkeys, the correlation between the variation in rainfall in the wettest month remained significant after the removal of the effects of latitude.

The evidence therefore suggests that both increased seasonality and cold weather are associated with a large body size, and that the influence of these two effects lead to a correlation between latitude and size.

The scaling of basal metabolic rate to body weight

As has been briefly discussed in Chapter 1, the basal metabolic rate of an animal can be predicted very accurately from a knowledge of its taxonomic group and its body weight. [N.B. See Chapter 2 for a discussion of the use of the term basal metabolic rate.] Kleiber [1961] described the scaling of basal metabolic rate [BMR] to body weight in eutherian mammals and noted that BMR does not increase linearly with body size but is proportional to the three quarters power of body mass. So that the relationship between the two parameters can be described by the equation linking basal metabolic rate [BMR] in mlO_2h^{-1} and body mass [M] in grams:

$$BMR = 3.2\ M^{0.756} \qquad [Eqn.\ 3.1]$$

This relationship has since been confirmed for larger samples of mammals [Stahl, 1967]. The precise significance of this scaling value is not clear, both because the usefulness of basal metabolic rate as a measure of an animals energy use is itself open to question and because there is no totally convincing explanation of the 0.75 exponent.

The question of the relevance of BMR arises because metabolic rate during activity is a major determinant of an animal's total energy requirements. But BMR is a measure of the energy use during rest only. It is therefore possible that an animal that has a low or high BMR for its size may not have an active metabolic rate that is different from other species of the same size. Although it has been stated that BMR is directly proportional to the actual daily expenditure [McNab 1980], some studies have shown that several species of mammals are capable of elevating their basal metabolic rates during pregnancy and lactation, whereas others apperently keep their metabolic rate at "normal" levels at these times [Thompson and Nicoll, 1986; Richard and Nicoll, 1987]. Such studies provide evidence that species have varying capacities to raise their metabolic rates and raise questions as to whether they would necessarily be expected to have a BMR that is proportional to their daily expenditure.

If one assumes that the use of BMR as a measure of metabolic rate is biologically relevant, then one must try to explain the 0.75 scaling exponent. As discussed by Calder [1984], there is no completely satisfactory explanation for the 0.75 exponent. One suggestion is that the surface area of an homiothermic animal will be a major determinant of the BMR, as the heat lost from the surface will be important in determining the energy needed to keep body temperature constant. As the animal's total mass will also be important in determining energy requirements, Kleiber [1961] suggests that the 0.75 exponent could arise as a result of a compromise between scaling to the mass of the animal [i.e. to $M^{1.0}$] and scaling to the surface area of the animal [i.e. $M^{0.67}$]. An important criticism of this explanation is that poikilothermic and ectothermic animals have also been found to have a metabolic scaling of $M^{0.75}$ [Calder, 1984].

A second explanation, the elastic similarity model of McMahon [1973, 1975] is also reviewed in Calder [1984], where a more detailed explanation of its derivation can be found. This model predicts that the energy requirements of muscles during activity will scale to the 0.75 of body weight, and hence that metabolic rate during activity will scale to $M^{0.75}$. If one assumes that BMR is proportional to metabolic rate during activity this explains the scaling exponent of BMR. However, both theoretical and empirical objections have been made made against this model and it is by no means generally accepted. It appears then, that a complete explanation of the scaling of BMR to body weight is yet to be found.

Chapter 3

Metabolic rate in the primates

Primates have been shown by Kurland and Pearson [1986] to have a metabolic rate that correlates with body weight in a similar way to that of other mammals, the regression equation for 28 species being:

$$\text{Metabolic rate} = kM^{0.80} \qquad \text{[Eqn. 3.2]}$$

[Where M is body weight and k is a constant, whose value depends on the units of metabolic rate and M used.]

However, there are several problems with Kurland and Pearson's study that should be noted. Firstly, the values of metabolic rate that have been used have not been measured under comparable conditions, in particular, several of the haplorhine species' measures are from immature animals [as evidenced from the body weights given] and there is evidence that suggests that immature animals tend to have higher BMRs than do adults. There is also a mixture of measures from resting, awake and anesthetized animals. Another problem is that Kurland and Pearson do not look at the haplorhine and strepsirhine species separately and therefore run the risk of confusing two separate "grades" of organization [see chapters 1 and 2 for a discussion of the problems of grades]. This grade confusion could be reason for the allometric exponent of Kurland and Pearson's analysis being slightly higher than the expected 0.75 value, [although the 95% confidence limits of the exponent value do include 0.75 (Kurland and Pearson, 1986)]. Finally, there is the question of whether regression analysis is the correct one for this type of data, with major axis analysis probably being more appropriate, although in this case the very high correlation found between log body weight and log BMR ($r=0.98$) will mean that there is virtually no difference between the best-fit lines obtained with the two methods [Harvey and Mace, 1982; this study, Chapter 2]. Because of these problems, and because data was available for some additional species, it was decided that it would be appropriate to carry out another analysis of the scaling relationship between metabolic rate and body weight in primates.

This study

Data on metabolic rate was collected for as many primate species as possible. The criteria used for selecting the data are described in Chapter 2. The data used and a summary of the conditions under which they were determined are listed in Appendix IV. As data measured under ideal conditions were difficult to find the analyses were carried out using two data sets [see Chapter 2 for details of the collection and sorting of BMR data]. Firstly, the major axis analyses were carried out using data that met most of the criteria needed to ascertain BMR accurately; these are data that are scored "good" [G] in Appendix IV [data set I]. The data that did not meet the criteria ideally needed to measure BMR [data set II] were then included in the figures of log BMR against log body weight to give some idea of where these species lay in relation to both the Kleiber line and the primate best-fit line. Data set I has data for 21 species and data set II includes a further 13 species. Strictly speaking, the data in data set II, and even some data in data set I, cannot be correctly referred to as basal metabolic rate data, but represent some other measure of metabolic rate. However, I have continued to refer to all the data as basal metabolic rate data so as to make the following section more readable.

The methods used for determining the scaling relationship between metabolic rate and body weight are the major axis methods described in Chapter 2.

Results of this study

Figure 3.4 shows the results of plotting log BMR against log body weight for 21 primate species as compared to the best-fit line found for a large number of mammal species. The major axis and correlation statistics [using accurate metabolic rate data only] are shown in table 3.4.

The very high correlation coefficients found indicate that the majority of the variation in BMR can be explained by variation in body weight. This is particularly true of the haplorhine species. Two further points should be noted about these figures. Firstly, in nearly all cases, the slope of the major axis line includes the value of 0.75 within its 95% confidence limits. Secondly, the slope value derived for the strepsirhines alone has a lower slope than 0.75. The reason for this lower slope value can be seen in figure 3.4, where all of the heavier strepsirhine species are shown to have a metabolic rate that is lower than would be predicted by the Kleiber relationship, whereas some of the smaller species have the expected metabolic rate for their body size.

Residual variation in basal metabolic rate

This study confirms the results of previous work [e.g. Kurland and Pearson, 1986] in indicating that most primates have a metabolic rate that is either as would be expected or is lower than would be expected for typical mammals of their size [figure 3.4].

Of the species in data set I, only one, the squirrel monkey [*Saimiri sciureus*], is found to have a high BMR for a mammal of its size, but the BMR is only about 6% above the predicted value. Although four other species also have metabolic rates that are further above [7-15%] than would be predicted from the Kleiber equation, the data from these species cannot be described as basal. Two studies, on *Saguinus geoffroyi* and *Papio cynocephalus*, use data from immature animals and the other three, on *Macaca fuscata*, *M. fascicularus* and *Papio cynocephalus*, use data from animals restrained in "chairs", which were most probably under a great deal of psychological stress. As the evidence for a higher metabolic rate than expected is slim for the primates, it will not be discussed further here, although it will be interesting to

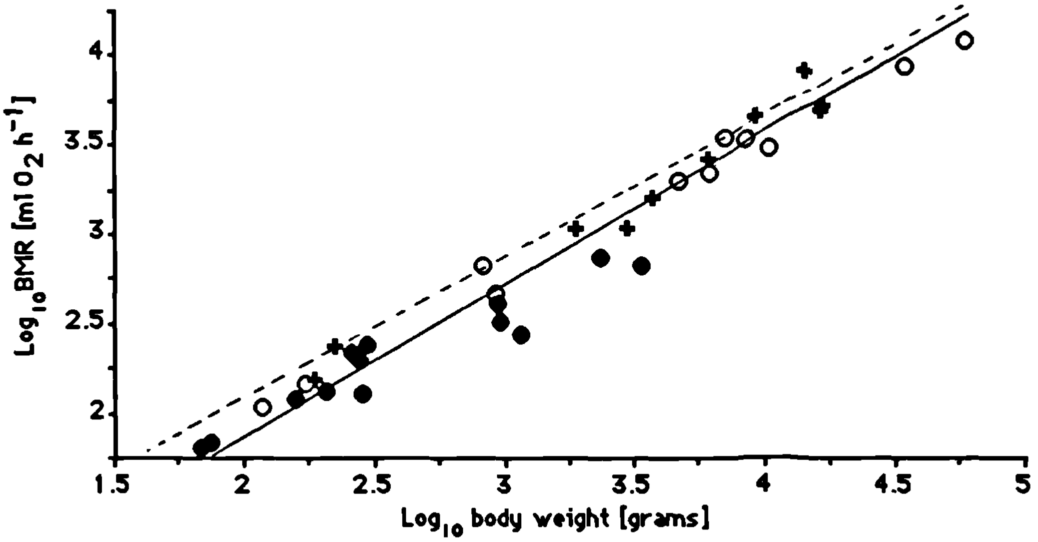
Table 3.4

Major axis statistics for $\log_{10}$ *basal metabolic rate vs.* $\log_{10}$ *body weight*

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	21	0.98	0.78	0.36	0.71	0.85
	genera	18	0.98	0.78	0.34	0.70	0.88
	subfamily	14	0.98	0.78	0.40	0.67	0.85
Strepsirhines:	species	11	0.96	0.59	0.79	0.47	0.74
	genera	8	0.94	0.54	0.75	0.35	0.77
	subfamily	5	0.95	0.54	0.97	0.26	0.91
Haplorhines:	species	11	0.99	0.76	0.46	0.70	0.83
	genera	11	0.99	0.76	0.46	0.70	0.83
	subfamily	9	0.99	0.76	0.48	0.71	0.82

Figure 3.4

Log_{10} basal metabolic rate versus log_{10} body weight



● **Strepsirhines [good data]**

○ **Haplorhines [good data]**

✚ **Haplorhines [data not used in analyses]**

——— Major axis best-fit line for primate species [calculated using "good data" only]

----- Regression line for mammals, from Kleiber [1961] see whether further studies on adult and unstressed macaques and baboons confirm that these species have elevated BMRs.

There are several primate species with BMRs that are considerably below the levels that would be predicted from the Kleiber equation, with 13 species from data set I having BMRs that are less than 80% of the predicted value. The majority of species with very low relative BMRs are strepsirhine species, although two haplorhine species [*Aotus trivirgatus* and *Colobus guereza*] also have low BMRs for their size. Several theories have been put forward to explain the low relative BMR of some species, and these are discussed here.

A lowered metabolic rate as a primitive trait

It has been suggested that a low basal metabolic rate is a primitive mammalian trait which has been retained by some primate species [Müller, 1985; Kurland and Pearson, 1986]. There are two facts that support this idea. Firstly, there is the observation that species with a low basal metabolic rate frequently have a body temperature that is not as constant as in species with a "normal" BMR. For example, several of the strepsirhine species that have been studied have a body temperature that drops by 1-3 °C during sleep or in very cold conditions [McCormick, 1981; Müller, 1975]. As it is generally believed that the ancestors of modern mammals had a less efficient homiothermic mechanism than is found today, it would seem reasonable to suppose that the combination of poor heterothermy and a low BMR is a primitive characteristic. In addition, it has already been noted that the majority of primate species with a low BMR are strepsirhines, a taxonomic group that is usually thought of as being generally primitive when compared to the haplorhines.

However, there are very good reasons for believing that a relatively low metabolic rate is a derived and adaptive characteristic. The main reason for thinking this is that the groups showing the most extreme hypometabolism are not necessarily those that are thought to be the most primitive. For example, the lorises and pottos have lower relative BMRs than do the bushbabies, although it is the bushbabies that are probably the closer to the ancestral primates in morphology and ecology [Charles-Dominique and Martin, 1970]. Although the bushbabies have some primitive features it could be argued that their metabolic rates have moved further from the ancestral state than have those of the lorises and pottos. However, further evidence that low metabolic rates can be selected comes from the two haplorhine species [*Aotus trivirgatus* and *Colobus guereza*] which have low metabolic rates, whereas other haplorhines for which data is available have "normal" metabolic rates for their size. It is therefore likely that both *Aotus trivirgatus* and *Colobus guereza* had ancestors with a normal metabolic rate.

If one accepts that a low metabolic rate is not a primitive trait, this implies that it is a character that has evolved in the primates, possibly as an adaptive character. The obvious advantage of having a low metabolic rate is that it means the animal requires less energy to live, it has therefore been suggested that a low metabolic rate has evolved in some species as an energy saving strategy [McNab, 1986b]. One reason for an energy saving strategy being particularly advantageous could be that the diet of the species limits resources in some way. This idea has led to a number of theories linking diet and BMR.

Diet and metabolic rate

Looking at the BMRs of a large number of mammals, McNab [1986b] concluded that certain diets are linked to low basal metabolic rates in mammals, whereas others are linked to high BMRs. Table 3.5 summarizes his conclusions. As can be seen, McNab's work suggests that large species that feed mainly on invertebrates, fruit, pollen and nectar and the leaves of woody plants [leaves] will have a low BMR for their size, although smaller species feeding on invertebrates, fruit and leaves will have a BMR that is as expected or higher than expected. Small species [100 grams or below] therefore tend to have a high BMR regardless of their diet, whereas larger animals appear to have a BMR that is correlated with their diet. McNab explains these patterns by suggesting that the foods that are associated with low BMRs have one or several of the following properties:

1. Low digestibility [some invertebrates, leaves].
2. Having chemical deterrents [some invertebrates, leaves].
3. Being seasonally available [invertebrates, fruit].
4. May be difficult to gather [invertebrates, small seeds].

Such foods are therefore have properties that "... may limit the rate at which energy is acquired by a mammal and therefore the rate at which the mammal can expend energy." [McNab 1986b, p.7]. Because smaller mammals need less total energy intake, they are less affected by the problems of obtaining such foods and therefore can afford to feed on them whilst still maintaining a normal or high BMR.

In addition to the association between diet and relative BMR, McNab also notes that there appears to be a link between an arboreal habitat and a low BMR. The evidence given for this idea is that in both frugivorous species and folivorous species the terrestrial species have a higher relative BMR than do the arboreal species.

Another theory linking diet and metabolic rate is discussed in relation to the primates by Kurland and Pearson [1986]. As discussed above, it has been suggested that diet is linked to body size because of the allometric relationship between body size and metabolic rate. If body size is related to dietary quality because of its relationship to metabolic rate, it follows that species that have either a high or a low relative metabolic rate will also be expected to have a diet that is not predictable from their size. This idea has been termed the "deviant-diet hypothesis" by

Table 3.5

Correlates of diet and basal metabolic rate in mammals

[from McNab, 1986b]

Diet	Observed BMR cf. Kleiber prediction	
	Body weight < 100g	Body weight >100g
Invertebrates	high [except bats]	low
Fruit	as expected	low
Nuts and seeds	high	high
Seeds in arid areas	low	-
Pollen and nectar	low	low
Grasses and herbs	high	high
Leaves of woody plants	high	low
Vertebrates	high	high

Kurland and Pearson. The hypothesis predicts that all species that have a diet that is deviant for their size will have a relatively low metabolic rate, whether the deviation means that the species has a higher quality or a lower quality diet then one would predict.

The correlation between a lowered metabolic rate and a poor quality diet for size is perhaps easier to understand. If a small species is feeding on a relatively low quality food it will have difficulty in harvesting sufficient calories per unit time to support a "normal" metabolic rate. However, if its metabolic rate is lowered it will require less energy and, other things being equal, a relatively low metabolic rate will be selected for. The second prediction, that feeding on a relatively high quality food will also be correlated with hypometabolism, results from the assumption that high quality foods will be rare. A large species feeding on high quality foods will therefore not be able to find enough of such food to support a normal metabolic rate and will only be able to support a lowered metabolic rate.

The main difference between the two theories of Kurland and Pearson and McNab is their predictions regarding animals eating low quality foods such as foliage. McNab believes that small animals feeding on low quality foods will be able to support a normal or elevated metabolic rate because their absolute resource requirements are low, whereas the Jarman-Bell theory predicts that small animals will not be able to process low quality foods fast enough to support their high relative metabolic rates and can only feed on such foods of they have a low metabolic rate. This difference arises because the two theories have different underlying assumptions about the way in which the rate of food acquisition varies with body size. Although it is intuitively obvious that larger animals can gather and eat more food in a given time than can smaller animals, it is not clear how this rate will vary with body size. A hypothetical example will illustrate the way in which the variation of food acquisition with body weight will affect the predicted metabolic rate of small animals eating low quality foods.

Take two animals, animal A weighing 1kg and animal B weighing 2kg. Both animals are seeking to survive on an abundant food supply, and have nine hours per day which they can afford to devote to food gathering and eating. Animal A needs 10 units of the food per day to survive. Assuming that the Kleiber relationship applies, animal B needs $(2^{0.75} * 10) = 16.8$ units of the same food per day. Assuming that animal B can eat 2 units of food per hour, it will spend 8.4 hours per day feeding and can therefore live on the food in question. Whether or not the smaller A can live on the food depends on how the rate of food acquisition is related to body weight. For example:

1) If food acquisition rate is directly proportional to body weight. Animal A can only gather 1 unit of food per hour, it will therefore need 10 hours a day to get enough food to live on. As it can only afford to spend nine hours a day processing food, it cannot survive by eating this food and must find a higher quality food where it can gather more resources per hour, unless it can

reduce its energy requirements, i.e. by lowering its metabolic rate.

2) If food acquisition rate is allometrically related to body weight. If animal B can only gather food 1.5 times faster than can A [i.e. food acquisition rate $=kM^{0.6}$, where k is a constant and M=body weight], then A will be able to process 1.33 units of food per hour. A will therefore be able to eat 10 units of food in 7.5 hours and will be able to survive on the low quality food. The hypothetical allometric relationship is such that the smaller animal will spend less time gathering food because the increase in metabolic needs of the larger animal are not offset by its increased ability to gather food.

If the number of hours available for collecting food were reduced to eight per day, B would no longer be able to survive and would have to switch to another food or lower its metabolic rate to decrease its energy requirements.

Example 1 illustrates the assumption of Kurland and Pearson, i.e. that smaller animals will have to reduce their metabolic rates if they are to survive on low quality foods. The second example illustrates the scenario predicted by McNab, where small species will be able to survive on low quality foods because of their lower absolute energy requirements. Which scenario is correct will depend on how the rate of food acquisition varies with body weight, a relationship that will depend on the type of food and the way in which it is harvested. To my knowledge the way in rates of food acquisition varies with body weight has not been investigated and the very many sampling regimes used to record feeding behaviour and a lack of detailed knowledge of the chemical content of foods eaten make simple comparisons difficult. Further development of this subject must therefore be considered outside the scope of this study.

As noted above, McNab's theory is developed from empirical observation, but his methods have been criticized by Elgar and Harvey [1987]. Elgar and Harvey suggest that correlations between ecology and phylogeny among mammals could lead to BMR variation that is due to differences in phylogeny being mistakenly taken as being due to ecological causes. For example, most of the arboreal frugivores in McNab's sample used are Carnivora and the terrestrial frugivores are all rodents. If the Carnivora have lower relative BMRs than do rodents it will appear as if arboreal frugivores have a lower BMR than do terrestrial frugivores. The observed differences in the relative basal metabolic rate of the two groups might therefore be due to differences that "..... could have arisen in the distant past and have been retained by inertia" [Elgar and Harvey; 1987, p.25]. Alternatively both BMR and habitat could be correlated with another difference found between the rodents and carnivores, such as group size, and the correlation between the two may have arisen as a consequence of this, rather than because of a direct relationship.

To test for these possibilities Elgar and Harvey looked at a similar [but larger] data set to that examined by McNab, using the same ecological categories. Although they also found that diet and habitat were linked to relative BMR, nearly all of these correlations were removed once phylogenetic influences were controlled. The only correlates remaining were between a high relative BMR and vertebrate-eating and a tentative link between a low BMR and invertebrate-eating. They therefore conclude "... that many of the correlations between diet and relative metabolic rates can equally well be described by taxonomic associations ... " [*ibid*p.30].

By restricting their sample to primates, Kurland and Pearson [1986] avoid some of the problems of common phylogeny and ecology found in McNab's work, although there could be a strong argument for treating haplorhine and strepsirhine species separately [see below]. Kurland and Pearson look at the diets and metabolic rates of 21 primate species. They test for a correlation between a species' deviation from its expected body size [predicted from the average body size of other primates with the same dietary quality and taxonomy] and a low relative metabolic rate [defined as a metabolic rate that is 20% below that predicted by Kleiber]. They conclude that there is a relationship between species with a relatively low metabolism and those with a size-diet pattern that deviates from the expected relationship.

There are several problems with this analysis that need to be addressed before the results can be taken as conclusive,. These problems arise in both the metabolic rate data [discussed above] and the dietary data used. To compare metabolic rates of species with different diets, Kurland and Pearson assign each of the 21 species to one of five categories. The problem is that the placing of each species in a dietary quality category does not appear to have been done in a consistent manner. For example, *Perodicticus potto* is classified as being predominantly insectivorous, despite its diet containing about 10% animal prey and 67% fruit [Charles-Dominique and Bearder, 1979], and *Lemur fulvus* is classified as being more folivorous than *Alouatta palliata*, although both species have diets that include similarly variable amounts of foliage and fruit [*L. fulvus* 9-67% fruit, 38-71% leaves (Tattersall, 1982); *A. palliata* 13-51% fruit, 48-69% leaves (Crockett and Eisenberg, 1986)]. The importance of exudate feeding in several species [e.g *Galago (Euoticus) elegantulus, Galago senegalensis*] is also ignored, with exudates appearing to be included under the category of animal prey. This is despite the fact that there is no evidence that exudates have a comparable dietary quality to insects and should probably be considered as having a similar, or possibly lower, dietary quality to fruit. [Exudates have a high carbohydrate content but are difficult to digest (Martin. pers. comm.).] These problems with Kurland and Pearson's work mean that their main conclusion [i.e. that the deviant-diet hypothesis is supported] should be viewed with some suspicion.

Because of the problems with both McNab's and Kurland and Pearson's work, it was felt that the relationship between diet and metabolic rate in the primates needed to be reexamined for this study. The following discusses only the results found when using species as independent data points, but the analyses were repeated using average subfamily data and none of the conclusions reached below was altered.

Figure 3.5 shows the relationship between diet and BMR for all the primate species for which good data is available. As has already been noted, nearly all primates in this study have a BMR that is lower than or about equal to that that would be predicted from data on all mammals. Nearly all the primates in this study are insectivores, folivores or frugivores, i.e. they are all in dietary categories that would be predicted by McNab [1986b] to lead to a lowered BMR and this result therefore seems to support McNab's theory. However, there is considerable variation in the relative BMR and it was therefore of interest to see if any link between diet and relative BMR could be uncovered within the primates.

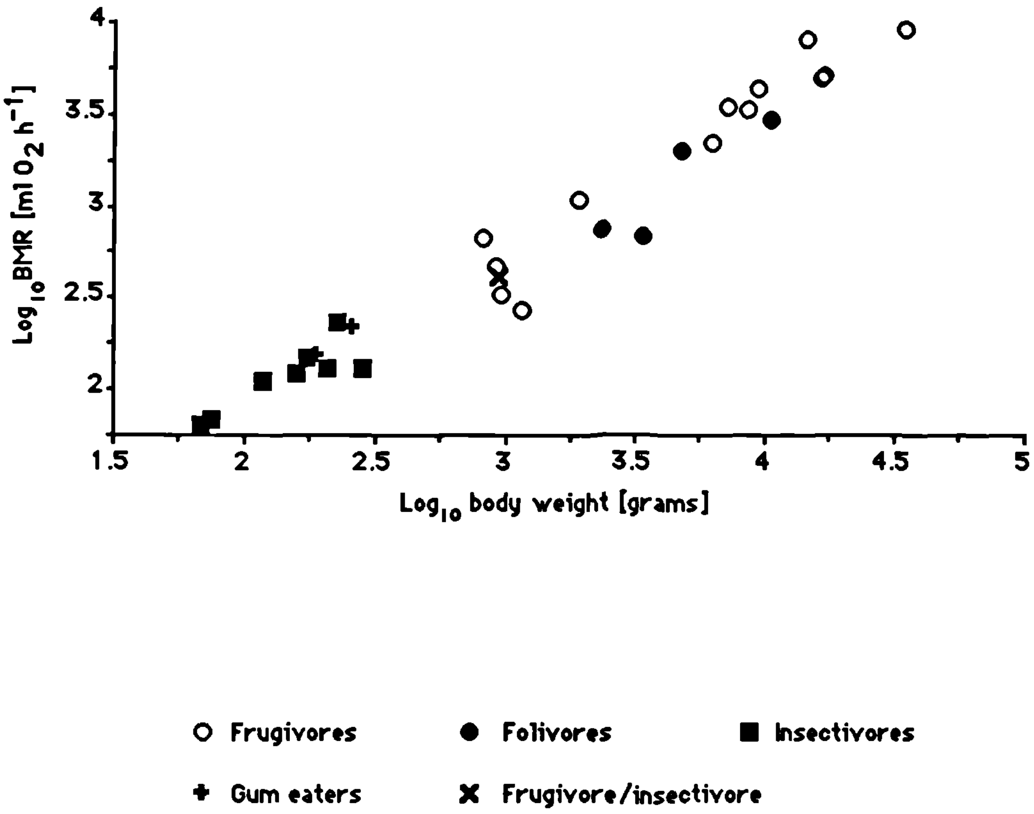
It can be seen that nearly all invertebrate-eaters have relatively low metabolic rates, a result that seems to support McNab's theory of invertebrate eaters being constrained, by their diet, to a low metabolic rate. However, when the data is examined more closely, it is found that all of the invertebrate eaters with a very low BMR are strepsirhine species. The two haplorhine species that eat predominantly invertebrates [*Tarsius spectrum* and *Cebuella pygmaea*] do not have low BMRs for primates, although they do have low BMRs for mammals [both having a BMR of about 84% of that predicted by Kleiber]. However, the data on the tarsier is based on data from only one adult animal, and the temperature at which the experiment was carried was probably below the thermoneutral zone. [Evidence that tarsiers have a low BMR is provided by Roberts (1988) who estimates that active *T. bancanus* consume only 60-80% of the energy requirements predicted for a resting mammal of its size.] More work is therefore needed to confirm that tarsiers have a "normal" BMR.

Two other haplorhines that are classified as frugivores but include a lot of insects in their diets [*Saimiri sciureus* and *Saguinus geoffroyi*] both have high BMRs for primates and indeed for mammals, of their size [although it should be noted that the data from *Saguinus geoffroyi* are from young animal and may not be representative of the adult BMR]. It therefore appears that the apparent link between a low relative BMR and insectivory in the primates may be due to the majority of insectivorous primates being strepsirhines. This impression is supported by the correlation coefficient between relative BMR and the proportion of insects in the diet being insignificant [$p>0.05$].

McNab [1986b] also found that folivorous mammals had relatively low BMRs. In the primate data used here there are four species that eat a high proportion of leaves; the brown lemur, the white sifaka, the guereza and the Guatemalan howler. Three of these species have a low BMR for primates and mammals, but the howler has the BMR one would expect. However, the BMR measurements on the howler monkey were made during the day, i.e. during its active

Figure 3.5

Log_{10} basal metabolic rate versus log_{10} body weight, showing diet



period", and the animals may not have been properly resting. If this is the case their metabolic rates would have been elevated above the basal level. With such a small sample it is impossible to tell if the folivory is linked to a low relative BMR in the primates, or if the two strepsirhine species have a low BMR primarily because of their strepsirhine heritage. It is interested to note that the colobus monkey has a very low relative BMR for a haplorhine species, with only the owl monkey being lower. McNab's theory would appear to be borne out by *Colobus guereza*, as it eats a very large proportion of mature leaves, i.e. leaves that would be expected to be particularly hard to digest [Glyn Davies, pers. comm.]. Despite this evidence that folivory is linked to a low relative BMR, there is no correlation found between relative BMR and the proportion of leaves eaten [p>0.05]. In addition, the howler monkey eats about 50% leaves but has a normal BMR. However, it eats mainly young leaves [Crockett and Eisenberg, 1986], which are probably easier to digest and higher in nutrients that more mature foliage [but see above comments on the BMR data].

No link between frugivory and relative BMR could be found. Frugivorous species do not appear to have a generally high or low relative BMR as compared to other primates and there is no correlation between the proportion of fruit eaten and relative BMR.

The evidence for a link between diet and relative BMR, of the type suggested by McNab, therefore appears to be tenuous. The reason for frugivorous primates not supporting McNab's theory could be due to tropical fruit being more abundant than fruit in other areas. McNab [1986b] suggested that the reason for frugivorous mammals having low relative BMRs was that fruit is a scarce resource, being seasonally available. As most primates live in the tropics, it might be expected that the effects of seasonality on the fruit supply will not be as great as in more temperate areas and this might explain the lack of correlation between frugivory and relative BMR in primates. There is some evidence that both insectivory and folivory are associated with a low BMR. However, the relationship is complicated by the majority of these species being strepsirhines, a group whose species appear to have a low BMR regardless of diet. Further evidence that diet is not very closely linked to relative BMR comes from the correlation of the dietary quality score and relative BMR, which is insignificant [p>0.05] for all primates together and for the two suborders separately.

As links between diet and relative BMR were not apparent, the next task was to investigate the links between diet <u>relative to body size</u> and relative BMR, and thus to test the deviant diet hypothesis of Kurland and Pearson [1986]. Two tests of the link between relative DQ and relative BMR were carried. Firstly, a correlation analysis was carried out between the residuals of BMR and relative DQ. As the deviant diet hypothesis predicts that both positive and negative deviations from the predicted diet will lead to a reduced BMR, the correlation was carried out firstly using the relative DQ values in the normal way [i.e. treating them as both positive and negative numbers] and secondly using only the size of the DQ deviation [i.e. treating all numbers as positive].

Secondly, the basic methodology of Kurland and Pearson's [1986] study was repeated, using the data of this work and calculating a dietary quality score [DQ] as described above. Although I felt that there were several basic flaws in this methodology it was used here, with only slight changes, so as to give a direct comparison between the two studies.

In Kurland and Pearson's study, the species were split into five groups that ate different foods. As mentioned above, it was felt that the placing of species into these groups was done without due consideration of the actual diets of the animals. As it was felt that a part of the problem could be the subjective nature of the categories used, the groups in this study were split by their DQ scores. The species were divided into five DQ groups representing species with different DQs, varying from group 1 with DQs of less than 140 to group 5 with DQs of 260 or over. This method had an advantage over that used by Kurland and Pearson in that species with a mixed diet could also be classified.

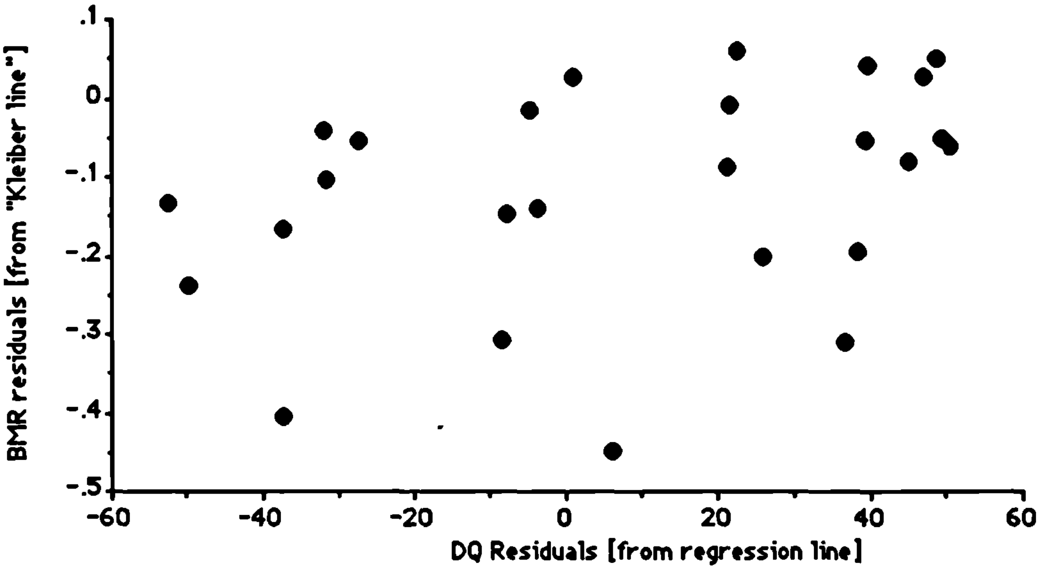
Using species for which BMR data was not available the expected body weight for a species in each group was calculated. Kurland and Pearson calculated the expected body weight by averaging the body weights for all species in a related group, in each of the DQ groups in which that group had members. For example, to find the expected body weight of a New World monkey in DQ group 4, the average body weights of all New World monkeys in group 4 excluding those for which BMR data was available was calculated. The (observed-expected) body weight could then be calculated for the species with BMR data. A similar method was carried out here with the expected body weights being calculated from the average of all species in the same family and DQ group [Kurland and Pearson did not split the species into families but into prosimians, New World monkeys, Old World monkeys and apes]. This set of residuals therefore measured the deviation of the observed body weight from the predicted body weight given a certain diet. This is in contrast to the DQ residuals used in the first correlation which measured the deviation of the observed diet from the predicted diet given a certain body weight. Correlation coefficients were calculated for this second set of residuals with the BMR residuals. As with the correlations above, this was done both using the actual value of the residuals and by treating all values as positive distances.

All the correlation analyses were carried out for all primates together and for the haplorhines and strepsirhines separately, for all New World species together, all Old World species together and for each family where there were three or more species.

Figure 3.6 shows a plot of the BMR residuals against the DQ residuals. There is no correlation between these figures, whether one takes the two suborders together or separately. [There is also no correlation when the residuals of DQ are treated as both positive and negative.] This lack of correlation was consistently found for all groups of primates and for both sets of

Figure 3.6

Basal metabolic rate residuals versus *dietary quality residuals*



residuals.

A further test done by Kurland and Pearson was also carried out. This involved the separation of the species into those with the expected BMR and those with a lower than expected BMR [hypometabolic species]. As with Kurland and Pearson's test, the hypometabolic species included all those with a BMR that is 20% or more below that that would be predicted from the Kleiber relationship. An analysis of variance was then carried out to see if the hypometabolic species had a greater deviation from the Jarman-Bell relationship than did the species with a normal BMR for their size.

It was found that there was some evidence that the hypometabolic species had lower-quality diets than would be predicted from their body weight, with hypometabolic primates having a significantly lower residual value than other primates [ANOVA, $p<0.02$ for both sets of residuals]. This was also found for the haplorhine species, but not for the strepsirhine species, when the two suborders were treated separately. However, the prediction that hypometabolic species would have a greater deviation [i.e. when positive and negative deviations were treated in the same way] from the predicted relationship between diet and body size was not found to be borne out.

The thermoregulatory hypothesis

Another possible correlate of the low metabolic rate of some primates is an adaptation to environments that subject the animals to heat stress [Charles-Dominique, 1974; Müller and Jaksche, 1980]. Kurland and Pearson [1986] also discuss this possible cause for hypometabolism, which they term the "thermoregulatory hypothesis".

A combination of nocturnal activity, a high degree of insulation and hypometabolism has been noted for several species. In addition, these species are generally found in tropical areas where the climate is warm and relatively stable, i.e. in areas where insulation would not be expected to be very important. Müller and Jaksche [1980] suggest that the stability of the temperature has "favoured a tendency towards lower body temperatures and a somewhat 'careless' thermoregulation" [p.276], thus allowing the species to decrease their metabolic rates and save energy. Their low body temperature is partially compensated for by their high insulation and partly by their nocturnal behaviour. By being active at night when temperatures are low, the animals increase their heat production at a time when they are most likely to need it, and their inactivity in the heat of the day means that they avoid heat stress at this time.

This study found that 14 species had BMRs that were 20% or more below the level that would be predicted by Kleiber. Of these, nine have the characteristics of nocturnality and good insulation predicted by the thermoregulatory hypothesis but five species are diurnal. The diurnal species are the sifaka [*Propithecus verreauxi*], the brown lemur [*Lemur fulvus*], a colobus monkey [*Colobus guereza*] and a marmoset [*Callithrix jacchus*]. The sifaka and the lemur are both strepsirhine species that have probably evolved from nocturnal species fairly recently in evolutionary terms. It is therefore possible that their low metabolisms have been retained despite their now being diurnal. It is also interesting to note that both of these species have a large proportion of leaves in their diet, and it is therefore possible that their low metabolic rates may have been originally selected in order to adapt them to hot climates but that this then pre-adapted them to be folivorous. The third diurnal species with a low BMR is a colobus monkey that is also highly folivorous. This also suggests that there could be more than one cause of a low BMR. The value for the marmoset is about 79% of Kleiber and may not be accurate as the experimental details are too sparse to understand the exact measurement conditions [for example, no precise body weight figures are given and the temperature at which the BMR was measured is not stated].

Some species that are tropical, nocturnal and well insulated do not appear to have a particularly low BMR for their size, these are a tarsier [*Tarsius spectrum*], a bushbaby [*Euoticus elegantulus*] and a dwarf lemur [*Cheirogaleus medius*]. The problem with these data is that it is difficult to tell if the BMR has been elevated because of the animals not being in fully basal conditions. With the dwarf lemur, the value for BMR was obtained by taking the metabolic rate for the animals when sleeping and multiplying this value by a correction factor, to take into account the animals lowered body temperature and thus give a BMR value for the animal at its active body temperature [McCormick, 1981]. Although McCormick [1981] argues that this correction factor should be used in order to give the metabolic rate whilst resting but not sleeping, there is evidence that a lowered body temperature is not necessarily linked to a lowered heat production [Müller, 1985] and this correction factor may therefore be incorrectly used in this case. If the actual sleeping metabolic rate of *Cheirogaleus medius* is taken, without any correction factor being applied, it is found to be about 73% of Kleiber and this species would therefore be classified as being hypometabolic. As discussed above, it is probable that the metabolic rate figure used for the tarsier is also too high.

Discussion

The variation in body weight follows some patterns reported by previous workers. Terrestrial species are larger than semi-terrestrial species, which are larger than arboreal species. In addition, the expected relationship between diet and body weight is found with folivores being the dietary group with the largest body size and insectivores and gum-eaters the smallest. It was also found that the habitat of a species can be used to predict its size, with forest and savannah species being large and edge species being small. Surprisingly it was found that the amount of leaves in the diet was not a good predictor of size within habitat groups that contained mostly large species [i.e. forest species, savannah species, semi-terrestrial and terrestrial species]. This may indicate that folivory only selects for an increase in body size in small species. With the exception of the 600g sportive lemur, species that eat over 40% leaves have a mean weight of over two kilograms in weight, and haplorhine species are over six kilograms. If a large size has already been selected for by another aspect of a species ecology, there would presumably be less selective pressure to increase in size because of an increase in folivory. In contrast, insectivory is associated with a small size within habitat groups, suggesting that a highly insectivorous diet requires a small size in all habitats.

Although the measure of dietary quality used was found to correlate highly with body weight, the correlation coefficient was no higher than that found when a multiple regression was carried out using the % animal food and % foliage eaten to predict body weight. The calculation of a dietary quality score and its subsequent correlation with size does not seem to offer any advantages over the use of a multiple regression of % animal food and % foliage eaten on body weight. As the assigning of quality weightings to different food is both time-consuming and based on some rather simplistic assumptions, it is recommended that the multiple regression technique be preferred.

Contrary to the predictions of Bergmann's rule, primates do not seem to increase in size with increasing latitude. Although a very few species groups did show positive correlations between latitude and size, these correlations were frequently low and could be due to chance. One indication that Bergmann's law is operating in these species is that those showing an increase in size with increase in latitude tended to be species whose ranges extended beyond the tropics, although it is notable that other species that are also found in more temperate areas do not show this increase in size. Correlations with climate were equally hard to find, although those that were found consistently suggested that size increased with decreasing temperature and increasing climatic variability.

These results should be viewed with some caution as the measures of latitude and climate used are crude. In particular there is no direct link between the animals used for the body weight measures and the latitude and climate measures used. This mismatch of data will be particularly important in species with a wide geographical range. Bergmann's rule would predict that such species would vary in body weight over their range and hence the data used may not be representative of the environmental measures used. A more precise test of the rule would be to look at the variation in body size of a single wide-ranging species at different latitudes. Despite this, it seems reasonable to assert that Bergmann's rule does not found to be true for the majority primates.

The basal metabolic rate of primates is shown to be about that that would be predicted or below that that would be predicted for a mammal of the same size. This supports the ideas of McNab [1986b] who suggested that mammals eating fruit, leaves and insects would tend to have relatively low metabolic rates. Despite this, there is very little evidence from this study that the diet of a primate has a direct influence on its metabolic rate. A number of tests failed to reveal any definite links between diet and metabolic rate, a result that is in contrast to several previous works on this topic. One possible reason for the contrasting results of this study may be that previous studies have not taken possible phylogenetic effects into account. It appears that, if one removes the confounding effects of phylogeny, there is very little evidence that mammalian metabolic rate is linked to diet [Elgar and Harvey, 1987] and a similar result is found in this study when strepsirhine and haplorhine species are treated as two separate groups.

Nearly all of the strepsirhine species tested so far have been found to have a low relative basal metabolic rate [BMR]. [The only exception found is the needle-clawed bushbaby, but given the consistently low BMR values found for other species of bushbaby I predict that further investigation of this species will contradict these results.] Interestingly the one measure that is available for a tarsier shows a "normal" BMR, a result that suggests that the lowered BMR of the strepsirhines arose in the ancestral stock after the splitting of the strepsirhine and haplorhine lines. However, the work of Roberts [1988] suggests that tarsiers have a low metabolic rate for their size, indicating that the ancestral haplorhines may have has relative low metabolic rates [or, of course, that they have converged with strepsirhines because of common ecological factors selecting for relatively low metabolic rates]. These alternatives await testing.

Whether tarsiers have a low metabolic rate or not, the generally "normal" metabolic rate of the monkeys and apes primates indicates that the low relative BMRs of two haplorhine species, *Colobus guereza* and *Aotus trivirgatus*, have arisen later in time as an adaptive characteristic. This evidence agrees with the assertion of Müller [1985] that a low relative BMR is not a primitive mammalian characteristic but it is adaptive in some way.

Most of the correlations between diet and BMR can be explained as a result of correlations between size, diet and phylogeny [e.g. strepsirhines tend to be comparatively small, small species are more insectivorous] and the fact that strepsirhine species tend to have a relatively low BMR. There does, however, appear to be some evidence that a high degree of folivory is linked to a low BMR, a result that supports McNab's ideas of low quality diets causing relatively low BMRs. However there is no direct evidence that a low quality diet, as measured by the DQ score, leads to a low relative BMR. Contrary to the findings of Kurland and Pearson [1986] there is no evidence that a relatively high quality diet leads to a low relative BMR, or indeed to high relative BMR. The theory that dietary quality is linked to body weight because of the way in which metabolic needs scale to body weight in different animals is therefore not upheld.

It appears, then, that knowing a species' phylogeny allows a better prediction of relative

BMR in the primates than does knowledge of diet. However, there is no satisfactory explanation of the low relative BMR of the strepsirhines that is totally consistent with the data. Variation in relative BMR within the strepsirhine species does not seem to follow any clear pattern or to correlate with environmental factors. Although the thermoregulatory hypothesis seems to explain the low relative BMR of the galagos, lorises and nocturnal lemurs, it cannot explain why the diurnal species of Malagasy strepsirhines also have a low relative BMR. It could be argued that the ancestral strepsirhines were probably tropical nocturnal animals and that their development of a low relative BMR as an energy-saving strategy has been retained by their descendants. If the diurnal lemurs have inherited a low relative BMR as a result of their ancestors being selected to have a poor thermoregulatory mechanism, one would expect that their powers of thermoregulation would also be poor. This poor homeostasis would be emphasized by the animals being diurnal, with inactivity in the coldest part of the day leading to a dropping of the body temperature and activity in the heat leading to a raising of body temperature. If this is the case, it offers an explanation for the rather unusual "sunning behaviour" of the diurnal lemurs, sifakas and indri, which presumably "sunbathe" in the morning in order to raise their body temperature. It may also help to explain the absence of diurnal strepsirhines on the mainland of Africa or Asia, as the disadvantages of imperfect thermoregulation for a diurnal species would be more highly selected against in areas with more competition than island Madagascar.

Although the thermoregulatory hypothesis can explain the low relative BMR of one haplorhine species, the owl monkey, it cannot explain that of the colobus, *Colobus guereza*. Given that this species is known to eat a lot of mature leaves, that are presumably difficult to digest, this suggests that its folivory may be the cause of its low relative BMR.

It therefore seems from the data available that there are two probable causes of a low relative BMR in primates, and in both cases a low relative BMR has evolved as a strategy to save energy. It is suggested that the strepsirhine species evolved a low relative BMR as a part of an adaptation to heat stress in tropical environments, and that although this adaptation was ideally suited to nocturnal living it has been retained in diurnal species because of a lack of variation or of strong selection to change species to having a more normal BMR. In addition a low relative BMR could have pre-adapted species to a low quality diet, such as folivory, as is found in *Lemur fulvus* and the indriids and these species will therefore be predicted to have a lower relative BMR than their less folivorous diurnal relatives. This could account for the comparatively small size of strepsirhines that eat a lot of leaves, as compared to haplorhines. Evidence that a low relative BMR is required for a highly folivorous diet is slim, and is mainly based on the observation that the two characteristics are found in *Colobus guereza*. The low relative BMR of the owl monkey is presumed to be a case of divergent evolution with the nocturnal strepsirhines.

Summary

Body weight is shown to vary with the degree of terrestriality, the habitat and the diet of species. There is no strong evidence to support the theory that body size increases with latitude, although it may do so in a few primate groups. Although there is little firm evidence that climate has a direct influence on body weight all correlations that are found between climate and size indicate that a low temperature and a high climatic variability will lead to a high body weight.

The scaling of metabolic rate to body weight is examined, and the major axis statistics reported. Contrary to the results reported in several recent works, there is no strong evidence that diet is closely lined to metabolic rate. It is suggested that the reason for the low relative BMR of the strepsirhine species is best explained as being an energy-saving adaptation that helps species cope with the heat stress of tropical areas. A folivorous diet may also be linked to the low relative BMR of some species.

Chapter 4

Life-history parameters

In this chapter the basic relationships of primate life-history parameters will be examined, both with respect to body weight and to each other. The relationships found will be compared to other similar studies that have been carried out on mammals, particularly primates. To a certain extent, this chapter repeats the methods of other primate studies, particularly the allometric analyses, which follow those of Rudder [1979], Harvey and Clutton-Brock [1985] and Martin and MacLarnon [1985; 1988]. However, the data set used here is both more up-to-date and considerably larger than those used previously, and it hence seemed advisable to repeat the analyses. This study also looks at the possible influences of taxonomy, diet and ecology on the parameters studied in far more detail than have previous studies.

The characters examined in this chapter are the basic life-history variables in the data set, i.e. neonatal weight, total litter weight, gestation period, litter size, age at first reproduction, interbirth interval, annual birth rate, weaning age and maximum recorded longevity. In addition, some derived parameters are also mentioned: these are r_{max}, prenatal growth rate and postnatal growth rate, although these measures are not discussed in any detail in this chapter, as they are dealt with at length in Chapters 5 and 6. The relationship of the life-history parameters to body weight, metabolic rate and to each other is considered and their variation with taxonomy and a number of environmental variables is discussed. A description of the definitions of the variables and the methods of calculating both the life-history and environmental measures can be found in Chapter 2.

This chapter falls into two sections, the first looks at the patterns of correlation between the life-history parameters, both before and after the effects of body weight have been accounted for and the second is an analysis of the scaling of the variables to body weight. Possible taxonomic, environmental and social correlates of these patterns are considered. The methodology and results are described separately for each section, but the implications of all the results are discussed together at the end of the chapter.

Chapter 4

Correlations between variables

Methods

Correlation coefficients were determined for pairs of variables using all species for which data were available. In all cases logarithmically transformed data were used. As has been discussed in the previous chapters, a large amount of the correlation between life-history variables may be due to their being independently correlated with other parameters, most notably body weight. Because of this problem, partial correlation analyses were carried out to remove the effects of body weight from the correlations between the pairs of parameters, again using the maximum possible number of species. Similarly, the effects of the other life-history parameters were removed from each pair of variables by partial correlation analyses. A discussion of the correlation methods used can be found in Chapter 2.

These analyses were carried out firstly on the haplorhine and strepsirhine data combined and then on the data for the two suborders separately. All correlation analyses were carried out on species data, average genus values and average subfamily values. The partial correlation analyses were carried out firstly on species data only and, if a significant partial correlation was found, the analyses were then repeated using average genus values and average subfamily values.

Results

Correlation coefficients between the logarithmically transformed life-history variables were nearly all highly significant [only three correlations were not significant at the $p<0.001$ level and, of these, only one, between the number of young per litter and the postnatal growth rate of the litter, is not significant at $p<0.05$]. The results for the species data set, the average genus and subfamily data being virtually identical.

The removal of the effects of body weight diminishes the correlations between the variables. The results of the partial correlation analyses can be seen in table 4.1. In the vast majority of cases, the removal of body weight effects leaves an insignificant correlation remaining between variables, although in some cases the correlations remain significant. A few of the significant correlations that remain are between variables that are directly related to each other in an obvious way. For example, it is no surprise to find that interbirth interval [IBI] is highly correlated with birth rate, even after removing body weight effects, as birth rate is calculated directly from IBI and the number of young per litter. Other remaining correlations are of more interest as they may tell us something about the physiological and/or evolutionary relationships between the parameters. It is these relationships that are discussed below.

Partial correlations were also carried out to remove the effects of other variables from pairs of parameters. In the vast majority of cases the large decreases in correlation found when

Table 4.1

Partial correlations of life history Characters, removing the effects of body weight(1)

Parameter	G	Lwt	FGR	IBI	AR	BR	L	WN	PNGR	LGR	RMAX	BMR
N	$0.355^{\dagger}$	$0.851^{\dagger\dagger}$	$0.673^{\dagger\dagger}$	0.005	$0.567^{\dagger\dagger}$	-0.005	0.254^{*}	0.339^{*}	$-0.464^{\dagger\dagger}$	$-0.455^{\dagger\dagger}$	$-0.321^{\dagger}$	$0.671^{\dagger}$
	(59)	(81)	(59)	(66)	(67)	(66)	(71)	(50)	(53)	(53)	(60)	(20)
G	-	0.176	-0.317^{*}	-0.006	$0.395^{\dagger}$	-0.126	0.103	$0.397^{\dagger}$	-0.210	-0.351^{*}	-0.264^{*}	-0.305
		(59)	(59)	(64)	(67)	(64)	(71)	(43)	(48)	(48)	(60)	(21)
LWt			$0.878^{\dagger\dagger}$	0.004	$0.522^{\dagger\dagger}$	0.190	0.129	0.150	$-0.372^{\dagger}$	-0.156	-0.121	$0.716^{\dagger\dagger}$
			(59)	(66)	(67)	(66)	(71)	(50)	(53)	(53)	(60)	(20)
FGR			-	0.010	0.280^{*}	0.174	0.006	0.015	-0.244	-0.004	-0.003	$0.779^{\dagger\dagger}$
				(52)	(54)	(52)	(55)	(43)	(44)	(44)	(50)	(18)
IBI				-	$0.351^{\dagger}$	$-0.893^{\dagger\dagger}$	0.211	0.117	-0.012	-0.007	$-0.845^{\dagger\dagger}$	0.337
					(73)	(84)	(73)	(48)	(49)	(49)	(73)	(23)
AR					-	$-0.321^{\dagger}$	0.279	$0.490^{\dagger\dagger}$	$-0.514^{\dagger\dagger}$	-0.470	$-0.672^{\dagger\dagger}$	0.339
						(73)	(77)	(46)	(52)	(52)	(73)	(21)

Table 4.1 [continued]

Parameter	BR	L	WN	PNGR	LGR	RMAX	BMR
BR	-	-0.262^{*}	-0.263	0.041	0.207	$0.911^{\dagger\dagger}$	-0.199
		(73)	(48)	(49)	(49)	(73)	(23)
L		-	0.190	0.047	-0.027	$-0.399^{\dagger}$	0.254
			(46)	(53)	(53)	(69)	(23)
WN			-	$-0.544^{\dagger\dagger}$	$-0.613^{\dagger\dagger}$	$-0.401^{\dagger}$	-0.052
				(38)	(38)	(45)	(18)
PNGR				-	$0.920^{\dagger\dagger}$	0.266	-0.471
					(58)	(47)	(17)
LPNGR					-	$0.377^{\dagger}$	-0.258
						(47)	(17)
r_{max}							-0.384
							(20)

N=neonatal weight, Lwt=litter weight; G= gestation length; FGR= foetal growth rate; IBI=interbirth interval; AR= age at first reproduction (female); BR= birth rate; L= 10=maximum recorded longevity; WN=weaning age; PNGR =post-natal growth rate, LGR = litter post-natal growth rate; BMR=basal metabolic rate.

*=0.05, †=0.01,††=0.001

(1) Figures in parenthesis indicate sample size

body weight was removed were not duplicated. However, the removal of neonatal weight [or total litter weight] also gave a large reduction in correlation coefficients, including the correlations found between many variables and body weight. Hence partial correlations removing these parameters are also discussed here.

Partial correlations with neonatal weight and litter weight

Previous work by Harvey and Clutton-Brock [1985] has suggested that relative neonatal weight is correlated with relative gestation length, relative weaning age, relative age at maturity and relative life span. However, Harvey and Clutton-Brock's study looked only at the primate sample as a whole and did not investigate the strepsirhine and haplorhine species separately. It has been demonstrated by Rudder [1979], and confirmed in this study [see later in this chapter], that strepsirhine species have significantly lower neonatal weights and litter weights than do haplorhines of the same size, with a haplorhine neonate being about three times heavier than a strepsirhine neonate weight from a mother of the same weight. As there is evidence that the two suborders show different relationships between neonatal weight and body weight it was felt necessary to investigate the two groups separately.

As with Harvey and Clutton-Brock's [1985] work, this study also finds that, when all primates are considered together, neonatal body weight and gestation length are significantly correlated once the effect of body weight are removed, i.e. for two primate species of a given body size one with a longer gestation length will tend to produce a larger neonate. This is a result that one might intuitively expect; it seems reasonable to suppose that one way of increasing neonate size would be to increase gestation length. What is more surprising is that the correlation is so low, with less than 13% of the residual variation in neonatal weight being accounted for by gestation length [$r=0.35$, $p<0.01$], and that there is no significant correlation found between relative <u>total</u> litter weight and gestation length [$r=0.17$, $r>0.1$].

When one looks at the two suborders separately, the positive partial correlation between litter weight and gestation is also significant for the haplorhines [$r=0.37$, $p<0.05$] and that for neonatal weight and gestation is also significant [$r=0.40$, $p<0.05$]. This indicates that the expected relationship is found in the haplorhines, i.e. that a longer gestation period is associated with heavier offspring, after the effects of body weight have been accounted for.

When one looks at the same relationships in the strepsirhine species, a rather surprising result is found. There is no significant correlation between neonatal weight and gestation length after the removal of body weight effects. It was thought that this might be due to many strepsirhine species having multiple litters and the resulting variation in litter size obscuring the relationship between neonatal weight and gestation. However, when the relationship between total litter weight and gestation length, removing the effects of body weight, was investigated, a negative partial correlation between litter weight and gestation length [r=-0.43, p<0.05] was found. This negative partial correlation is also found when using average genus or average subfamily values [and in fact the partial correlation coefficient is higher at these levels]. It appears then, that strepsirhines with a relatively long gestations actually produce relatively lighter litters than do those with relatively short gestation periods.

Foetal growth rate is calculated from dividing neonatal weight by gestation length. As might be expected,from this a significant partial correlation of litter weight [and neonatal weight] and foetal growth rate is found for all groups and at all taxonomic levels, i.e. a species with a relatively high neonatal weight will have a relatively high foetal growth rate. However, when the haplorhines are looked at, this correlation is surprisingly low, with only about 15% [r=0.39, p<0.05] of the variation in relative foetal growth rate being accounted for by variation in relative litter weight. This is presumably because the variation in relative litter weight can be counteracted by the variation in gestation length, as a haplorhine species with a high relative litter weight will tend to have a relatively short gestation length and hence will not necessarily have a high foetal growth rate. Similarly, there is a low correlation between relative gestation length and relative foetal growth rate in the haplorhine species, as the effect on foetal growth rate of an increase in gestation length may be counteracted by an increase in neonatal weight.

In the strepsirhines, the negative correlation between relative litter weight and relative gestation length is reflected in the very high partial correlation coefficients found between foetal growth rate and litter weight [r=0.87, p<0.001] and foetal growth rate and gestation length [r=-0.82, p<0.001], as species will tend to have relatively short gestations, large litter weights and hence high foetal growth rates, or the converse set of characters.

The relationship between body weight, neonatal weight, litter weight and gestation length is further clarified when one looks at the correlation between body weight and gestation length with the effects of neonatal weight [or litter weight] removed. This partial correlation is insignificant for all primates and for strepsirhines and haplorhines separately, whereas the correlation between body weight and neonatal weight [or litter weight] with the effects of gestation length removed remains highly significant in all cases. These results indicate that gestation length is correlated with body weight *via* the correlation between neonatal [or litter] weight and body weight, so that the links between the three parameters can be represented as:

Gestation length ⟷ **Litter weight** ⟷ **Adult body weight**

Given this relationship it is difficult to understand how a larger litter weight could lead to a longer gestation length in haplorhines but to a shorter gestation length in strepsirhines. One possible complicating factor is metabolic rate. Neonatal weight and litter weight both have significant positive partial correlations with basal metabolic rate [BMR] when the whole primate sample is considered and when the strepsirhine species are considered separately [although not when the haplorhine species are considered separately]. It therefore appears that a low relative BMR in the strepsirhines is associated with a low relative litter weight. In addition it was noted that some strepsirhine species with particularly low BMRs, mainly the Lorisinae, also had much longer gestation lengths than other strepsirhines of the same size. It was therefore thought that the negative correlation between relative litter weight and gestation length in the strepsirhines could be due to some species increasing their gestation times so as to compensate for the low foetal growth rate imposed on them by a low metabolic rate, but still having to produce litters of a low weight.

There is a highly significant negative correlation between gestation length and BMR after the effects of neonatal weight have been removed in both suborders [r= -0.60, p<0.01 for haplorhines and r= -0.67, p<0.01 for strepsirhines]. This indicates that, for the production of a infant of given weight, an increased BMR will lead to a shorter gestation length. However, the partial correlation of gestation length and BMR after the effects of litter weight have been removed is not significant in strepsirhines [p>0.05], although it is in haplorhines. Partial correlations removing the effects of both body weight and litter weight from the correlation of gestation length and BMR were found not to be significant.

To test whether BMR did have a positive correlation with litter weight, once confounding variables were removed, a partial correlation of BMR and litter weight, removing the effects of both gestation length and body weight, was carried out. Although this partial correlation was significant for the whole sample [r=0.54, p<0.01, one-tailed test], the low sample size engendered by the use of four variables meant that a similar partial correlation coefficient for the strepsirhine species was insignificant [r=0.51, p>0.05]. No correlation was found for the haplorhine species [r=0.361, p>0.05].

Although the statistical evidence that a low BMR will lead to a low litter weight and low gestation length is slim, further evidence of the links between a low BMR, a long gestation and a low litter weight are found when the effects of BMR and body weight are removed by a partial correlation from the correlation between litter weight and gestation period. This partial correlation is insignificant [p>0.05] indicating that the reason for the negative correlation between relative gestation length and relative litter weight in the strepsirhines could be due to the influence of metabolic rate on both of these parameters. These relationships are discussed further below and in Chapter 6.

Neonatal weight also correlates positively with age at first reproduction and weaning age, and negatively with postnatal growth rate. When one looks at the correlations between these parameters in the haplorhine group separately, most are also found to be significant, but in the strepsirhine species no correlations are found. A haplorhine, of a given size, with a large neonatal weight will therefore be expected to mature relatively slowly. [Similar results are found if one looks at litter weight rather than neonatal weight, although the correlations with postnatal growth rate are not found.] The strepsirhine species do not show this link between a large infant [or litter] weight and slow maturation, and in fact there is a significant positive correlation between litter weight and postnatal growth rate in the strepsirhine species. This will be discussed further in Chapter 6.

After the removal of body weight, the following variables were found to have significant positive correlations with age at first reproduction; neonatal weight, litter weight, gestation length, weaning age and foetal growth rate [FGR]. Age at first reproduction also has significant negative partial correlations with; interbirth interval, birth rate, postnatal growth rate [of both the individual offspring and the total litter] and $r_{max.}$ Correlation of age at first reproduction with the first two variables in the above list has already been discussed. The correlation with FGR is very low [r=0.28] and is not found when the effects of neonatal weight are removed. The correlation with r_{max} is expected, as age at first reproduction is one of the variables used to calculate r_{max}. Therefore, these parameters are not discussed here [but see Chapter 5 for further consideration of the variation in r_{max}]. This leaves six parameters to be discussed, four closely related developmental variables [gestation length, PNGR, LPNGR, and weaning age] and two variables relating to rate of production of offspring [IBI and birth rate].

The results show that, for primates overall, a relatively early age at first reproduction is linked to a relatively short gestation period, a relatively rapid postnatal growth rate, relatively early age at weaning and a high birth rate. However, it is interesting to note that none of these relationships is found when the strepsirhine species are considered separately, although they are all found when only the haplorhine species are looked at. This lack of correlation within the strepsirhine species could be due to their very small degree of variation in age at first reproduction. Of the 21 strepsirhine species for which data is available, ten start breeding in their first year and all of the remaining species [except *Propithecus verreauxi*, which starts breeding at about 3.5 years] first produce young in their second year.

Two other partial correlations that are found only for haplorhine species are negative relationships between weaning age and r_{max} and longevity and r_{max}. This indicates that rapid infant development is linked to high rate of population increase and a long lifespan in the haplorhine primates. In the strepsirhines, weaning age is found to be positively correlated with gestation length and negatively with postnatal growth rate after the removal of body weight effects. This indicates that species with a long gestation will also have a late weaning age and a slow postnatal growth rate. These relationships are discussed further in Chapter 6.

Chapter 4

Bivariate analyses

Methods

The methods used here, and the reasons for using them, are described in detail in Chapter 2. Briefly, a bivariate [major axis] analysis was carried out on logarithmically transformed data to determine the relationship of each parameter to body weight. Once the basic form of the allometric relationship between the parameters and body weight was determined the effects of taxonomy and ecological variables on these relationships were investigated, particularly with respect to the relative values of the parameter in question.

For the following bivariate analyses, the plots of the life-history parameters against body weight show the species points about the major axis best-fit line for average species values. This is done to enable comparisons with other studies, the majority of which use statistics based on the assumption that species' values can be treated as independent points. As discussed in Chapter 2, there is some justification for using the average subfamily values rather than species values for this type of analysis. All analyses were therefore repeated using average genus and subfamily values. Although the equation that is discussed is that found using average species values, the major axis best-fit lines obtained using either average genus or average subfamily points are not usually significantly different from these. For reference, the statistics for the major axis best-fit lines at each taxonomic level can be found in results tables given in this, and following, chapters. The number of species considered varies according to the parameter under discussion and the precise make-up of the data set for each parameter or groups of parameters can be found by referring to the data lists in the appendices.

In some cases, the possible presence of grades of organisation is discussed. To test for significant differences between groups that show a similar scaling exponent, but that are thought to be different in the elevation of their best-fit lines, the "ANOVA test of residuals" described in Chapter 2 is used. This tests for differences between groups by first taking residuals from a best-fit line of average slope through the means of the whole sample [i.e. all groups together]. The residuals are then tested with an analysis of variance to see if the groups have significantly different residual values. If the test shows significant differences between groups they are treated separately for further analyses.

When looking at the possible relationships between the life-history variables and the ecological variables, three measures of the species' ecological type were examined: diet, habitat type and degree of arboreality. The procedure used was basically the same as that used in the previous chapter to examine the variation in body weight and BMR. For diet, two tests were carried out. Firstly, the proportion of each diet component eaten was correlated with each set of residual values. Secondly, an analysis of variance was carried out to test whether species classified in different dietary categories had different residual values of the parameter in question. For habitat type and degree of arboreality only the analysis of variance tests were carried out. Both parameters were classified as discussed in Chapters 2 and 3. Habitat type was tested using both the "broad" and "narrow" categories.

As mentioned in previous chapters there is good reason for supposing that phylogeny will be reflected in the scaling relationships of life-history parameters. Previous work has suggested that the main division in the primate order is between the strepsirhine and haplorhine primates [e.g. Rudder, 1979; Leutenegger, 1973] and this is examined here. In addition work by Kirkwood [1985] on growth rate has indicated that further grades of organisation may be found. Kirkwood's work found that when looking at the growth rate of primates the data could usefully be split into prosimians, New World monkeys, Old World monkeys and apes. In the light of this, tests were also made to see if these groups could be separated out in this way for any of the parameters discussed in this thesis. Similarly, the possibility of the primate families representing different grades of organisation was investigated. Further details of the way in which this was carried out can be found in Chapter 2.

Results

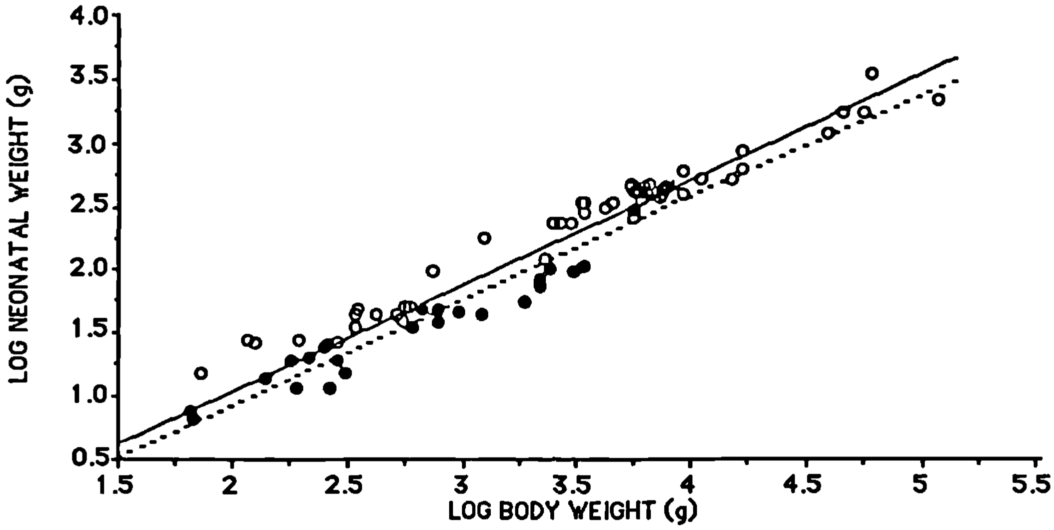
Individual neonatal weight and total litter weight

The weight of the neonate is a measure of the total parental investment made in the young up to birth. Although parental investment will also include other uses of resources [e.g. investment in the placenta] neonatal weight is a commonly measured parameter and species can easily be compared. Two measures of offspring weight at birth can be used, the individual neonatal weight or the total weight of the litter. For the rest of this chapter, and indeed this thesis, the term "neonatal weight" will be used to describe the individual neonatal weight and the term "litter weight" the total weight of the litter. Further discussion on the question of parental investment can be found in Chapter 6, which is solely devoted to the variation in different measures of parental investment.

Data on neonatal weight was available for 81 species, representing 44 genera and 18 subfamilies. The relationship of neonatal weight to body weight in the primates can be seen in figure 4 1 and table 4.2. As expected from previous work [e.g. Rudder, 1979] the correlation between log neonatal weight and log body weight is high, with approximately 95% of the variation in log neonatal weight being predictable from variation in log body weight. The relationship between neonatal weight and body weight for primate species is described by the equation: $N = 0.23\ M^{0.84}$, where N= neonatal weight in grams and M = average adult body weight in grams. The value of the slope for subfamily values is just within the 95% confidence limits found by Harvey and Clutton-Brock [1985], who obtained a slope value of 0 93 for the average subfamily values. As this study contains more species [81 rather than 70] than does the previous study, the exponent value of 0.83 is probably the more accurate. The close agreement

Figure 4.1

Log$_{10}$ neonatal weight versus *log$_{10}$ mean body weight for primate species*



● **Strepsirhine species**

○ **Haplorhine species**

——— Major axis best-fit line for primates, data from this study

--- Best-fit line for mammals from Martin and MacLarnon [1988], using fixed slope of 0.85.

between the exponent value obtained in this study and those found by Martin and MacLarnon [1985] for 74 primate species and by Martin and MacLarnon [1985, 1988] for a large sample of mammals gives further support for its preference over that obtained by Harvey and Clutton-Brock [1985]. However, if the two primate suborders are considered separately there is evidence for a slope of even lower value.

Table 4.2

Major axis statistics for log_{10} *neonatal weight vs.* log_{10} *body weight*

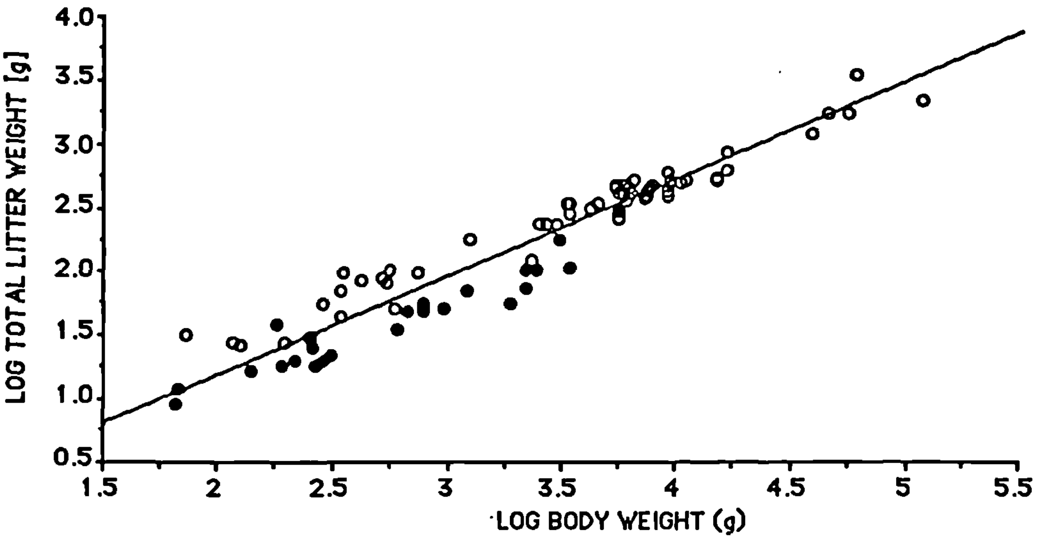
Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	81	0.97	0.84	-0.63	0.79	0.89
	genera	44	0.97	0.83	-0.61	0.77	0.89
	subfamily	18	0.98	0.84	-0.62	0.75	0.94
Strepsirhines:	species	23	0.96	0.73	-0.50	0.65	0.83
	genera	13	0.95	0.76	-0.57	0.61	0.94
	subfamily	5	0.99	0.76	-0.57	0.63	0.92
Haplorhines:	species	58	0.98	0.75	-0.28	0.71	0.80
	genera	31	0.98	0.74	-0.22	0.69	0.79
	subfamily	13	0.99	0.77	-0.33	0.69	0.86

From figure 4.1 it can be seen that there is some indication that strepsirhine species have a relatively lower neonatal weight than do haplorhine species. This view is supported when the residuals [from the best-fit line for all primates] are examined, as all except one of the strepsirhine species represented show a relatively low neonatal weight [*Cheirogaleus medius* is the exception, with a neonatal weight very slightly larger than would be expected for its size]. The 95% confidence limits of the lines calculated for the two groups separately show considerable overlap, indicating that the slope of the two lines is not different. When the residuals are calculated from the average slope, the two groups are found to be significantly different [ANOVA, $p < 0.05$]. It can be said, therefore, that a strepsirhine will tend to have a relatively smaller neonatal weight than will haplorhine species. It is interesting to note that consideration of the two orders separately leads to both groups showing scaling of neonatal weight to the power of approximately $^3/_4$ body weight, i.e. the same exponent as is found for metabolic rate. This is discussed below. No systematic phylogenetic differences in relative

Figure 4.2

Log_{10} total litter weight versus *log_{10} mean body weight*

for primate species



● **Strepsirhine species**

○ **Haplorhine species**

—— Major axis best-fit line for primates, data from this study neonatal weight within the strepsirhines or the haplorhines could be found.

The allometry of total litter weight [i.e. litter size X neonatal weight] in primates and in the mammals generally has been well documented by several people [e.g. Leutenegger, 1973, 1976, 1977; Stearns, 1983; Harvey and Clutton-Brock, 1985]. The results obtained here are in basic agreement with these studies.

Data on litter weight were available for the same 81 species as used for neonatal weight [i.e. representing 44 genera and 18 subfamilies]. The relationship of litter weight [T] to average adult body weight in grams [M] in the primates can be seen in figure 4.2 and table 4.3 and is described by the equation:

$$T = 0.48\, M^{0.76}.$$

Table 4.3

Major axis statistics for $\log_{10}$ litter weight vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	81	0.96	0.76	-0.32	0.71	0.81
	genera	44	0.96	0.75	-0.28	0.68	0.81
	subfamily	18	0.97	0.77	-0.36	0.68	0.87
Strepsirhines:	species	23	0.95	0.66	-0.20	0.57	0.77
	genera	13	0.94	0.69	-0.27	0.54	0.87
	subfamily	5	0.98	0.64	-0.12	0.44	0.89
Haplorhines:	species	58	0.94	0.67	0.04	0.63	0.72
	genera	31	0.98	0.66	0.11	0.61	0.71
	subfamily	13	0.98	0.73	-0.17	0.64	0.84

As noted by Leutenegger [1973] and Rudder [1979] there is evidence that this relationship is better described by taking the strepsirhine and haplorhine species separately [see figure 4.2]. Taking the residuals from about a average value fixed slope of 0.66, it was found that the relative total litter weight of the strepsirhine species was significantly lower than that of haplorhines [ANOVA, $p<0.05$]. As in previous studies, the data used here give a lower allometric exponent value [about 0.66] when the two groups are treated separately. No systematic phylogenetic differences in relative litter weight within the strepsirhines or the haplorhines could be found.

These analyses therefore raised two questions. Firstly, why do neonatal weights and total litter weights scale to body size in the way that they do? Secondly, why do strepsirhine species have lower relative neonatal weights and total litter weights than do haplorhine species?

The first question is complicated by the fact that the allometric exponent varies depending on whether one takes the primate group as a whole or whether one looks at the haplorhines and strepsirhines separately, and on whether one looks at individual neonatal weight or total litter weight.

It was considered that the difference in relative neonatal weights could be related to the strepsirhine group containing a number of species that produce more altricial young than do other primate species. In the mammals, there appears to be a dichotomy between those species that produce precocial young and those that produce altricial young [Martin and MacLarnon, 1985; 1988]. Altricial mammals produce larger litters of less well developed young than do precocial mammals, and the size of each neonate, relative to the maternal size, is therefore smaller in altricial mammals. Although the criteria used by previous workers who were looking at all mammals [e.g. Martin and MacLarnon, 1985; 1988; Case, 1978], classify no primate species as altricial, it is acknowledged that some primate species cannot be classified as being completely precocial [Case, 1978].

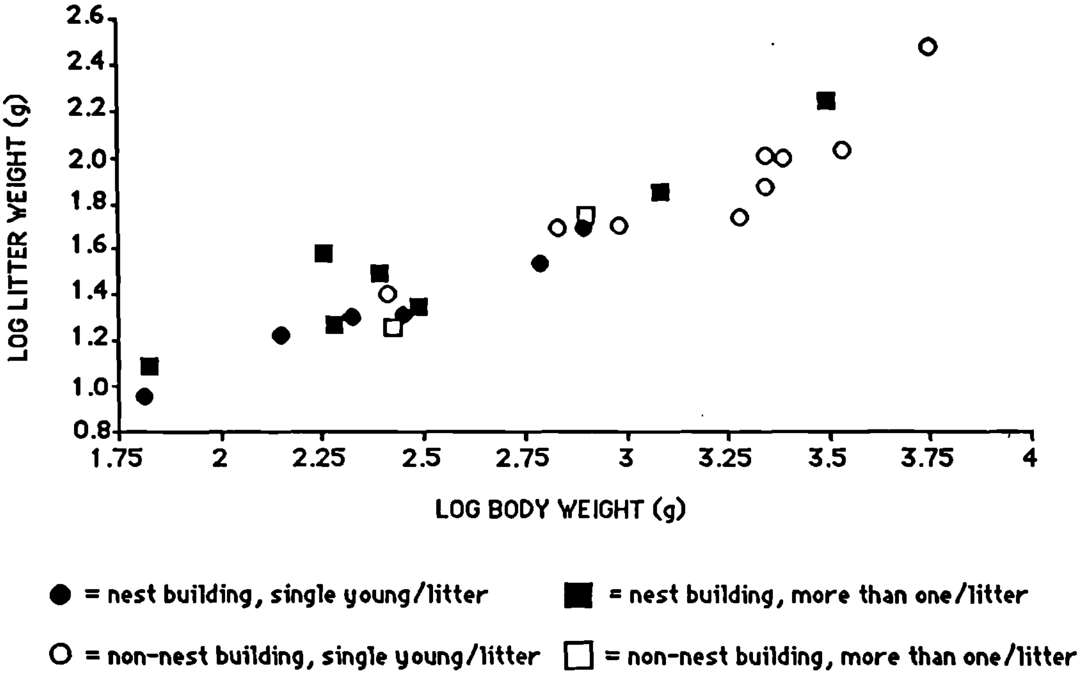
Figure 4.3 shows the strepsirhine species split into two groups, 1 and 2. Group 1 species are the "true precocial" species and group 2 species the "partially altricial" species. The "partially altricial" species were taken as those that give birth to their young in nests, and whose young do not have their eyes open at birth, they therefore include *Varecia variegatus*, *Galago* species, *Microcebus* species, *and Cheirogaleus* species. As can be seen, there is no evidence that the more altricial strepsirhine species give birth to smaller young than do the precocial species, whether size is taken as individual neonatal weight or total litter weight. The four species of *Lemur* all produce relatively small neonates, despite their producing young that are born with their eyes open and developed enough at birth to be carried clinging to the mother's fur. This result is not changed if a third criterion, the production of multiple litters, is added to the definition of "altricial" primates, as the *Galago* species that tend to produce singletons [*G. demidovii*, *G. senegalensis*, *G. zanzibaricus* and *G. garnetti*] also have relatively small neonates and litter weights for primates.

Other factors that could influence neonatal size are diet, habitat type or the social structure of the population. All of these factors could influence the quality and quantity of resources available to the mother and hence could influence selection on neonate size. However none of these factors were found to have any correlation with either relative neonatal weight or relative litter weight.

The scaling of individual neonate weight to the 0.75 power of body weight, when

Figure 4.3

Log_{10} total litter weight versus *log_{10} mean body weight for strepsirhine species, showing nest-building and litter size*



strepsirhines and haplorhines are looked at separately, indicates a possible link between metabolic rate and neonate size [Rudder, 1979; Martin, 1975 (but see below)]. If metabolic rate and neonate weight were linked, their connection could also offer a possible explanation for the smaller size of strepsirhine primate neonates, in that strepsirhine species tend to have both a relatively low neonate weight and a low metabolic rate. Some evidence that the two parameters are connected is discussed above, i.e. that when a partial correlation between $\log_{10}$ BMR and $\log_{10}$ litter weight is carried out for strepsirhine species, removing the effects of body weight, the result is a significant positive correlation indicating that about 60% of the variance in one parameter can be accounted for by the variance in the other. It therefore appears that there is some evidence linking relative litter weight with relative BMR, at least in the strepsirhine species. However, when the partial correlation between neonatal weight and BMR is looked at for the strepsirhines and haplorhines separately, there is found to be no significant correlation between the two parameters. It seems, then that if BMR is linked to the weight of the offspring at birth it is to the total litter weight and not to individual litter weight. In fact the 95% confidence limits of the best-fit lines for log litter weight *vs.* log body weight include 0.75 in most cases [see table 4.3], and there is therefore no reason to assume that total litter weight is not correlated with metabolic rate. Indeed it seems more likely that total litter weight would be a better measure of the mother's energy input into pregnancy than would individual neonatal weight and therefore the former measure would be the one expected to correlate with metabolic rate.

One objection to this theory is that although the haplorhine species have a BMR that scales to the 0.75 power of body weight, the strepsirhine species do not [see Chapter 3, this work]. It might therefore be expected that the litter weight would similarly scale differently in the two groups. Although there does not seem to be this expected difference, the confidence limits for the exponent values are quite wide for both groups and it is therefore impossible to say whether or not this is the case. There is also evidence from this study that species with particularly low BMRs do not necessarily have very low neonatal weights for their size. For example, *Loris tardigradus* has both a low relative BMR and a low relative neonatal weight, but *Nycticebus coucang* has a low relative BMR and a high relative neonatal weight [for a strepsirhine]. Similarly, when one looks at the two haplorhine species with known to have a relatively low BMR, the colobus monkey [*C. guereza*] has a low neonatal [and litter] weight for a haplorhine of its size, but the other, the owl monkey, has a slightly heavier litter weight than one would predict for a haplorhine of its size.

However, as has already been mentioned, the variation in gestation length is a further complication in this relationship and there is also the possibility that BMR does not reflect the metabolic rate during pregnancy. These questions are pursued further in Chapter 6.

Another explanation for the relationships found between of litter weight and body size was suggested by Leutenegger [1973]. He suggested that the weight of the litter was determined by the surface area of the placenta. The evidence for this is that litter weight scales to body weight to the power of $^{2}/_{3}$ i.e. in the same way as surface area scales to volume. However, as pointed out by Rudder [1979] this explanation assumes that the placenta weight scales isometrically to adult body weight. However, Rudder's investigations indicate that placental weight scales isometrically with neonatal weight. Hence, if Leutenegger's argument is correct, the surface area of the placenta [S] would scale to adult body weight [M] in the following way:

$$S = kM^{(0.75)0.67} = kM^{0.50}$$

[where k is a constant that would be different for strepsirhines and haplorhines].

This gives allometric exponent value [0.50] that is outside the 95% confidence limits of the empirically determined exponent of either suborder.

Another explanation for the difference found between strepsirhines and haplorhines is given by Leutenegger [1973]. He suggests that the difference is due to strepsirhines and haplorhines having different types of placentation. Strepsirhine species have a non-invasive, epithelioclorial placentation, a type that is often considered to be less efficient than the invasive, haemochlorial placentation found in the Haplorhini. Leutenegger therefore suggests that the haplorhine type of placentation allows faster transfer of nutrients from the mother to the developing foetus and thus allows the production of larger neonates. However, when looking at other placental mammals Martin and MacLarnon [1988] found that several groups with a non-invasive, epithelioclorial placentation had relatively large neonates as compared to any primates, despite having similar relative gestation lengths. They therefore conclude that ".... there is no evidence that the non-invasive epithelioclorial type of placentation constrains either the rate or the extent of foetal development ....". This conclusion is further supported when the rate of primate foetal growth is looked at when it appears that the rate of foetal growth is not correlated with the placental type.

It therefore appears that neither the "metabolic rate" nor the "surface area" hypotheses adequately account for the observed relationships between neonatal [or litter] weight and body size. This point has also been made Martin and MacLarnon [1985; 1988], who suggest that there is evidence that a exponent value of approximately 0.8 to 0.85 for individual neonate scaling will be theoretically predicted. Martin and MacLarnon show that gestation length [G] in mammals can be taken to scale to approximately the 0.1 power of adult body weight [M], so that:

$$G = kM^{0.1}$$ [Where k is a constant]

Within species gestation length is also predictable from the relationship between neonatal weight [N] and gestation length [g]:

$$N=aG^3$$

Where a is a constant known as the foetal growth factor [this is an approximated equation that ignores the time lag between conception and the start of growth].

The foetal growth factor [a] also scales allometrically to body weight, so that:

$$a= k_2M^{0.5} \qquad \text{Where } k_2 \text{ is a constant.}$$

A combination of equations above leads to:

$$N \; = aG^3 = (k_2M^{0.5}) (kM^{0.1})^3 \qquad = kk_2M^{0.8}$$

Similarly, the value of the scaling exponent of either gestation length or the foetal growth factor can be predicted if the scaling exponent of neonatal weight and the other parameter is known.

The scaling parameters for neonatal weight found by Martin and MacLarnon [1985; 1988], for all mammals, are similar to those found in this study. The 95% confidence limits of the major axis slope for all primates together and for strepsirhines and haplorhines separately all include the value of 0.8. Hence, use of this approach does not help to explain the difference between strepsirhines and haplorhines, but does indicate that, if the two groups are treated separately they results are consistent with the work of Martin and MacLarnon.

Gestation length

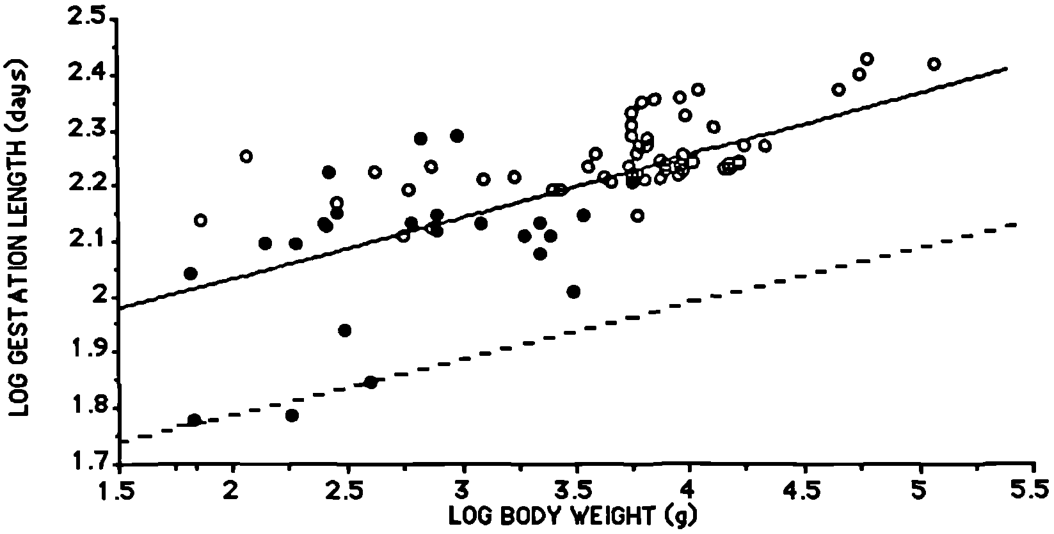
Data on gestation length were available for 78 species, representing 44 genera and 18 subfamilies. Figure 4.4 and table 4.4 show the relationship between gestation length and average adult body weight. These results are in agreement with those found by Martin and MacLarnon [1985] for slightly fewer species [74] and with Harvey and Clutton-Brock [1985].

It might be expected, from their relatively lower neonatal and litter weights, that the strepsirhine species would tend to have relatively low gestation lengths for their body sizes. Although some strepsirhine species do have shorter gestation periods for their body size than haplorhines it is notable that 3 out of the 4 lorisid species show a gestation length that is relatively longer than most haplorhines, whereas other strepsirhine species have similar relative gestation lengths to haplorhine species. Other conspicuous features of figure 4.4 are the exceptionally short relative gestation lengths of the Cheirogaleinae, and the very long relative gestation length of the only tarsier for which data is available [*Tarsius bancanus*]. If one looks at

Figure 4.4

Log_{10} gestation length versus *log_{10} mean body weight*

for primate species



● **Strepsirhine species**

○ **Haplorhine species**

——— Major axis best-fit line for primates, data from this study

\--- Best-fit line for mammals from Martin and MacLarnon [1988], using fixed slope of 0.85.

the data with these Cheirogaleinae and *Tarsius* outliers removed, there is no significant difference between the relative gestation lengths of haplorhine and strepsirhine species [ANOVA, $p > 0.05$, at all taxonomic levels].

Table 4.4

Major axis statistics for $\log_{10}$ gestation length vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	78	0.69	0.11	1.81	0.09	0.14
	genera	44	0.67	0.11	1.85	0.07	0.14
	subfamily	18	0.74	0.12	1.81	0.06	0.18
Strepsirhines:	species	24	0.41†	0.11	1.79	0.00	0.21
	genera	13	0.35†	0.11	1.80	-0.08	0.30
	subfamily	5	0.53†	0.15	1.67	-0.32	0.70
Haplorhines:	species	54	0.66	0.07	1.98	0.05	0.09
	genera	31	0.77	0.08	1.97	0.60	0.11
	subfamily	13	0.82	0.09	1.95	0.05	0.13

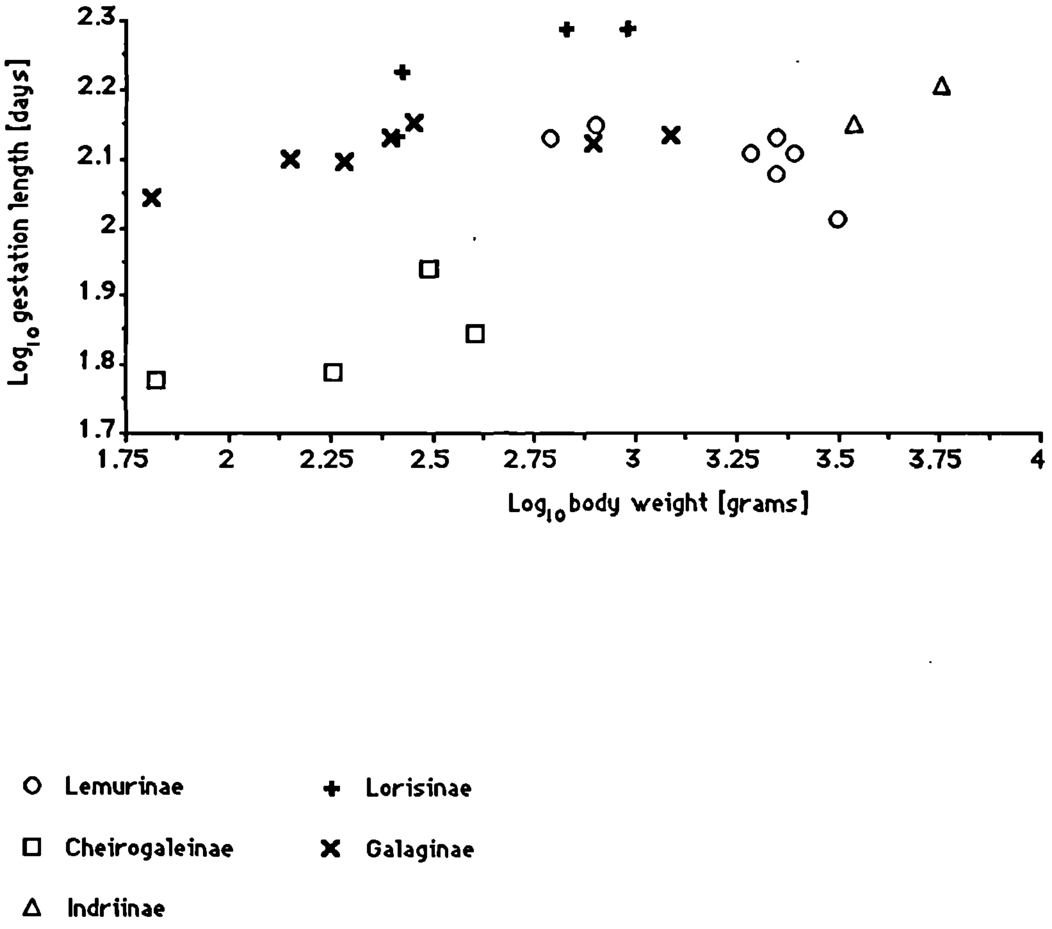
†=not significant [$p > 0.05$]

Within the strepsirhines, there is no significant correlation between body size and gestation length at any taxonomic level [see table 4.4] and even this insignificant correlation is reduced when the Cheirogaleinae are removed. However, this surprising lack of an association between gestation and body weight is explained when one looks at the two main taxonomic groups of the strepsirhines separately. As shown in figure 4.5, in both the Lorisidae and the Lemuridae, there is evidence of gestation length scaling to body size with the Lorisidae having a relatively longer gestation length than do the Lemuridae. [This difference is significant for both species and genus points (ANOVA of residuals $P < 0.01$) and nearly significant at the subfamily level where the very small sample size reduces significance ($p = 0.06$).] This relatively short gestation in the lemur family is significantly below that of the haplorhine species [ANOVA, $p < 0.05$], whereas the longer gestation of the loris family is statistically indistinguishable from that of the haplorhines.

Figure 4.5

Log_{10} gestation length versus *log_{10} mean body weight*

for strepsirhine species



Within the **Haplorhini**, there is evidence of gestation length being related to taxonomic position. Within the three monkey families [**the Cercopithecidae, the Cebidae and the** Callitrichidae] there are groups with both relatively long and relatively short gestation lengths. Within the Old World monkeys the two colobine species for which data is available [*Presbytis entellus* and *Pygathrix nemaeus*] have relatively long gestations, whereas the Cercopithecinae are characterized by short gestation periods for their body size. Similarly, in the cebid monkeys the Atelinae have relatively long gestations whereas *Cebus* species and *Aotus trivirgatus* have relatively short gestations. As noted previously, *Tarsius bancanus* stands out as having a very long gestation period for a small primate. The apes and humans have gestation periods that are longer than would be expected for haplorhines of their size. This difference is significantly different when the gestation residuals of apes and humans together are compared to other haplorhines [ANOVA, $p=0.027$].

When investigating the effects of diet, habitat and social system the results tended to reflect these taxonomic divisions between the species. The main folivorous groups in the Old and New World monkeys [the Colobinae and the Alouattinae respectively] are represented by two colobine monkeys [*Presbytis entellus* and *Pygathrix nemaeus*] and three species of howler monkey [*Alouatta* species.]. The former two species have relatively long gestation periods whereas the gestations of the latter three are about what would be expected for animals of their body size. The other folivorous species included in the analyses are four strepsirhine species [*Lemur fulvus*, *Indri indri*, *Hapalemur griseus* and *Lepilemur mustelinus*] and three haplorhines: the siamang, [*Symphalangus syndactylus*], the gorilla, [*Gorilla gorilla*] and the graminivorous gelada baboon [*Theropithecus gelada*]. Of these species, all have relatively long gestation periods, except for *Lemur fulvus* and *Theropithecus gelada*. The evidence for a link between folivory and long gestation periods is therefore somewhat tenuous. [It should be noted that the gelada baboon is not folivorous in the same way as the other species (as it eats mostly grasses and not leaves of woody plants) and therefore it might not be predicted to have a long gestation]. No link between relative gestation period and frugivory or insectivory could be found. As might be expected from these results, there was also no significant correlation between the proportion of different food eaten and relative gestation period. No link between habitat type, or social structure, and relative gestation length could be found.

Parameters relating to the rate of increase

As explained in Chapter 2, the rate of increase of a population will be represented in this work by the parameter r_{max}. To calculate r_{max} one needs to know three other parameters, the age at first reproduction, the birth rate and the age at last reproduction. The variation in these parameters is therefore discussed here, variation in r_{max} itself is dealt with in Chapter 5.

Chapter 4

Age at first reproduction

The female age at first reproduction is particularly important as it has more influence on r_{max} than do the other two parameters used to calculate r_{max} [birth rate and age at last reproduction]. [From now on female age at first reproduction will be referred to as simply age at first reproduction.] In the primates, variation in age at first reproduction is likely to be even more influential on the variation in r_{max} than in other mammals, as the small litter sizes of primates mean that they have less scope for changing r_{max} by varying the birth rate than do species with a higher number of young per litter. Several previous studies have looked at the variation of age at first reproduction with body size and these can be compared to those found in this study [given in table 4.5]. The studies by Rudder [1979], for primate species, give results that are similar to those found here, with a slope value of around 0.35. The slope value of 0.44 found by Harvey and Clutton-Brock [1985] for primate subfamilies appears to be rather high [although it does fall with in the 95% confidence limits of the subfamily line obtained in this study]. As this study is based on a much larger sample [83 as opposed to 47 species] it is used in preference to that of Harvey and Clutton-Brock [1985].

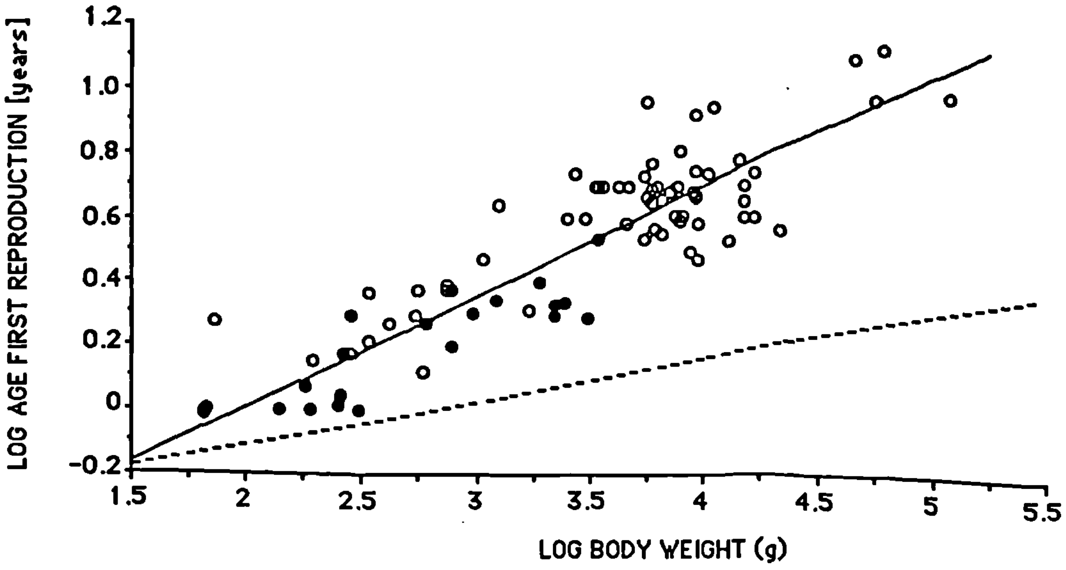
Table 4.5

Major axis statistics for log_{10} mean age at first reproduction [in females] vs. log_{10} body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	83	0.88	0.34	-0.66	0.30	0.38
	genera	43	0.89	0.34	-0.64	0.29	0.40
	subfamily	18	0.94	0.39	-0.82	0.32	0.47
Strepsirhines:	species	21	0.87	0.28	-0.55	0.20	0.35
	genera	11	0.89	0.30	-0.61	0.19	0.43
	subfamily	5	0.99	0.39	-0.86	0.31	0.48
Haplorhines:	species	62	0.82	0.30	-0.46	0.24	0.35
	genera	32	0.85	0.31	-0.50	0.24	0.38
	subfamily	13	0.92	0.37	-0.73	0.27	0.48

Figure 4.6

Log_{10} age at first reproduction versus *log_{10} mean body weight for primate species*



● **Strepsirhine species**

○ **Haplorhine species**

——— Major axis best-fit line for primates, data from this study

--- Major axis best-fit line for mammals from Wootton [1988]

Comparing the results with those obtained for all mammals by Wootton [1987], it appears that the line for primates is above that found for mammals over the complete primate size range [figure 4.6]. This indicates that a typical primate will have a later relative age at first reproduction than does the "average" mammal. This result agrees with those obtained by previous studies, that looked at a smaller sample of species, [Western, 1979; Wootton, 1987] and supports the idea that primates are relatively slow to grow to maturity. In addition, the primate equation differs from that found by Wootton in having a higher allometric exponent, 0.35 as compared to 0.25. This means that as size increases the difference between an "average" mammal's age at first reproduction and an "average" primate's age at first reproduction is greater at larger body sizes.

It was considered that one reason for the difference in slope of the primate and the mammal line could be that the higher slope of the primates is due to grade difference within the primates. The slope values for the haplorhines and strepsirhines separately do indeed show lower slope values, which include 0.25 in their 95% confidence limits. However, the best-fit lines for both the strepsirhines and haplorhines are above that found for mammals.

There is some indication that strepsirhines tend to breed earlier than do haplorhines of the same body size [figure 4.6]. This was tested for by comparing the residuals obtained form a line of average slope [as 80% of the variation in age at first reproduction residuals is accounted for at the generic and species levels the following analyses were not carried out at subfamily level.] The residuals of the two suborders were found to be significantly different when both species and average generic data were compared [ANOVA, $p<0.05$], indicating that strepsirhines tend to have a lower relative age at first reproduction than haplorhines. The two suborders were therefore treated separately in the analyses of differences between dietary and habitat groups.

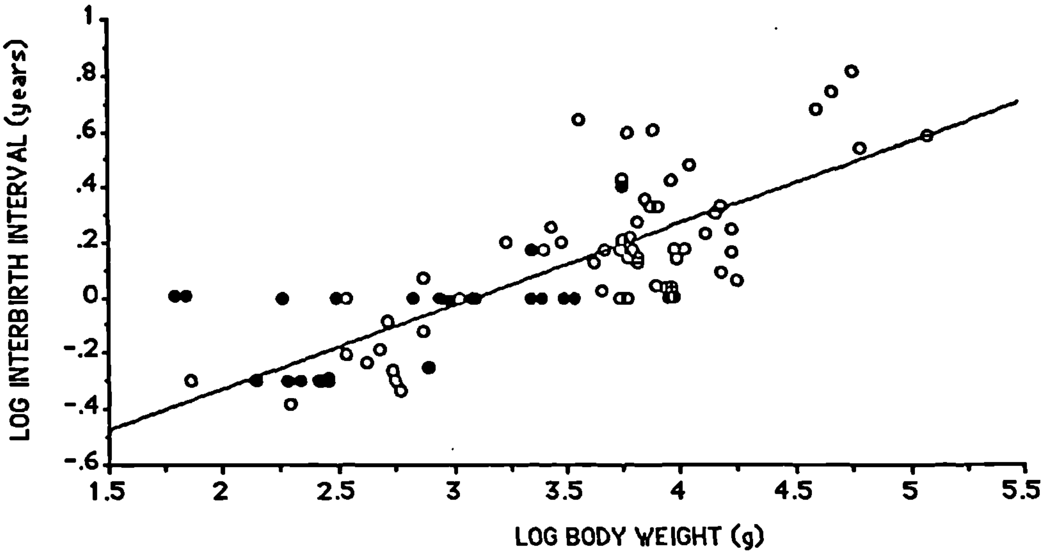
As discussed in the methods chapter, there is a tendency for captive animals to have a lower age at first reproduction than do wild animals. This difference was found to be significant when the residuals of wild and captive species were compared [ANOVA, $p<0.05$ although there was no difference between the residuals of wild and free-ranging provisioned species. When the two suborders were looked at separately, there was no difference found within the strepsirhines and a barely insignificant difference found in the haplorhines [$p=0.06$, for captive data compared to wild and free-ranging data]. However, the strepsirhine data contains very few data from wild animals [4 out of 21 species] and it is therefore difficult to be certain that wild strepsirhines do not breed later than captive ones. Because of the possible difference between the captive and wild species shown by these results, the comparison of different groups was carried out both on the complete data set and on the wild and free-ranging species only. The second "wild data set" contained 32 species [4 strepsirhines and 28 haplorhines].

When the whole data set was considered, there were no differences found between species with different diets or those in different habitats. There was also no correlation found between

Figure 4.7

Log_{10} interbirth interval versus *log_{10} mean body weight*

for primate species



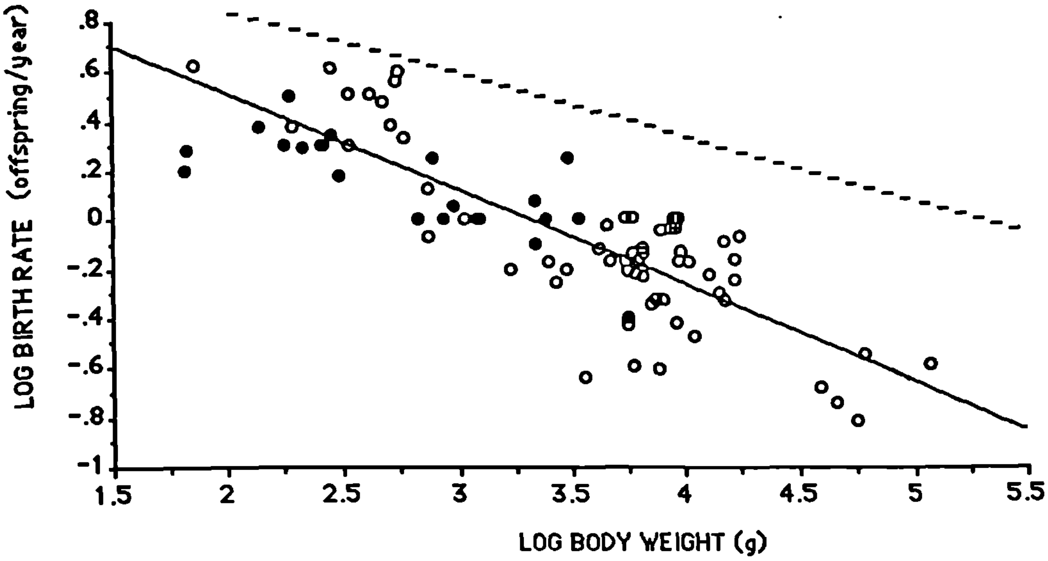
● **Strepsirhine species**

○ **Haplorhine species**

——— Major axis best-fit line for primates, data from this study

Figure 4.8

Log$_{10}$ birth rate versus log$_{10}$ mean body weight for primate species



● **Strepsirhine species**

○ **Haplorhine species**

____ Major axis best-fit line for primates, data from this study

\-\-\- Best-fit line for mammals from Western [1979], using regression statistics

Chapter 4

Table 4.6

Major axis statistics for $\log_{10}$ interbirth interval vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	84	0.76	0.30	-0.91	0.24	0.35
	genera	44	0.85	0.32	-0.99	0.26	0.38
	subfamily	18	0.90	0.34	-1.06	0.26	0.43
Strepsirhines:	species	21	0.59	0.22	-0.66	0.08	0.36
	genera	12	0.66	0.25	-0.74	0.06	0.45
	subfamily	5	0.68	0.18	-0.54	-0.17	0.58
Haplorhines:	species	63	0.76	0.34	-1.09	0.27	0.42
	genera	32	0.87	0.35	-1.12	0.28	0.43
	subfamily	13	0.94	0.39	-1.27	0.29	0.50

Table 4.7

Major axis statistics for $\log_{10}$ birth rate vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	84	-0.82	-0.39	1.30	-0.45	-0.34
	genera	44	-0.87	-0.40	1.31	-0.47	-0.33
	subfamily	18	-0.92	-0.41	1.30	-0.50	-0.32
Strepsirhines:	species	21	-0.74	-0.28	0.92	-0.41	-0.16
	genera	12	-0.74	-0.30	0.97	-0.51	-0.12
	subfamily	5	-0.81	-0.25	0.84	-0.62	0.00
Haplorhines:	species	63	-0.82	-0.47	1.59	-0.55	-0.39
	genera	32	-0.88	-0.44	1.47	-0.53	-0.36
	subfamily	13	-0.92	-0.44	1.43	-0.56	-0.33

the proportion of different foods eaten and relative age at first reproduction. However, differences between the forest and savannah habitat groups were revealed within the wild data set at both the species and genus levels of analysis [ANOVA; $p<0.05$, $p<0.075$ respectively], this was true for all 32 wild species and for the 28 haplorhine species [there were not enough wild strepsirhine species for comparison].

Interbirth interval and birth rate

Interbirth interval is an factor in the determination of birth rate, which in turn is a determinant of r_{max}. In species with a small litter size interbirth interval [IBI] will have a greater influence on the birth rate than will the latter's other component, the number of young per litter. As no primate species regularly gives birth to more than two offspring at a time IBI will be expected to exert a large influence on the birth rate.

The results of the scaling analyses of log IBI against log body weight are shown in figure 4.7 and table 4.6 and those for log birth rate against log body weight are shown in figure 4.8 and table 4.7. Figures 4.7 and 4.8 indicate that there is no difference between the relative interbirth intervals or the relative birth rates of strepsirhine and haplorhine species. This impression is supported by the results of analyses of variance carried out on the residuals of these parameters, which indicate that there is no significant difference between the two groups for the residuals of either parameter [$p<0.05$ at all taxonomic levels].

As with age at first reproduction, it was considered that data from captive animals might not be representative of the inter-birth intervals found in the wild. When the data were split into captive, provisioned and wild species, it was found that wild animals had longer interbirth intervals and lower birth rates for their body size than either captive or free-ranging animals. Because of this the data was split into two groups: "wild species" and "free-ranging and captive species". Within these two categories, there were still no differences found between the haplorhine and strepsirhine species and the data for both was therefore used together.

Within the wild data set it was found that species that are found in "forest" habitats had longer relative interbirth intervals and lower relative birth rates than "savannah" species, This was also true when average generic values were compared [ANOVA, $p<0.05$]. No links between diet or social structure and either relative IBI or relative birth rate were found.

Longevity

The way in which maximum recorded longevity scales to body weight is seen in table 4.8 and figure 4.9. As can be seen in figure 4.9 longevity in the primates scales to body in a similar way as it does in other mammals, but the best-fit line for primates is above that of other mammals indicating that primates tend to live longer than mammals of the same size. The 95% limits of the scaling exponent found here includes the value of 0.23 found by Rudder [1979] for 40 species and 0.29 found by Harvey and Clutton-Brock [1985] for 17 subfamilies. The significance of this exponent is discussed below, in the section on physiological time.

Table 4.8

Major axis statistics for $\log_{10}$ maximum recorded longevity versus $\log_{10}$ body weight

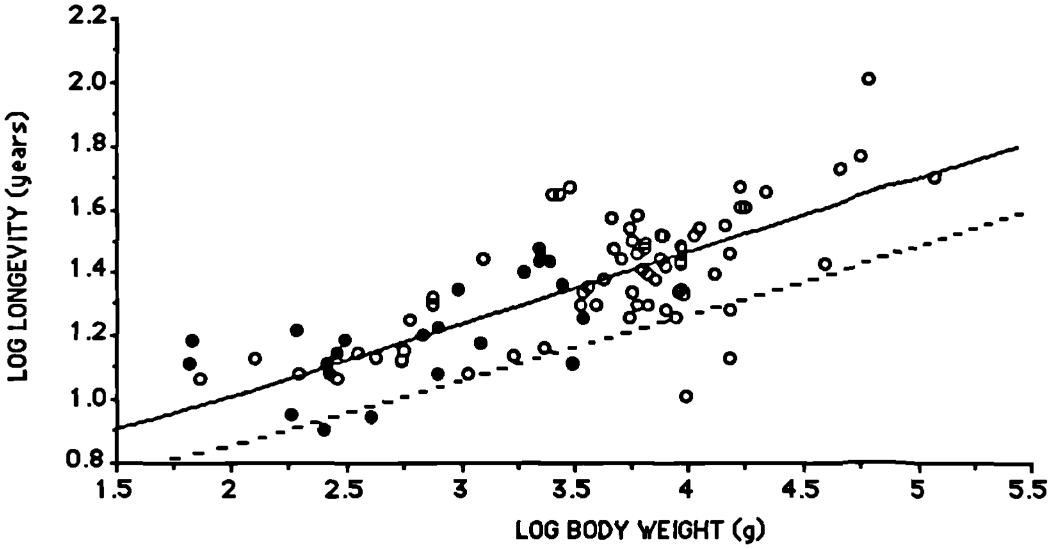
Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	92	0.75	0.22	0.58	0.18	0.26
	genera	46	0.64	0.19	0.66	0.12	0.26
	subfamily	19	0.81	0.26	0.47	0.16	0.35
Strepsirhines:	species	22	0.61	0.20	0.64	0.08	0.32
	genera	12	-0.03†	0.00	1.21	-0.17	0.16
	subfamily	6	0.48†	0.12	0.83	-0.19	0.45
Haplorhines:	species	70	0.68	0.22	0.57	0.17	0.28
	genera	34	0.70	0.22	0.59	0.14	0.30
	subfamily	13	0.82	0.26	0.46	0.14	0.38

†=not significant [p>0.05]

No correlations were found between relative longevity and habitat, diet or social structure. Although some taxonomic groups had a higher relative longevity than others, [for example, *Cebus* monkeys had a very long life span for their size], this may simply be a reflection of their surviving better in captivity and not necessarily relevant to animals in the wild. No significant difference was found between the relative longevity of strepsirhines and haplorhines [ANOVA, p<0.05].

Figure 4.9

Log_{10} maximum recorded longevity versus *log_{10} mean body weight for primate species*



● **Strepsirhine species**

○ **Haplorhine species**

——— Major axis best-fit line for primates, data from this study

--- Best-fit line for mammals from Stearns [1983], using regression statistics

Weaning age

The relationship between weaning age and body weight can be seen in table 4.9 and figure 4.10. Figure 4.10 seems to suggest that strepsirhine species wean their young at a relatively earlier age than do haplorhine species, although the difference between the species residuals calculated from an average fixed slope is just outside the 95% significance level [p=0.054 for species data]. It was also noted that the marmosets and tamarins have an earlier relative weaning age than do the other haplorhines, and when these species were included with the strepsirhines this group was found to have a significantly earlier weaning age than the remaining haplorhines [[P=0.0047].

The question of weaning age and its relevance to parental investment is discussed in some detail in Chapter 6, and therefore is not considered in depth here. However, it should be noted here that no correlations between relative weaning age and diet, habitat, social structure or living conditions [i.e. wild, captive etc.] could be found. The major axis slope found in this study is somewhat lower than that reported by Rudder [1979] of 0.51 for 30 species and Harvey and Clutton-Brock [1985] of 0.56 for 17 subfamilies. The former figure is just outside the 95% confidence limits and the later inside the 95% confidence limits of this study. The scaling of weaning age to body weight is also discussed in Chapter 6.

Weaning weight

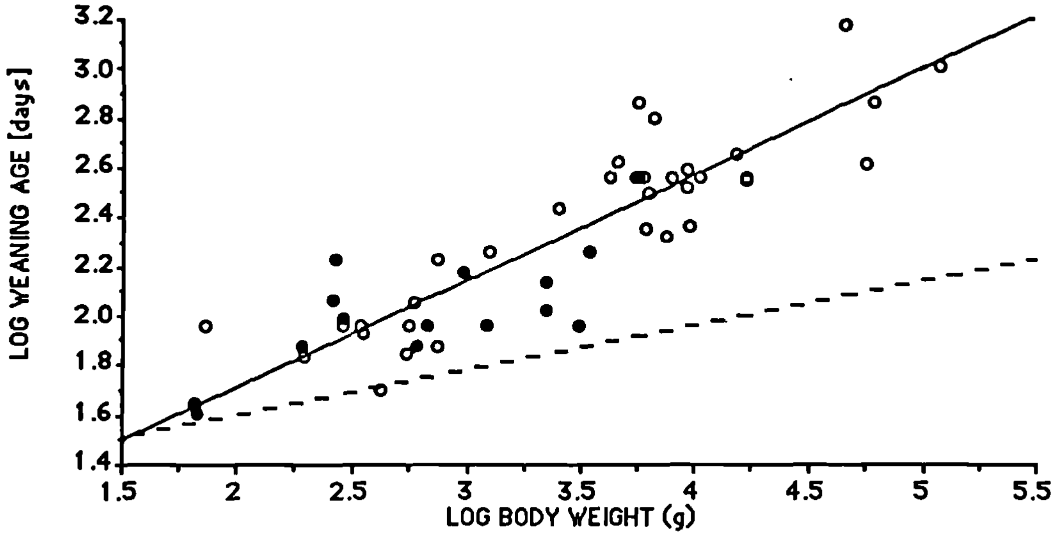
The scaling of weaning weight to body weight was considered for 22 mother-reared species only. Although additional data are available for seven hand-reared species these are not used in the analyses, although the data can be found in Appendix III. Table 4.10 and figure 4.11 show the relationship of weaning weight to body weight. The statistics in table 4.10 suggest that the relationship between the parameters may be different for the two suborders, with strepsirhines scaling to a higher exponent value. It appears from figure 4.11 that the higher slope of the strepsirhine species is caused by three larger species [*Varacia variegatus, Nycticebus coucang* and *Perodicticus potto*] having particularly high weaning weights for their adult body size. However, the small sample sizes and wide confidence limits preclude any firm conclusions. There is no evidence that strepsirhines and haplorhines have different relative weaning weights [ANOVA of residuals from fixed slope or from major axis line through whole sample, p>0.1]. No correlations between relative weaning weight and diet, habitat, social structure or living conditions [i.e. wild, captive etc.] could be found.

These results are in general agreement with those reported by Rudder [1979], who also concluded that there was no difference between the relative weaning weights of haplorhines and strepsirhines. The question of variation in weaning weight is discussed further in Chapter 6, and is therefore not discussed in detail here.

Figure 4.10

Log_{10} weaning age versus $\log_{10}$ mean body weight

for primate species



● **Strepsirhine species**

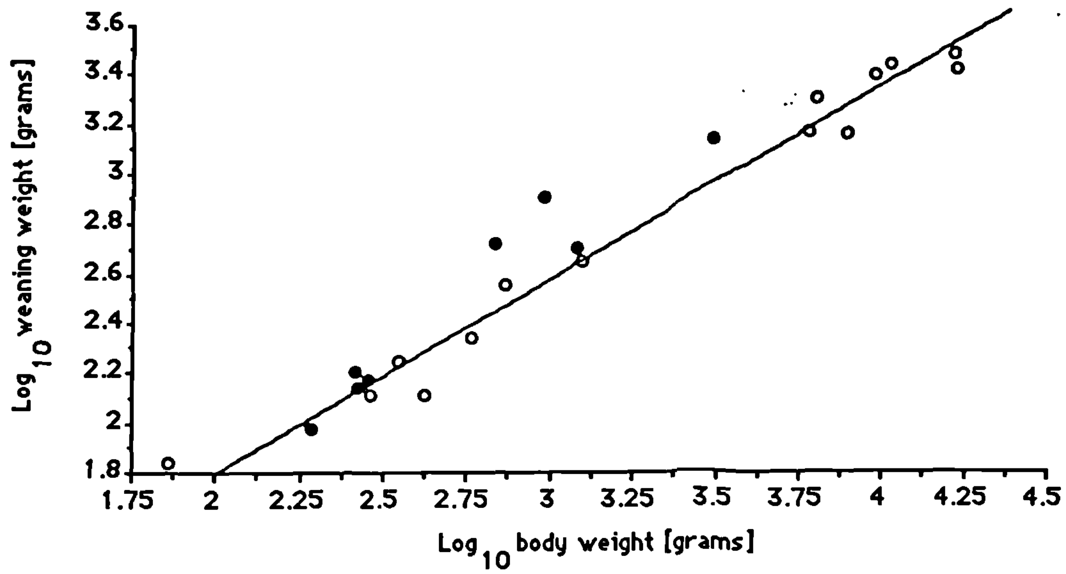
○ **Haplorhine species**

——— Major axis best-fit line for primates, data from this study

\- - - Best-fit line for mammals from Stearns [1983], using regression statistics for duration of lactation.

Figure 4.11

Log_{10} weaning weight versus log_{10} mean body weight



● **Strepsirhine species**

○ **Haplorhine species**

—— Major axis best-fit line for primates, data from this study

Table 4.9

Major axis statistics for $\log_{10}$ weaning age vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	51	0.89	0.43	0.85	0.37	0.50
	genera	38	0.88	0.41	0.91	0.34	0.49
	subfamily	17	0.93	0.47	0.75	0.37	0.57
Strepsirhines:	species	15	0.72	0.30	1.17	0.13	0.49
	genera	11	0.69	0.32	1.13	0.08	0.60
	subfamily	5	0.90	0.39	0.91	0.06	0.71
Haplorhines:	species	36	0.89	0.44	0.85	0.36	0.51
	genera	27	0.89	0.41	0.94	0.32	0.50
	subfamily	12	0.92	0.46	0.78	0.33	0.62

Table 4.10

Major axis statistics for $\log_{10}$ weaning weight vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	22	0.98	0.76	0.33	0.69	0.85
	genera	16	0.97	0.75	0.39	0.65	0.85
	subfamily	7	0.97	0.78	0.24	0.62	1.01
Strepsirhines:	species	8	0.97	0.99	-0.23	0.75	1.30
	genera	6	0.98	0.99	-0.22	0.66	1.51
	subfamily	3	0.98	0.87	0.01	0.87	0.87
Haplorhines:	species	14	0.99	0.76	0.29	0.68	0.84
	genera	10	0.99	0.74	0.36	0.67	0.82
	subfamily	4	0.99	0.76	0.29	0.76	0.76

Chapter 4

Physiological time: evidence for a constant ratio with life span?

In 1981 Linstedt and Calder compiled a list of the scaling of various life processes to body mass. These parameters were all measures of the time taken for physiological processes to occur, ranging from the contraction times of muscles to the maximum recorded life span. The most striking result of their work was the conclusion that the vast majority of these processes scaled to approximately the 0.25 power of body weight, and in virtually all cases, 0.25 was included in the 95% confidence limits of the exponent value. As longevity was also found to scale to the 0.25 power of body weight they could conclude that ".... each life comprises about the same number of physiological events or actions; in other words, each animal lives its life faster or slower as governed by size, but accomplishes just as much biologically whether larger or small." [Calder, 1984; p.141]. For example, the equation relating the time of the circulation of blood volume [B in seconds] to body mass [M in kg] in mammals is:

$$B = 21M^{0.21} \qquad \text{Eqn. 4.1}$$

Whereas that relating life span [L in years] to body mass in mammals is:

$$L = 11.6M^{0.20} \qquad \text{Eqn. 4.2}$$

Converting equation 4.1 to the same units [years] as equation 4.2 and dividing one by the other allows the computation of the number of circulations of blood volume per life [L/B] for an animal of a given size.

$$\frac{L}{B} = \frac{11.6\,M^{0.20}}{(6.65 * 10{-}7)\,M^{0.21}} \qquad = (1.7 * 10^{7})\,M^{-0.01}$$

The allometric exponent of equation 4.3 is nearly zero, showing that there is virtually no variation with body mass for L/B, i.e. there are about (1.7 X 10^{7}) circulations of blood volume per lifetime for a mammal, whatever its size. Similar calculations can be done for other mammalian and avian parameters showing that they too have a constant relationship to life span, whatever the animal's size.

Since Linstedt and Calder's [1981] publication there have been other studies that have also found that parameters measuring time scale to the 0.25 power of body weight, e.g. Stearns [1983] for several mammalian characters. However, a recent study by Martin and MacLarnon [1985] looked at the scaling of gestation length to body weight and suggested that the 0.25 slope found when log gestation length is plotted against log body weight is due to the data for altricial and precocial mammals being mistakenly treated as a single data set. When altricial and precocial mammals are treated separately, there is strong evidence that the slope of the best-fit line is about 0.1, rather than the higher value suggested by previous workers. It was of interest to see if similarly low slope values would be found for other life-history parameters, when precocial and altricial mammals were treated separately. As primates are all precocial, as compared to other mammals, looking at the primate group alone gives an exponent value that is not affected by the possible grade differences between precocial and altricial mammals. Table 4.11 lists the allometric exponents for the measures of physiological time found for primate species in this study.

Looking at the whole primate group, only three of the seven parameters listed [longevity, breeding life and interbirth interval] include the figure of 0.25 within the 95% confidence limits for the allometric exponent value. As expected, gestation length has a exponent value of about 0.1, but three measures of the speed of postnatal development [age at first reproduction, age at reaching adult weight and age at weaning] all have exponent values that are above 0.25. However, when the haplorhines and strepsirhines are considered separately, the 0.25 exponent value is included in several of these cases [see table 4.11].

As several parameters examined are not found to scale to a similarly low power in the primates,the ratio between most time periods and life span varies with body size. As noted by Martin and MacLarnon [1985] gestation length scales to about the 0.1 power of body weight for most mammalian orders, and this includes the primates. Gestation period shows a decrease in proportion to life span as size increases for both strepsirhines and haplorhines, but the difference this incurs is very slight over the primate size range. For example, from the equations above, a one hundred gram primate would be expected to have gestation period of about 2.8% of its life span whereas a ten kilogram primate would have a gestation that was about 1.3% of its life span. The proportion of the life span spent at breeding age appears to be a constant in all primates, regardless of size. The figures given in the above table indicate that a typical primate will spend about 90% of its total life at between age at first breeding and age at death. The figures for this parameter thus appear to support Lindstedt and Calder's ideas.

Age at first reproduction, age at reaching adult weight and age at weaning are measures of the time taken for an animal to reach maturity or independence from its parents. In the haplorhines, all of these parameters show an increase in proportion to the total life span with increasing body size, i.e. a large primate will be predicted to spend a greater proportion of its total lifetime maturing than will a smaller one. For example, a four hundred gram animal such as a tamarin will be predicted to have lived about 2% of its life up until weaning, 10% of its life before reaching adult weight and 16% of its total life at pre-breeding age, whereas a four kilogram guenon will have lived about 3% of its life before weaning, 17% before gaining adult weight and 20% of its life before age at first reproduction.

In the strepsirhine species, age at first reproduction and age at weaning show some increase relative to life span with increasing body size, and age at reaching adult weight shows a similar relationships to that found in the haplorhine species. For comparison with the above figures, a four hundred gram strepsirhine such as a greater dwarf lemur will be predicted to have lived about 1.7% of its life up until weaning, 6.5% of its life before reaching adult weight and 11% of

Table 4.11

Physiological time as a function of body mass for primates

Period	Scaling equation[1]	95% C.L.s	Life span/period time
Maximum recorded Life span [L]	$L = 3.80 M^{0.22}$	0.18-0.26	1
Breeding life[2] [B/years]	$B = 3.68 M^{0.21}$	0.16-0.26	$1.1 M^{0.01}$
Gestation length [G/days]	$G = 64.6 M^{0.11}$	0.09-0.14	$21.5 M^{0.11}$
Age at first reproduction [A/years]	$A = 0.22 M^{0.34}$	0.30-0.38	$17.3 M^{-0.12}$
Age reaching adult weight [WA/years]	$WA = 0.05 M^{0.50}$	0.43-0.59	$70.0 M^{-0.28}$
Age at weaning [W/days]	$W = 7.1 M^{0.43}$	0.37-0.50	$196.0 M^{-.21}$
Interbirth interval [I/years]	$I = 0.12 M^{0.30}$	0.24-0.35	$30.8 M^{-0.08}$
Strepsirhines			
Maximum recorded Life span [L]	$L = 4.37 M^{0.20}$	0.08-0.32	1
Breeding life[2] [B/years]	$B = 4.68 M^{0.17}$	0.03-0.32	$0.93 M^{0.03}$
Gestation length [G/days]	$G = 61.66 M^{0.11}$	0.00-0.21	$25.9 M^{0.08}$
Age at first reproduction [A/years]	$A = 0.28 M^{0.28}$	0.20-0.35	$15.6 M^{-0.08}$
Age reaching adult weight [WA/years]	$WA = 0.06 M^{0.46}$	0.17-0.82	$72.8 M^{-0.26}$
Age at weaning [W/days]	$W = 14.6 M^{0.30}$	0.13-0.49	$109.3 M^{-0.10}$
Interbirth interval [I/years]	$I = 0.22 M^{0.22}$	0.08-0.36	$19.9 M^{-0.02}$
Haplorhines			
Maximum recorded Life span [L]	$L = 3.72 M^{0.22}$	0.17-0.28	1
Breeding life[2] [B/years]	$B = 3.07 M^{0.23}$	0.15-0.30	$1.21 M^{-0.01}$
Gestation length [G/days]	$G = 95.50 M^{0.07}$	0.05-0.09	$14.22 M^{0.15}$
Age at first reproduction [A/years]	$A = 0.35 M^{0.30}$	0.24-0.35	$10.62 M^{-0.08}$
Age reaching adult weight [WA/years]	$WA = 0.10 M^{0.44}$	0.36-0.50	$37.2 M^{-0.22}$
Age at weaning [W/days]	$W = 7.04 M^{0.44}$	0.36-0.51	$193.0 M^{-0.22}$
Interbirth interval [I/years]	$I = 0.08 M^{0.34}$	0.27-0.42	$46.5 M^{-0.12}$

[1] Where body mass [M] is measured in grams.

[2] Where B = [life span - age 1st reproduction] except in Homo sapiens where B = [50 years - age 1st reproduction].

its total life at pre-breeding age, whereas a four kilogram sifaka will have lived about 2% of its life before weaning, 12% before gaining adult weight and 13.5% of its life before age at first reproduction.

Interbirth interval [IBI] as a proportion of life span was also examined. This value is almost a constant for strepsirhine species but for haplorhines it varies more with body size. The ratio of total life span: IBI is a partial measure of the total number of litters an animal would be expected to produce in its lifetime, but the actual number of litter produced also depends on age at first reproduction. The number of litters per lifetime as a function of body size in strepsirhine species can thus be calculated as:

$$\text{Number of litters per lifetime} = \frac{\text{Breeding life}}{\text{IBI}} + 1$$

$$= \frac{4.68\,M^{0.17}}{0.22\,M^{0.22}} + 1$$

$$= 21.3\,M^{-0.05} + 1 \qquad \text{Eqn. 4.3}$$

The very low exponent value of equation 4.3 above means that the predicted difference in number of litters per lifetime for a small and a large strepsirhine is very small. For example, a 100 gram bushbaby would be predicted to have 18 litters in a lifetime whereas a 6000 gram indri would be predicted to have between 14 and 15 litters. For strepsirhines, therefore, the fact that interbirth interval is an almost constant proportion of life span means that all strepsirhines could have about the same number of litters if they lived to their maximum life span, regardless of size.

For haplorhine species there is a higher negative scaling exponent for the ratio life span:IBI against body weight. The number of litters per lifetime as a function of body size in haplorhine species can be calculated as:

$$\text{Number of litters per lifetime} = \frac{3.07\,M^{0.23}}{0.08\,M^{0.34}} + 1$$

$$= 38.37\,M^{-0.11} + 1 \qquad \text{[Eqn. 4.4]}$$

The higher negative value of the exponent value and constant value of equation 4.4, as compared to that of 4.3, means that the number of litters per lifetime varies more with size in the haplorhines. This can be shown by comparing the predicted number of litters for haplorhines with the same sized animals as used in the strepsirhine example above. A 100 gram tarsier would be predicted to have about 23 litters if it lived and reproduced up until its maximum life span whereas a 6000 gram haplorhine [such as a cercopithecine monkey] would produce only about 16 litters in its life time. There is hence a difference of seven litters as compared to a difference of only two or three litters for two strepsirhines of the same sizes.

It appears then, that the general predictions of Linstedt and Calder [1981], that physiological time periods are a constant proportion of life span, are not found to be true for several primate life-history characters. Although the differences between animals of different sizes are frequently small, there is a consistent trend towards a longer developmental time in larger primates, so that the time to weaning, the time to gaining adult weight, age at first reproduction and interbirth interval are found to represent a larger proportion of total life span as size increases in the haplorhine primates. The combination of the later age at first reproduction and the longer interbirth interval, relative to life span, in the larger haplorhines means that they will be expected to produce less litters per lifetime than will smaller haplorhine species. In the strepsirhines, however, there is less range in the total number of litters produced in a lifetime, over the same body size range.

Discussion

The allometric and correlation analyses presented in this chapter consistently show two things. Firstly, that although the two groups of primates, the strepsirhines and the haplorhines, can be separated by the ways in which some of their life-history parameters scale to body weight other parameters scale in the same way for both groups. Generally speaking, strepsirhines have a lower neonatal weight, lower litter weight, later age at weaning, and earlier age at first reproduction than do haplorhine species of the same size, but gestation period, birth rate and longevity scale in the same way in the two groups.

The reason for the apparent partial correlations between several parameters, after the removal of body weight effects, may be due to the basic differences between strepsirhine and haplorhine species. For example, the high partial correlation between relative BMR and relative litter weight is not found within the strepsirhine and haplorhine groups when taken separately. This indicates that the reason for the correlation when the whole primate data set is used is because the strepsirhines have a low relative BMR and a low litter weight compared with the haplorhines.

Some partial correlations are found to remain significant even when the haplorhine and strepsirhine groups are treated separately. These correlations indicate that in the haplorhine species there are negative correlations between the postnatal developmental time and a neonatal weight, so that species giving birth to relatively large infants will develop relatively slowly. This negative correlation between total maternal investment in young and the rate of maternal investment in young supports the predictions of most life-history theories, which suggest that species with a large investment in single offspring will have a slow developmental time.

In the strepsirhines the picture is more complex, with the opposite pattern seeming to emerge in several cases. For example, relative litter weight is found to correlate negatively with relative gestation length and positively with relative postnatal growth rate, so that species with a relatively low litter weight would be expected to have a relatively long gestation and relatively slow growth rate [both pre- and postnatally].

A possible complicating factor in the strepsirhine species may be their variable relative metabolic rate. However, the results of both the partial correlation analyses and the bivariate analyses do not give a clear picture of how BMR is acting on these parameters. Even when the effects of both gestation length and body weight are held constant, there is no clear relationship between litter weight and BMR in the strepsirhine species. Several possible explanations could explain this situation. It is possible that there is no direct relation between the developmental variables discussed and metabolic rate and that another variable is influencing these parameters. Another possibility is that the measure of metabolic rate used here [BMR] is not a good measure of the actual metabolic rate of the strepsirhine species during gestation and/or lactation. As has been discussed earlier there is evidence that at least one strepsirhine species, a sifaka, elevates its metabolic rate during pregnancy [Richard and Nicoll, 1987]. If other species can also do this, and if the amount of increase is not directly proportional to BMR, it would be expected that BMR would not correlate with factors such as gestation length and litter weight.

An unexpected correlation result was that birth rate did not appear to be closely correlated to other life-history parameters, once body weight effects have been removed. This result is surprising because theories of life-history evolution predict that a high birth rate will be linked to rapid development and high maternal investment. These questions are discussed in more detail in chapters 5 and 6, which deal with the rate of increase and maternal investment.

Within the two suborders [i.e. the strepsirhines and the haplorhines] there are very few consistently observed differences found between other phylogenetically related groups, such as the loris and lemur family or the Old World and New World monkeys. There is, however, some indication that the lemur family [lemurs and mouse lemurs] have relatively short gestation lengths compared to other strepsirhines, and indeed to all other primates, whereas tarsiers have a very long gestation for their body size. There is also evidence that the marmosets and tamarins have a relatively high birth rate as compared to other haplorhines, this result being expected given the capacity of these species to produce up to four offspring in a year.

It has been suggested that the production of twins in the marmosets and tamarins is as a result of their being selected for smaller infants and it was therefore of interest to see if the marmosets and tamarins produced smaller neonates than other haplorhines. Leutenegger [1973] argues that the scaling of litter weight to body weight in the haplorhine monkeys means that smaller monkeys producing single infants will tend to give birth to babies that are very large in comparison with their body size. For example, a 500 g haplorhine will produce a litter weighing about 11% of its adult weight whereas a 5 kg haplorhine's newborn young will weight only 6.5% of the adult weight. Leutenegger suggests that the proportionately larger size of the smaller species' young means that they will experience difficulty giving birth and will therefore be selected to produce two smaller neonates rather than a single large neonate.

When the size of the individual neonates of marmosets and tamarins are looked at, they are found to be slightly below that that would be predicted from their body size. A relatively small neonate is also found in Goeldi's monkey [*Callimico geoldii*],a species that is of uncertain relationship to other marmosets and tamarins but that produces only one infant per litter. However, the difference between the observed and expected neonatal weight is small and there are two tamarin species [*Saguinus fuscicollis*and *S. nigricollis*] that have neonatal weights that are slightly above that that would be predicted. These results show that the production of relatively small infants is not only found in species that produce twins [as evidenced by *Callimico geoldii*] and that species that produce twins do not necessarily have relatively small infants [as evidenced by two tamarin species]. In addition, the total litter weights of the marmosets and tamarins are higher than would be predicted from their body size, suggesting that there has not been a simple reduction in neonate size due to the production of twins, but that twinning has been accompanied by a marked increase in the total amount of resources put into the offspring during gestation. Further evidence that a small size does not necessarily prevent haplorhines from producing single offspring comes from the tarsiers. Although these species are smaller than the marmosets and tamarins they usually produce only one infant which is relatively large for a haplorhine species. Similarly, it appears then, that some other explanation must be found for twinning in marmosets and tamarins, this will be discussed further in later chapters.

The way in which the variables scale to body size is not completely in agreement with Lindstedt and Calder's suggestion that the number of "life events" is the same for all species. Instead it appears that larger species take a larger proportion of their lifetimes to mature and will produce less litters. This result does not agree with previous studies on mammals, which have found that most measures of physiological time scale to about the 0.25 of body weight [e.g. Stearns, 1983; Wootton, 1987]. With the exception of gestation length, the measures of physiological time in primates scale to a higher exponent of body weight than do the same parameters when all mammals are considered. The difference between the exponent found for gestation length for all mammals and for primates alone has been explained by Martin and MacLarnon [1988] as being a result of taking all mammals together rather than treating them as two separate groups, altricial and precocial. However, the differences in the exponent values of age at first reproduction, age at weaning and interbirth interval cannot be thus explained. If these exponent values for altricial and precocial mammals treated separately were to be higher than when all mammals were treated together, one would predict that precocial mammals would have an earlier age at first reproduction, earlier age at weaning and shorter interbirth interval than would altricial mammals of the same size. The evidence of this study suggests that, if anything, the opposite is true, with the primates being a highly precocial group that has a later age at first reproduction, a later age at weaning and and longer interbirth interval than would a typical mammal of the same size. If one looks at the plots of log age at first reproduction, log weaning age and log interbirth interval against log body weight [figures 4.6, 4.10 and 4.8] it can be seen that the best-fit lines for mammals and primates converge at small body sizes. It therefore appears that the reason for the steeper slopes found with the primates is that the larger primates have a slower development and longer birth spacing than do mammals of the same size, whereas smaller primates are more like typical mammals, this pattern is found in both strepsirhine and haplorhine species.

There is very little evidence to suggest that the life-history parameters discussed vary with any of the ecological variables used. It has been suggested [McNab, 1980; 1984] that diet could effect life-history variables *via* basal metabolic rate [BMR] but in no case was a correlation found between diet and a life-history variable. In the light of the lack of solid evidence linking BMR to diet that we saw in Chapter 3, this result is not perhaps surprising. However, it is perhaps worth noting that BMR itself was found to be correlated with neonatal weight, litter weight and foetal growth rate, after the effects of body weight were removed. The fact that none of these three parameters was found to be correlated with diet, once body size effects had been removed, is perhaps a further indication that diet and relative BMR are not closely associated.

To return to the question of there being very little correlation between the life-history parameters and ecological factors: there was no correlation found between either habitat or degree of arboreality and neonatal weight, litter weight, gestation period or weaning age. The fact that there does not appear to be a connection between relative litter weight and any ecological variable appears to suggest that the difference found between strepsirhine and haplorhine species is not due to small neonate and litter weight being a directly adaptive character. A low litter weight is found for nearly all strepsirhine species, regardless of their habitat or the precociality of their young, indicating that it is a very conservative character. As can be seen from figure 4.2, the weight of strepsirhine offspring tends to fall on or below the best-fit mammalian line, whereas that for haplorhine species tends to fall above this line. Neither group shows any obvious divergence from the mammalian pattern and hence this information cannot be used an indication as to whether the ancestral primates had litter weights that were closer in relative size to the haplorhines or to the strepsirhines.

Some rather tenuous connections appeared to suggest that forest-dwelling species had a later age at first reproduction and a longer interbirth interval than species found in the savannah and woodland. These differences in forest and open country species were reflected in a difference between arboreal and terrestrial species. It is therefore possible that the reason for forest species breeding later and more slowly is due to a connection with savannah living and terrestriality, with terrestriality being the cause of the observed life-history characteristics. These results indicated that a more thorough investigation of the variation of age at first reproduction and birth rate was called for, in particular their relationships to habitat type and environmental predictability. This is carried out in the next chapter, where the variation in the intrinsic rate of natural increase [r_{max}], a parameter which incorporates both age at first reproduction and birth rate, is discussed.

Summary

Primates are shown to have large infants, slow developmental times and long lives as compared to other mammals of a similar size. Within the order, there is clear evidence that the strepsirhine and haplorhine primates have different reproductive strategies. The strepsirhine primates tend to breed younger, and have smaller neonates and smaller total litter weights than do haplorhine species. There is also a tendency for the strepsirhines to wean their young at an earlier age. The Malagasy species also have shorter gestation lengths than do haplorhine species but the lorises, pottos and bushbabies have gestations that are indistinguisable statistically from those of haplorhine species. It is suggested that the ancestral strepsirhines had shorter gestation lengths for their body size than did the ancestral haplorhines, but that the relatively low metabolic rate of the loris group has led to a corresponding increase in gestation length.

The lack of correlations between life-history variables and environmental variables suggests that the differences between strepsirhine and haplorhine species cannot be explained by theories of life-history evolution that attempt to directly link life-history variation with environmental variation. Instead it is thought that the majority of differences between the two groups arose in the ancestral stock and have been retained by phylogenetic inertia. This idea does not exclude the possibility that the ancestral differences arose as an adaptive response.

Although the majority of parameters examined do not seem to vary with ecological variables in any predictable way, there is some evidence that two parameters that influence the capacity for population increase, age at first reproduction and birth rate, may be correlated with habitat type. This subject is to be investigated further in Chapter 5. The relationships between developmental variables are complex, particularly in the strepsirhine species where they influenced by metabolic rate. This is discussed further in Chapter 6.

Chapter 5

The rate of population increase

In this chapter the variation in the intrinsic rate of natural increase [r_{max}] will be examined. The chapter starts by looking at the relationship between r_{max} and body weight, including a description of the scaling of r_{max} to body weight in primates. This is compared to the scaling found in mammals. There follows a discussion of the relationship between r_{max} and metabolic rate and between r_{max} and other life-history parameters.

As has been previously stated, one of the aims of this work is to investigate whether the relationship between environmental predictability and r_{max} is as predicted by theories of life-history evolution. In accordance with this aim several measures of environmental predictability have been used and their relationship to r_{max} examined. Relationships between r_{max} and other ecological variables are also examined.

The value of r_{max} was calculated for each species as described in Chapter 2. Data on this parameter were available for 73 species [representing 40 genera and 18 subfamilies]; the data are listed in Appendix III. The methods of this chapter are basically those used in chapters 3 and 4 and will not be explained in further detail here.

The relationship between r_{max} and body weight

As has been mentioned in previous chapters, several studies have noted that there is an allometric relationship between r_{max} and body weight, this being found for a wide range of organisms. Table 5.1 shows the results found by previous studies.

Rudder [1979] carried out a study of r_{max} and body weight for primates, which indicated that the slope of the major axis best-fit line was steeper than the best-fit line found for other organisms. It was considered that this relationship should be investigated for the larger number of primates found in this study [73 as compared to 31 in Rudder's study], and the major-axis statistics were therefore calculated, as in previous chapters. Table 5.2 and figure 5.1 show the

Table 5.1

Results of previous analyses of the relationship between r_{max} and body weight

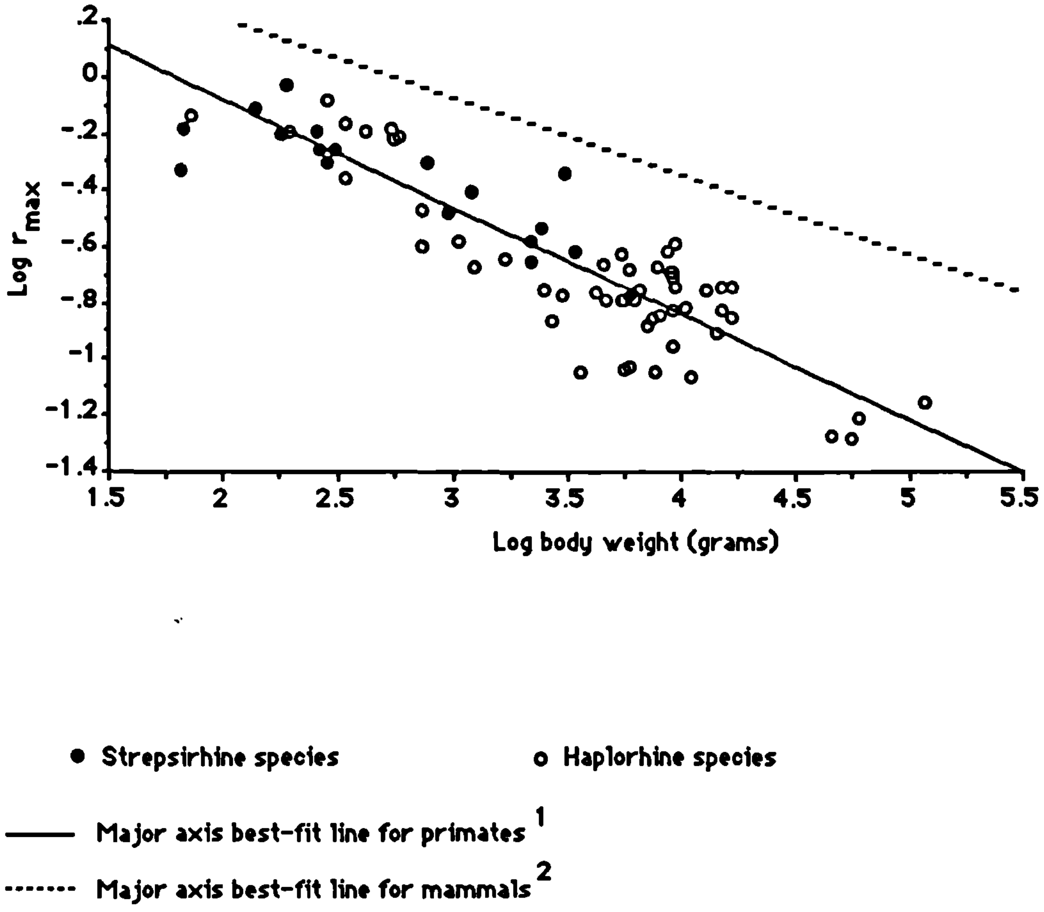
Group studied	b[1]	n	type of analysis	Reference
Unicellular organisms	-0.28	-	regression	Fenchel [1974]
Heterotherm metazoa	-0.27	-	regression	Fenchel [1974]
Wide range of organisms	-0.28	-	regression	Blueweiss *et. al.* [1987]
Mammals	-0.26	44	regression	Hennemann [1983]
Mammals	-0.28	44	major axis	This study [using data from Hennemann, 1983]
Atricial mammals	-0.29	19	regression	Hennemann [1984]
Precocial mammals	-0.13	30	regression	Hennemann [1984]
Primates	-0.35	31	major axis	Rudder [1979]
Haplorhine primates	-0.39	19	major axis	Rudder [1979]
Strepsirhine primates	-0.15	12	major axis	Rudder [1979]

[1] Allometric exponent of r_{max} against body weight, to two significant figures.

Figure 5.1

$Log_{10}\, r_{max}$ versus log_{10} mean body weight

for 73 primate species



1. This study
2. This study, using data from Hennemann [1983].

relationships found.

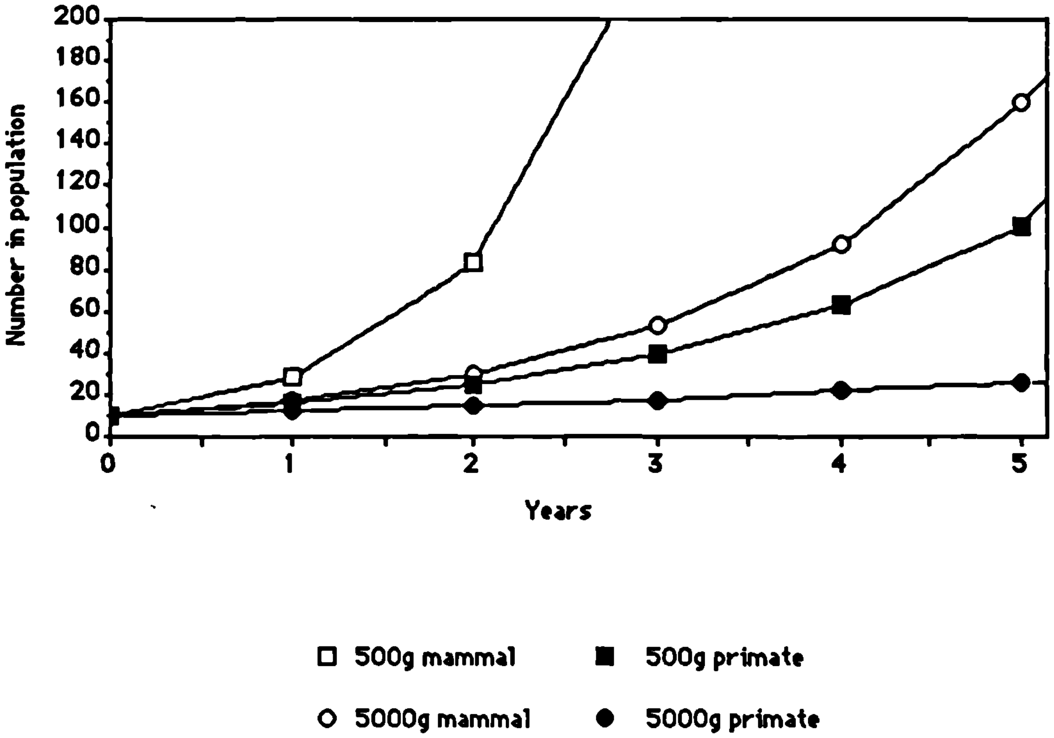
The correlation between the log values of r_{max} and body weight is high, with about 80% of the variation in log r_{max} being explained by variation in log body weight. As expected from previous studies the correlation is negative, indicating that larger primates will have a lower capacity for population increase than will smaller ones. This study agrees with that of Rudder in finding that primates have a lower r_{max} than non-primate mammals of the same size. The slope value for primates is higher than that found for mammals, and the mammalian value is outside the 95% confidence limits of the primate slope. This relationship means that the difference between the value of log r_{max} of larger primates and other mammals will be greater than the difference found between a smaller mammal and a primate of the same size. This is illustrated in figure 5.1 where the two best-fit lines can be seen to converging at smaller body weights. This result is not surprising, as the two main determinants of r_{max} [age at first reproduction and birth rate] also show divergence of the mammalian and primate log-log best-fit lines at high body weights [see figures 4.6 and 4.8]. These results are therefore compatible with those of previous studies on r_{max} and with the results for other life-history parameters presented in the previous chapter of this thesis.

The effect of the differences of the scaling relationship of r_{max} to body weight in mammals and primates can be illustrated by considering the population growth of a typical primate and a typical mammal of the same body size. Table 5.3 and figure 5.2 show the population growth of a hypothetical typical primate population where the adults weigh 500 grams and 5000 grams, respectively, and compares them with hypothetical typical mammals of the same size. Assuming that there are a ten breeding individuals in each population in year 0, the expected r_{max} of each population can be used to calculate how large the population will be in each successive year.

It can be seen that the rate of reproductive output of a typical primate is much reduced as compared to other mammals, in both the comparison of 500g animals and that of 5000g animals. However, the different scaling relationships between r_{max} and body weight in the two groups mean that the ratio of population numbers of smaller mammals: small primates are proportionately greater than large mammals: larger primates. This difference would still arise if primate r_{max} was below that of mammal r_{max} but scaled to the same allometric exponent [i.e. -0.28]. However, as primate r_{max} scales to a more negative value of body weight [i.e. -0.38] larger primates have an even lower r_{max} than they would if primate r_{max} scaled to the same exponent as mammal r_{max}.

Figure 5.2

Population growth for a typical mammal and a typical primate of 500 grams and 5000 grams [1]



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1. Assuming the expected r_{max} and a starting population of 10 individuals, see text for further details.

Table 5.2

Major axis statistics for $\log_{10} r_{max}$ vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	73	-0.89	-0.38	0.69	-0.43	-0.34
	genera	40	-0.91	-0.39	0.71	-0.45	-0.34
	subfamily	18	-0.95	-0.42	0.80	-0.49	-0.35
Strepsirhines:	species	17	-0.79	-0.26	0.36	-0.37	-0.15
	genera	9	-0.86	-0.27	0.40	-0.41	-0.13
	subfamily	5	-0.97	-0.28	0.43	-0.42	-0.15
Haplorhines:	species	56	-0.87	-0.40	0.75	-0.47	-0.34
	genera	31	-0.91	-0.40	0.72	-0.47	-0.33
	subfamily	13	-0.95	-0.43	0.82	-0.52	-0.34

Table 5.3

The increase in population numbers of a typical primate and a typical mammal of 500 grams and 5000 grams

Year	Number in population[1]				Difference		Ratio	
	Mammals		Primates		Mammal - primate nos.		mammal: primate nos.	
	500g	5000g	500g	5000g	500g	5000g	500g	5000g
0	10	10	10	10	0	0	1.0	1.0
1	29	17	16	12	13	5	1.8	1.4
2	83	30	25	15	28	15	3.3	2.0
3	239	53	40	18	199	35	6.0	2.9
4	689	92	63	22	626	70	10.9	4.2
5	1983	160	101	26	1802	134	19.6	6.2
10	393401	2572	1015	68	393386	2504	387.6	37.8

1) Assuming "typical" r_{max} for mammals and primates, rounded to the nearest whole number.

For example, if r_{max} scaled to (body weight)$^{-.28}$ and the r_{max} of a 100g primate was 0.85 [i.e. the r_{max} that is actually found], the r_{max} of a 5000g primate could be calculated in the following way:

$r_{max} = a(\text{body weight})^{-.28}$

For a primate of 100 grams: $0.85 = a(100)^{-.28}$

$\log a = \log(0.85) - (-0.28 * \log(100)) = 0.489, \therefore a = 3.086$

Hence, for a primate of 5000 grams: $r_{max} = 3.086(5000)^{-.28} = 0.28$

With an r_{max} of 0.28 a starting population of ten would increase to about 172 after 10 years. In fact, the scaling relationship of r_{max} to body weight that is actually found gives a primate of 5000 grams a r_{max} of 0.20 and a starting population of ten increases to only 68 after 10 years. It appears therefore that larger primates are selected to have an even lower r_{max} than one would predict if the primates differed from mammals only by a grade difference. This is discussed further at the end of this chapter.

As about 80% of the variation in r_{max} is explained by body weight, some 20% of the variation is accounted for by the residual values, it is these values that are now discussed.

Residual variation in r_{max}

The following sections look at the variation in r_{max} that cannot be accounted for by variation in body weight, i.e. the residual variation. As over 60% of the residual variation [i.e. about 12% of the total variation] in r_{max} is due to differences at the species level, species are treated as independent data points for the residual figures. A small amount of r_{max} variation [about 23% of the residual variation or 4.6% of the total variation] is accounted for by differences between genera within subfamilies and the results were therefore checked using average generic figures. No differences in the overall conclusions were found using the average genus figures and these results are therefore not reported here. As no extra variation is added by averaging data to the subfamily level and only 3.4% of the total variation [17% of the residual variation] can be accounted for by variation in average family points the residual data was not averaged beyond the genus level.

Chapter 5

Taxonomy and r_{max}

If the primate species are split into their two suborders it is found that the major axis best-fit line for the strepsirhines has a low slope, as compared to that of other primates [see table 5.2]. [The slope value for strepsirhines found in this study is, in fact, higher than that of -0.15 reported by Rudder [1979]. The difference can be accounted for by the extra data included in this study, in particular more accurate data for larger strepsirhine species which indicate that their rate of increase is slower than previously thought.] It can be seen that the 95% confidence limits of the strepsirhine and haplorhine lines overlap, and if the outlier *Varecia variegatus* [which falls far above the primate best-fit line] is removed from the strepsirhine data the 95% confidence limits of the allometric exponent include that found for the whole primate sample.

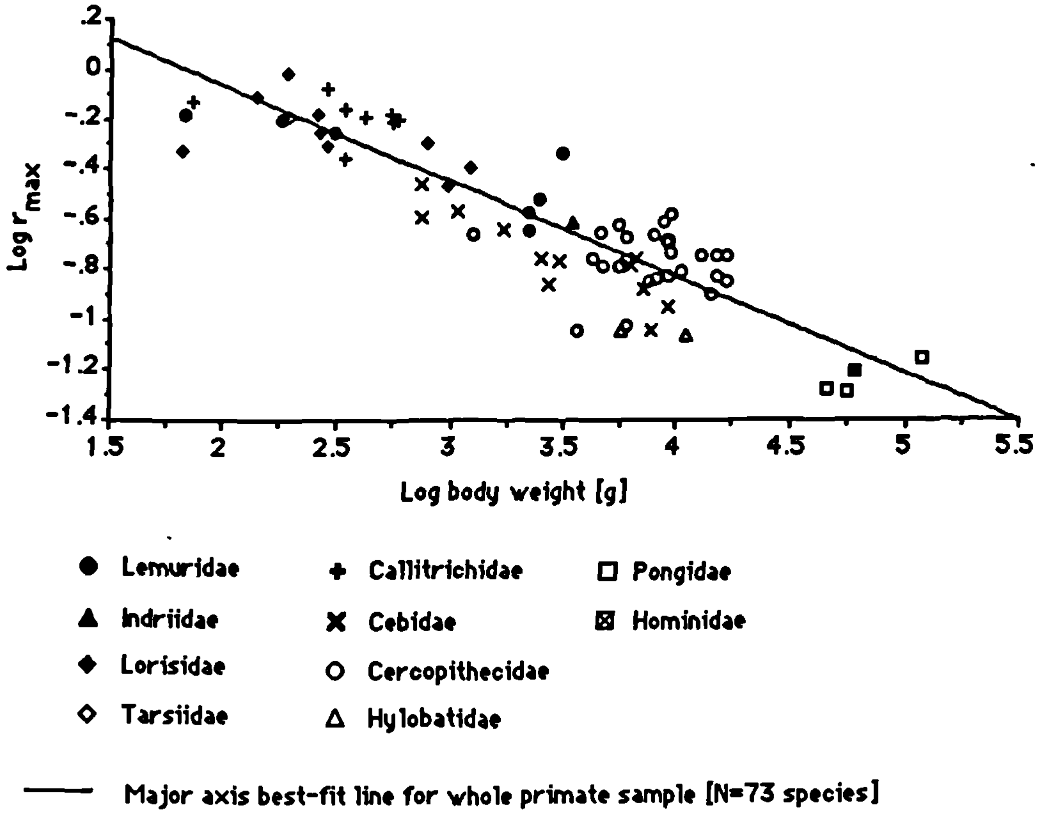
Rudder suggests that the strepsirhine species have a higher r_{max} than do haplorhines of the same size, and that this difference is a result of their being more r-selected than the haplorhine species. However, this difference is not apparent in figure 5.1, and statistically no difference could be found between the two suborders. This was the case regardless of whether the residuals were taken from a line of fixed slope of the strepsirhine and mammal value (-0.28), the haplorhine value (-0.38) or the mean of the two values (-0.33), [ANOVA, $p>0.1$ in all cases]. The two groups are therefore treated together for most of discussion of the variation in r_{max}. However, in some other parameters strepsirhines and haplorhines have different scaling relationships. Hence, when looking at the relationships between r_{max} and such parameters the two groups are separated.

Looking at smaller taxonomic groups several trends can be seen. This is illustrated in figure 5.3. Of the primate families, the cebid monkeys and the gibbons tend to have particularly low r_{max} values for their size, whereas the callitrichid monkeys [the marmosets, tamarins and Geoldi's monkey] and the cercopithecine monkeys [i.e. all Old World monkeys] are generally found to have higher r_{max} values than one would predict from their body size. The strepsirhine families show no clear tendencies to have a high or low relative r_{max} There is some indication that the lemurs [*Lemur* spp and *Varecia variegatus*] tend to have a high r_{max} for their size, with *L. catta*, *L. macaco*, and *V variegatus* having high residual r_{max} values, although *L. fulvus* has about the expected r_{max} for a primate of its size.

Within these families there are no clear distinctions between the subfamilies, as would be expected from the results on the nested analysis of variance that indicate that nearly all residual variation is due to variation of species within genera and genera within subfamilies [see above].

Figure 5.3

$\log_{10} r_{max}$ versus $\log_{10}$ mean body weight for primate species, showing families.



Chapter 5

Correlations between r_{max} and other life-history parameters

The correlations between individual life-history parameters have already been discussed in Chapter 4. However, specific correlations with r_{max} were not discussed and will be dealt with here. As shown in tables 4.1 and 4.2, r_{max} correlates highly with other life-history parameters; but many of these correlations become insignificant once body weight effects have been removed by partial correlation, indicating that they occur only because both r_{max} and the second parameter are independently correlated with body weight.

After body weight effects have been removed, r_{max} is negatively correlated with neonatal weight, gestation length, inter-birth interval, age at first reproduction, longevity and weaning age, and positively correlated with birth rate and litter post-natal growth rate. [All correlations refer to logarithmic values.] Hence primates with relatively high r_{max} values have relatively low neonatal weights, relatively high pre-natal and post-natal developmental times, relatively short life-spans and relatively high birth rates.

The correlations with age at first reproduction and birth rate are not surprising as these parameters are used to calculate r_{max}, and the correlations are in the direction expected. However, it is worth noting that relative longevity is <u>negatively</u> correlated with relative r_{max} despite the fact that, for a given age at first reproduction and birth rate, longevity will be <u>positively</u> correlated with r_{max}. This pattern is that which would be predicted by most theories of life-history evolution, with both r- and K-selection theory and bet-hedging theory predicting that rapid development, a high birth rate and a sort lifespan will be linked

The haplorhine and strepsirhine species were also considered separately as the analyses of Chapter 4 reveal that the two groups show different scaling relationships between body weight and several life-history parameters Within the haplorhine group the partial correlations found to be significant were almost the same as were found for all primates, the only difference being that there was not a significant partial correlation between log gestation length and log r_{max}. This indicates that haplorhine primates with relatively high r_{max} values have relatively low neonatal weights, relatively high post-natal developmental times, relatively short life-spans and relatively high birth rates. In contrast, when the strepsirhine species were considered it was found that the only partial correlations with log r_{max} that were significant were with interbirth interval and birth rate

These results indicate that the haplorhine primate species fit with accepted theories of life-history evolution, with a high rate of increase being linked to rapid development, a high birth rate and a short life, both before and after the removal of body weight effects. The strepsirhine species, however, do not show any correlations between developmental rates and r_{max} or between lifespan and r_{max} after body weight effects have been removed, although species with relatively high r_{max} values do have a high birth rate. These results are discussed further at the end of this chapter.

Diet, basal metabolic rate and r_{max}

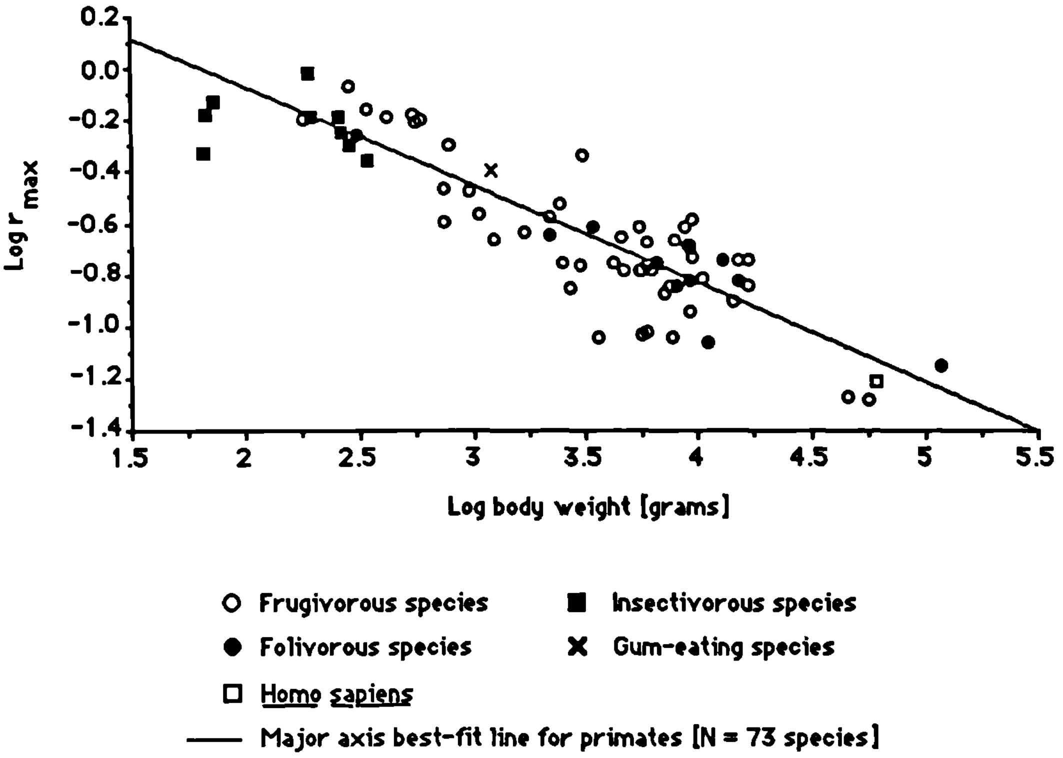
It has been suggested that diet and r_{max} will be related to each other via a connection between diet and basic metabolic rate [BMR] [McNab, 1980]. As discussed in Chapter 3, McNab [1980, 1986a, 1986b] postulates a link between diet and metabolic rate, with certain diets [e.g. folivorous, insectivorous, frugivorous] being associated with low relative metabolic rates and others [e.g. carnivorous] with high relative metabolic rates. He also argues that BMR is correlated with two measures of developmental rate, [post-natal growth and gestation length] and with birth rate. Hence species with a relatively high BMR will be expected to have a relatively high post-natal growth rate, a relatively short gestation length and a high birth rate, whereas species with a low relative BMR will have the opposite characteristics. In species with a high relative BMR, the increased post-natal growth rate and a short gestation length would be expected to decrease the generation time and hence increase r_{max} and the additional effect of an increased birth rate will increase r_{max} still further.

The relationship between diet and BMR in primates has already been discussed in Chapter 3, and it was concluded that there is very little evidence to suggest that diet is directly linked to BMR, at least in the species examined. However, there was some slim evidence that linked a low BMR to a folivorous diet and it is therefore possible that one might find a link between folivory and r_{max} The relationship between diet and r_{max} in primates is therefore discussed here. This relationship was investigated in the same way as was that between diet and body weight in Chapter 3 and diet and other life-history parameters in Chapter 4 This involved correlating the proportions of different food eaten with residual r_{max} and an analysis of variance to test whether species eating mainly one type of food have a significantly different residual r_{max} than other species A correlation between the relative dietary quality score [see Chapter 3 for an explanation of this parameter] and relative r_{max} was also calculated.

Figure 5.4 shows the relationship between diet and relative r_{max} for the 71 primate

Figure 5.4

$\log_{10} r_{max}$ versus $\log_{10}$ mean body weight for primate species, showing diet



species for which r_{max} data and a dietary category is available. It can be seen from this diagram that there is no clear link between any of the dietary categories and either a high or a low residual r_{max}. Of the nine insectivorous species, two are above the primate best-fit line, five are below it and two fall on the line. There are three folivores with high relative r_{max} values, two with the expected r_{max} and three with a low relative r_{max}. The frugivores are evenly distributed above and below the best-fit line. As one might expect from these observations, no distinction between the species in different dietary category groups could be discerned by the ANOVA and there was no correlation between the proportion of any food type eaten and the residual values of r_{max}. A correlation between residual r_{max} and the dietary quality score was also insignificant. A similar lack of correlation between diet and relative r_{max} is found when the haplorhines and strepsirhines are dealt with separately.

Although diet does not appear to be correlated with relative BMR, it is still possible that relative BMR is correlated with relative r_{max}. As already mentioned McNab [1980] proposed that a link between BMR and developmental variables could be found in mammals, once size effects had been controlled, and that this would lead to a correlation between relative BMR and relative r_{max}.

One problem with the work of McNab [1980] is that he presents no statistical evidence to support his argument that these life-history parameters are linked to BMR after body weight effects have been removed. His evidence that this is the case is presented in the form of plots of a life-history parameter against BMR, without the effects of body weight being removed. To control for body weight effects he compares only species of a similar body weight. For example, precocial species of weight 21-38 grams are treated as one group and it can be seen that, within this group, there is an decrease of gestation length with increased BMR [per unit weight]. The problem with this method is that one would expect that the species weighing 38 grams would have a lower BMR [per unit weight] and a longer gestation length than a species of 21 grams, and it is difficult to separate out this expected correlation between the actual values of BMR and gestation length from the correlation between the relative values that McNab claims can be found [the original data set is not given so one cannot check this point]. In addition the groups of species of a similar size are often very small, with six out of twelve groupings used containing only two or three species, and only three containing more than six species.

In addition McNab [1980] does not directly test the theory that relative r_{max} is correlated with relative BMR, as data on r_{max} itself is not used However, Hennemann [1983] does consider relative r_{max}. Hennemann calculated the expected BMR [from the Kleiber relationship] and the expected r_{max} [from the empirically determined regression line] for 44 mammal species. The observed value is then expressed as a percentage of this expected value, thus giving relative measures. Hennemann found a significant correlation between the % expected BMR and % expected r_{max}, although the correlation was low [Spearman rank correlation, r= 0.25, increased to r= 0.34 when 6 aquatic species were omitted].

It appears then that there is some evidence linking relative r_{max} to relative BMR in mammals. The reason why these two parameters should be linked is presumed to be due to species with a high metabolic rate being able to support a higher rate of chemical synthesis and thus to grow their infant faster [McNab, 1980]. McNab points out a high BMR will require a large amount of resources and thus one will only expect species with access to abundant resources to be able to support a relatively high BMR. The relatively high metabolic rate of such species would allow them to support rapid physiological reactions and they could therefore have rapidly developing young and hence a relatively high r_{max}. However, this would require that the resources to nurture the young [both before and after birth] would be available. If resources are limiting the mother may be selected to put them into activities other than raising infants rapidly and hence a relatively high r_{max} would not necessarily be achieved by an animal with a relatively high BMR, so that; "All r-selected species may have high rates of metabolism, but not all species with high rates may be r-selected." [*ibid*, p.117]. McNab further argues that species with a low relative BMR will not be able to support rapid chemical synthesis and therefore cannot have a relatively high r_{max}, and hence one would expect that species with relatively low BMRs will not have relatively high r_{max} values.

We have already seen that primates are a group with both a low relative BMR and a low relative r_{max} as compared to other mammals, so to some extent McNab's theory is borne out. However, the previously mentioned work of Elgar and Harvey [1987] should be reiterated at this point. Elgar and Harvey show that variation in BMR can be explained by taxonomic differences in BMR, with some groups having a low relative BMR and others a high relative BMR. If similar differences in r_{max} occur between groups, it may be that the correlation found by Hennemann is due to the disproportionate effect of a few groups with a low relative BMR and low relative r_{max} and/or groups with the opposite characteristics.

To test for a direct link between BMR and r_{max} in primates the following tests were carried out. The residual BMR was plotted against residual r_{max} and the correlation coefficient of these two residual data sets was found. The partial correlation of BMR and r_{max}, removing the effects of body weight, was also calculated. In order to directly compare the primate results with those found by Hennemann [1983] for mammals, another test of the correlation between relative BMR and relative r_{max} was also carried out. This involved calculating the expected values of both r_{max} and BMR and then the percent of the expected value actually found for the two parameters. The percent of expected r_{max} and percent of expected BMR values were then correlated. [Hennemann carried out rank correlations on these data as he was unsure of their suitability for a product-moment correlation test. Both rank correlations and product-moment correlations have been employed here; the first to give a direct comparison with Hennemann's work, the second because the data is considered to be approximately normal in distribution and therefore product-moment correlations are considered to be appropriate, see Chapter 2.] All of these tests were carried out with the whole primate sample and with the strepsirhines and haplorhines separately, as although the scaling of r_{max} to body weight appears to be the same for the two groups it has been shown that BMR scales differently. Data on 28 species were available for both BMR and r_{max}, but only 20 of these had BMR data that was of good quality. The analyses were all repeated twice, firstly with all the available BMR data and secondly with only the better quality data. As the results were qualitatively the same only the results from the second, better data set are reported here.

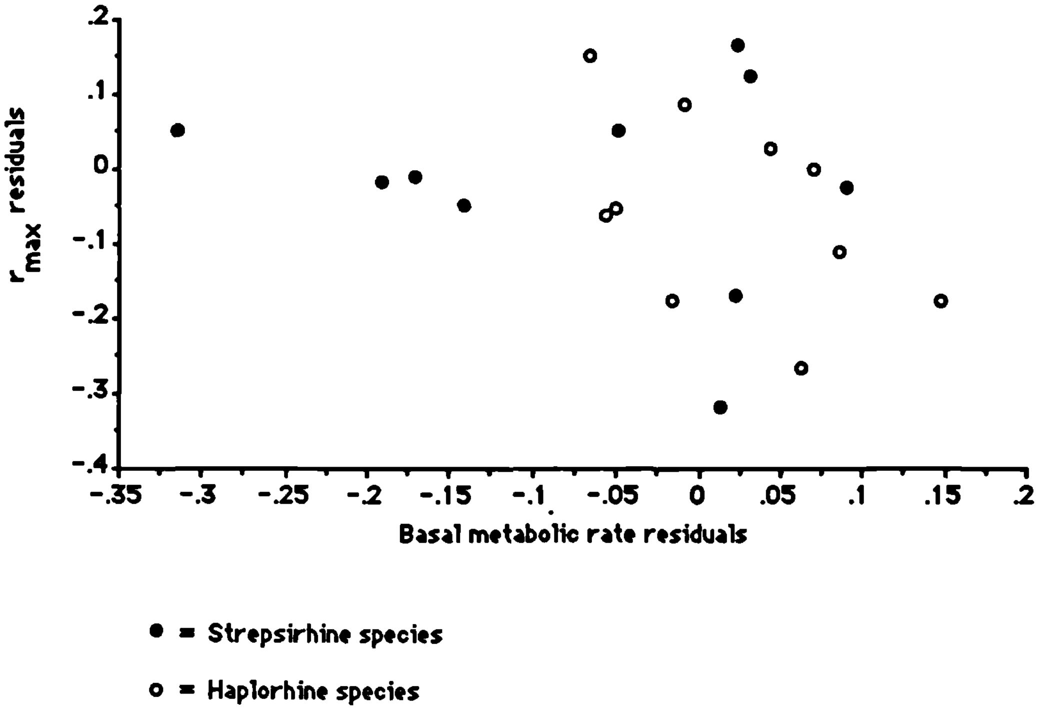
Figure 5.5 shows a plot of the residual r_{max} values against the residual BMR values, both being taken from the primate best-fit line. It is clear from this figure that there is no correspondence between the two sets of residuals and the correlation between them is not significant [$r=-.29$, $p>0.20$]. The correlation between the percent of expected BMR and percent of expected r_{max} was also insignificant [$r=-.35$, $p>0.10$], as was the partial correlation between BMR and r_{max} with body weight effects removed [[$r=-.38$, $p>0.05$]. The equivalent correlations were also insignificant when the haplorhine and strepsirhine species were considered separately.

McNab's proposed that all species with a low relative BMR would be constrained to have a low relative r_{max}, but that only some species with a high relative BMR would be able to support a high relative r_{max}. This might provide a possible explanation for the lack of correlations between relative BMR and relative r_{max}, as although all those species with a low relative BMR would be expected to have a low relative r_{max}, some of those with a high relative BMR might not support a high relative r_{max} because of resource limitations.

However, when one looks more closely at the data the hypothesis that a low relative BMR

Figure 5.5

Residual r_{max} versus residual basal metabolic rate for 20 primate species



must be associated with a low relative r_{max} is not supported. Several species with a low relative BMR have the expected r_{max} or a high r_{max} for their size [e.g. *Galago moholi, Propithecus verreauxi, Arctocebus calabarensis, Colobus guereza*]. This indicates that a low relative BMR is not always associated with a low relative r_{max}. It is therefore concluded that no direct link between r_{max} and diet or between r_{max} and BMR can be found in primates.

Environmental predictability and r_{max}

Two important theories of life-history evolution predict that there will be a link between the rate of population increase and environmental predictability. The way in which environmental predictability is thought to affect the rate of increase depends on the theory in question. The theory of r- and K-selection predicts that species found in unpredictable environments will be selected to have a high rate of increase. Alternatively, bet-hedging theory predicts that unpredictable environments will select for a high rate of increase if adult mortality is increased by the unpredictability of the environment, but that a low rate of increase will be selected if juvenile mortality is increased. Both theories predict that species in predictable environments will be selected to have a low rate of increase. These theories are discussed in detail in Chapter 1.

In this section several measures of environmental predictability will be looked at, and their relationship to the rate of population increase [as measured by r_{max}] will be investigated. The hypothesis that environmental predictability is correlated with the intrinsic rate of natural increase will be tested in an attempt to determine whether r/K theory or bet-hedging theory is supported by the primate data. The environmental measures that will be discussed are latitude, climate and habitat type, these have already been described in previous chapters and hence will not be defined here.

Latitude

Since Dobzhansky's [1950] work, suggesting that species in the tropics experience different selection pressures than do those in the equator, there has been an interest in the way in which life-histories vary with latitude [e.g. Chapman, 1984; Zeveloff and Boyce, 1986].

The relationship between body weight and latitude has already been discussed in detail in Chapter 3, where previous work on Bergmann's rule [that predicts that animals in colder climate will be larger] is summarized and the rule is tested for primates. It is found that there is little evidence of Bergmann's rule operating in primates, although a few groups do show the expected increase in size with increasing latitude. The reason for this size increase with latitude is unclear but it could be due to increased cold at higher latitudes and/or increased climatic variability at higher latitudes.

From r/K theory one would predict that species in higher latitudes would breed faster, and hence have a higher r_{max}, than would species living nearer to the equator. However, given the negative correlation between r_{max} and body weight, Bergmann's law would seem to predict the opposite. This apparent conflict between the two theories could be resolved by considering relative r_{max}, rather than the actual r_{max}. If selection operates to increase the average body size of a species allometric scaling of reproductive parameters will also be operating to decrease r_{max}. However, if there is also selection to increase the breeding rate of the organism, r_{max} may be increased by selection operating to "decouple" the strong links between body weight and the reproductive parameters. In this way the species would be selected to have a high relative r_{max}. Whether such a process can take place is dependent on how close are the links between body size and reproductive parameters i.e. whether one can change independently of the other. It may be that the links between r_{max} and body weight are very strong in primates and that the selection for an increased r_{max} at high latitudes also means that a small body weight is selected and this partially counterbalances the selection for a large body weight. These opposing selective forces could therefore be the reason that no clear trend of increasing body size with latitude is found in primates.

Alternatively the conflict may not arise if either body weight and/or r_{max} do not vary with latitude. We have already seen that the evidence for Bergmann's rule operating in primates is not very convincing and it may be that latitude does not influence body weight to any significant degree. If this is the case, and latitude does effect r_{max}, then one would expect that r_{max} will correlate with latitude. However, the scaling of r_{max} to body weight would then predict that body weight would decrease with increasing latitude, a correlation that was only found to be true for one primate group, the howler monkeys [see Chapter 3]. It may be that selective forces other than latitude differences are preventing primates in high latitudes from having a small body weight in response to selection for a high r_{max}. One would therefore predict that residual r_{max} would increase with increasing latitude if high latitudes select for a high r_{max}. A final possibility is that neither body weight nor r_{max} are varying with latitude and one would therefore predict that body weight, r_{max}, and residual r_{max} would all have insignificant correlations with latitude.

The methods of analysis were basically those of correlation described previously. All analyses were carried out on the whole primate data set, on the strepsirhines and haplorhines separately and on lower taxonomic groups [i.e. families, subfamilies, genera] which contained three or more species. The two measures of latitude [range centre and range limit] were correlated both with log r_{max} and with relative r_{max}.

The correlations found between latitude and log r_{max} mirrored those found between latitude and body weight [listed in Chapter 3]. Most groups that showed an increase in body size with latitude also showed a decrease in r_{max} with latitude. There were no significant positive correlations found between r_{max} and latitude. In all cases the negative correlations between log r_{max} and latitude were removed by a partial correlation removing the effects of body weight. These results indicate that the negative correlations found between r_{max} and latitude can be explained as being a result of the negative correlations found between r_{max} and body weight and the positive correlations found between body weight and latitude.

In nearly all cases there were no significant correlations between latitude and residual r_{max}, whether the measure of latitude used was range centre or range limit. This supports the idea that latitude does not correlate directly with r_{max} and that the few correlations that are found are due to the correlation of body size with both parameters. The only exception to this lack of correlation was a very weak correlation with range centre for all species [$r=0.247$, $0.02< p <0.05$]. However, as is discussed below, this correlation is probably due to the correlations between habitat and relative r_{max} and between habitat and latitude.

These results show that latitude, or at least the latitude measures used here, cannot be used to predict relative r_{max} in primates.

Climate

Although there were few indications that latitude correlated with r_{max}, it was felt that the relationship between climate and r_{max} needed to be investigated. Climate can vary for reasons other than latitude, e.g. with altitude or position in relation to large land masses. The climatic conditions that a species is found in will have an influence on several important parts of its life, including the predictability of its resources, i.e. factors that are postulated to effect r_{max}. Climate will influence the type of plants that can grow, and hence will effect those animals feeding on, and living among this vegetation. The availability of prey for insectivorous and carnivorous animals will be both directly effected by the climate, and indirectly via the plant life. The two most important variables influencing resource levels are water availability and temperature and, as detailed in previous chapters, the climatic variables used include measures of both the average conditions of precipitation and temperature and of their variability and predictability.

Chapter 5

As discussed in Chapter 2, the measures of climate used are correlated with each other, with colder climates generally being more variable. The theory of r- and K- selection predicts that those species suffering from unpredictable population crashes will have a higher r_{max} than those living in a more stable environment. If high climatic variability is a cause of high variability in mortality then the theory predicts that a variable climate, as measured by the variation in rainfall and temperature through the year, will be associated with a high r_{max}. However, as noted by Zammuto and Miller [1985a, 1985b] variability is not necessarily synonymous with predictability. A temperate climate is more variable than a tropical climate, but the seasons may be regular and predictable, thus allowing animals to evolve to cope with the variation in climate and not suffer undue mortality because of seasonality. It is only if seasonality is associated with unpredictable fluctuations in climate, and hence with increased mortality, that one would predict that they would be associated with r-selection. To assess predictability, several measures of inter-year climatic variability have been used [discussed in Chapter 2 and listed in table 2.1] and these are tested to see if they show the predicted correlation with log r_{max} and residual r_{max}.

The results of the correlations between climate parameters and log r_{max} and climate parameters and residual r_{max} are listed in table 5.4. As can be seen from this table, there are only three significant correlations between log r_{max} and climatic parameters. Two of these are positive correlations between log r_{max} and the variation of temperature in the hottest month, i.e. macaque and colobus species that live in climates where hot weather is unpredictable tend to have high r_{max} values. The third correlation is between log r_{max} and the variation of rainfall in the wettest month for cebus monkeys, where a negative correlation suggests that cebus monkeys that are found in areas with variable rainfall in the wet season have a lower r_{max} than do those in less variable areas. However, the correlations found with the cebus monkeys and the colobus monkeys include exceptionally small numbers of species [N=3 in both cases] and should therefore be viewed with caution.

There are several correlations between residual r_{max} and climatic parameters. There are eight correlations with measures of variability, all of which are positive, indicating that a variable climate is associated with a high residual r_{max} in bushbabies, the Lorisinae, tamarins, mangabeys and colobus monkeys. In the bushbabies and the lorisines dry weather is linked to a high r_{max} whereas in the colobines the opposite is the case. There is also a correlation between the average temperature in the coldest month and residual r_{max} for the mangabeys, indicating

Table 5.4

Correlations of climate parameters with log r_{max} and residual r_{max}

a) Correlations of log r_{max} and climate parameters

Climatic variables[1]	Groups with significant correlations	N	r	Significance level
Precipitation variables				
HI.CV.$_{ppt}$	*Cebus* species	3	-0.999	0.02
Temperature variables				
HI.CV.$_{t}$	*Macaca* species	8	0.711	0.05
	Colobus species	3	0.997	0.05

b) Correlations of residual r_{max} and climate parameters

Climatic variables[1]	Groups with significant correlations	N	r	Significance level
Precipitation variables				
HI.AV.$_{ppt}$	*Galago* species	6	-0.949	0.01
HI.CV.$_{ppt}$	*Galago* species	6	0.929	0.01
	Colobus species	3	1.000	0.01
LO.CV$_{ppt}$	*Saguinus* species	3	1.000	0.01
AN.AV$_{ppt}$	*Galago* species	6	-0.947	0.01
	Lorisinae species	3	-0.990	0.10
	Colobus species	3	1.000	0.01
Temperature variables				
HI.CV.$_{t}$	Lorisinae species	3	0.997	0.05
	Saguinus species	3	1.000	0.01
	Colobus species	3	0.999	0.02
LO.AV.$_{t}$	*Cercocebus* species	3	-0.999	0.02
LO.CV.$_{t}$	*Saguinus* species	3	0.999	0.02
MNTH.CV$_{t}$	*Cercocebus* species	3	0.995	0.05

1) Abbreviations for climate parameters are given in table 2.1

that they have a higher relative r_{max} in colder areas. However, as with the results found for r_{max} and climatic parameters, the significant correlations found between relative r_{max} and climatic parameters are mostly based on samples containing only three species.

It therefore appears that, where there are links with climate, there is some indication that residual r_{max} increases with increasing climatic variability and decreases in drier areas. The exception to this is found in the colobus monkeys where annual rainfall is positively correlated with a high r_{max}. Although the majority of these results are based on very small sample sizes, it is notable that there are no significant correlations indicating that increasing climatic variability is associated with decreasing relative r_{max}.

Habitat

A preliminary study of the variation in r_{max} looked at species in "predictable" and "unpredictable" habitats, with the former being forest species and the later being edge and open country species [Ross, 1988]. The study found that those species in "unpredictable" habitats tended to have a high r_{max} for their size whereas the forest species had r_{max} values that were both above and below levels predicted from their weight. In an attempt to look at this problem in more detail, this study looks at r_{max} in relation to the six more accurate habitat categories used in earlier chapters.

The categories of habitat used are described in Chapter 2. The six categories include habitats of varying predictability. It is usually considered that tropical forests [the first habitat category] in general, and in particular primary rainforests, are a stable environment, with secondary forest and forest edge being less predictable and more ephemeral. Such predictions are made because of the known patterns of succession found in many habitats, where secondary growth is more transient and is succeeded by a longer lasting primary stand [Odum, 1971]. The second habitat category, which includes species found in a variety of forest habitats including secondary forest, is therefore considered to be more unpredictable than than habitat category 1. Still more variable is the third category, which includes species found mainly in edge and secondary forest, i.e forest that consists almost entirely of secondary growth that may be unpredictable in both time and space. Between this and the last category are two groups of species that are found in varying amount of edge, woodland and savannah habitats. The most unpredictable habitat is probably the sixth and last category, which includes species found in savannah and open grassland, areas that are frequently subject to drought and extremes of temperature. These categories are also combined to give three broader habitat definitions; forest species, edge species and open country species [details in Chapter 2].

The relationship of body weight, r_{max}, and residual r_{max} with habitat can be seen in figures 5.6 and 5.7. As already noted in Chapter 3, there is a variation of average body weights of species from habitat to habitat and this variation is also found in the smaller sample of species for which r_{max} data are available. As would be expected from the negative correlation between body weight and r_{max}, the average r_{max} varies in the opposite way [figure 5.6]. Generally speaking, forest habitats and savannah habitats seem to produce species with higher body weights and lower r_{max} values than do edge habitats. This trend is also seen in the comparisons between the broader habitat groupings where "forest" species are found to have a larger mean body weight and lower r_{max} values than species found in other habitat types. The relationship between habitat and body weight has already been discussed in Chapter 3 and, given the high negative correlation between r_{max} and body weight, it is not surprising that r_{max} varies with habitat in the opposite way to body weight.

The residual variation of r_{max} with habitat is of interest, as it may show up specific adaptations that are independent of body weight variation. Figures 5.6c and 5.7 seem to suggest that species found in primary forest habitats have a low relative r_{max} whereas those that are found in savannahs and open grassland have a high relative r_{max}. However the difference between the groups was not found to be significant, even at the 10% level. Given the apparently very clear differences between primary forest and savannah and open grassland species it seemed strange that these groups were not significantly different from each other. Inspection of the data revealed that for the "primary forest" species only one, *Varecia variegatus* had a residual r_{max} that was positive, being the highest residual value of any of the 73 species examined.

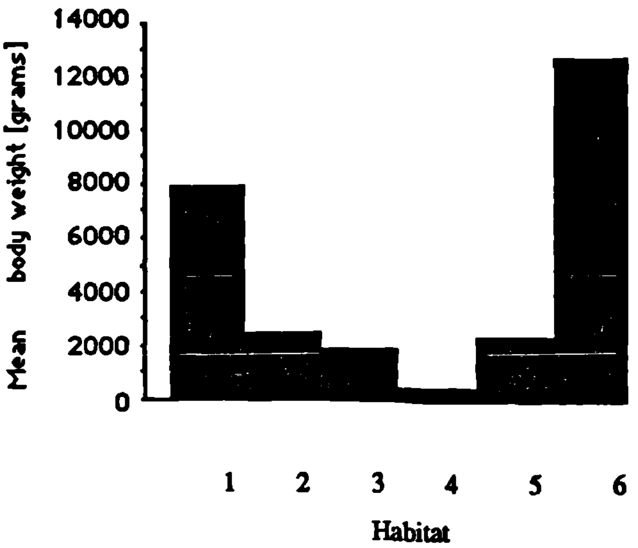
The exclusion of *Varecia variegatus* decreases the average residual r_{max} of the "wet forest" species from -0.055 to -0.108 and decreases the variance from 0.03 to 0.007. It was therefore felt that the removal of *Varecia variagata* might reveal a significant difference between the habitat types and the ANOVA was therefore repeated without this species. As predicted, the remaining primary forest species were then shown to have a significantly lower residual r_{max} than both savannah species and edge species [$p<0.05$]. When looking at the broad habitat divisions, a significant difference between the forest and the open grassland habitat groups was found [$p<0.05$], but again this was only significant after the removal of *Varecia variagata*

Within smaller taxonomic groupings [i.e. suborders, families, subfamilies, genera] very few significant differences could be found between the residual r_{max} values of species in

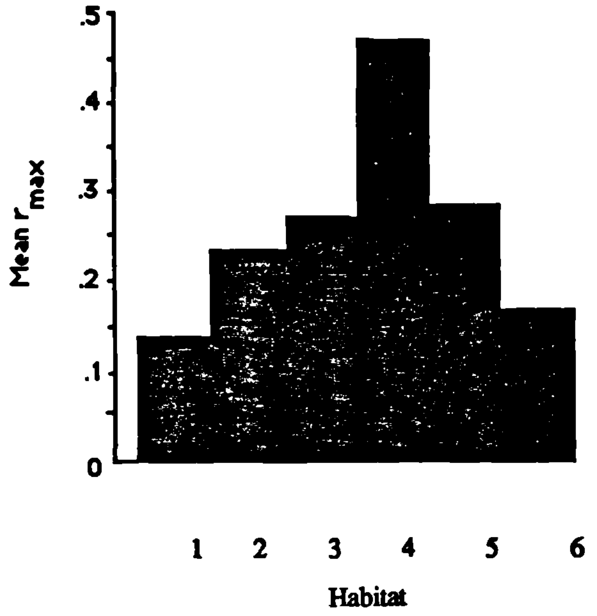
Figure 5.6

Habitat type, body weight, r_{max} and residual r_{max}

a) Mean body weight and habitat [calculated from log species values)



b) Mean r_{max} and habitat [calculated from log species values]

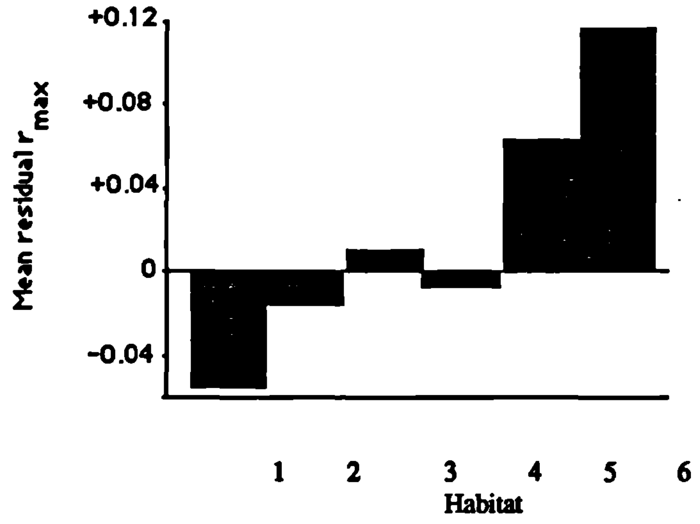


1=primary forest ; 2= general forest; 3= edge; 4= edge and woodland; 5= woodland and savannah; 6=savannah and open country.

Figure 5.6 (continued)

Habitat type, body weight, r_{max} and residual r_{max}

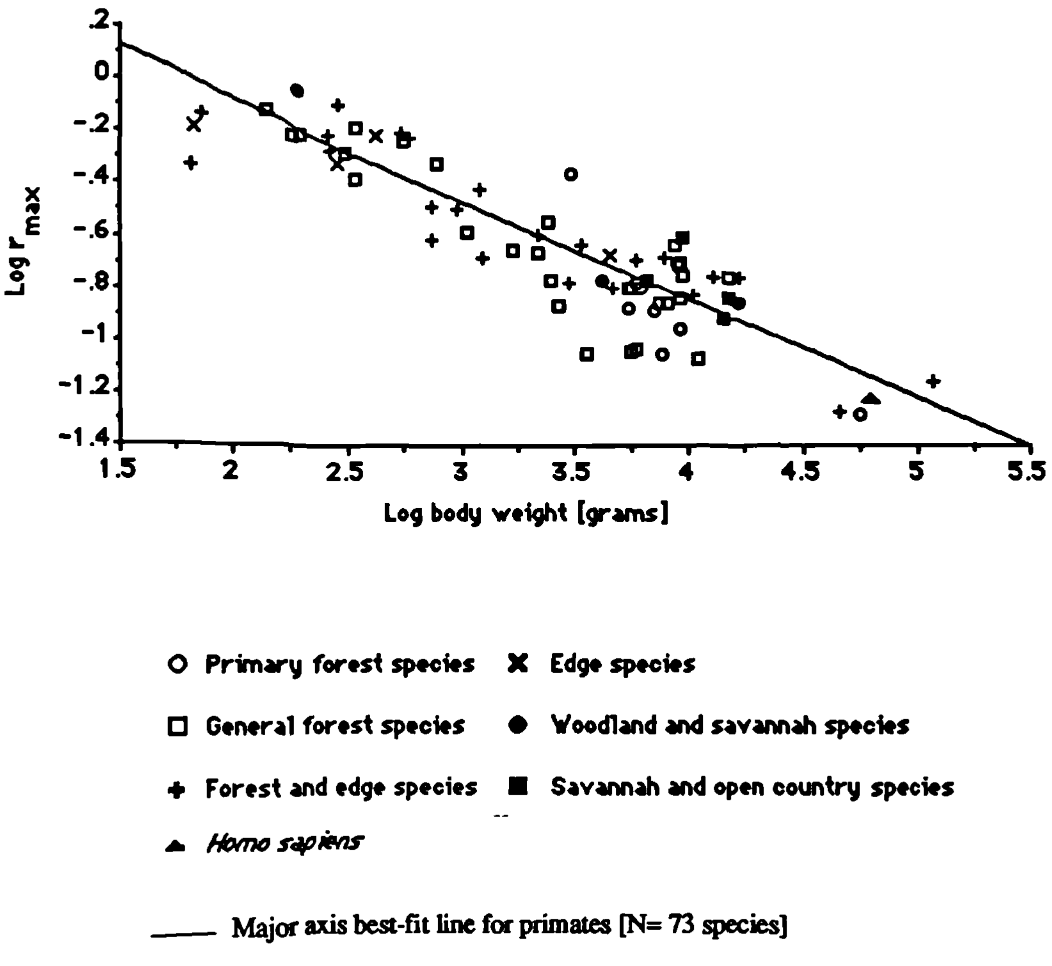
c) Mean r_{max} residuals and habitat



1=primary forest ; 2= general forest; 3= edge; 4= edge and woodland; 5= woodland and savannah; 6=savannah and open country.

Figure 5.7

Log r_{max} versus log body weight for primate species, showing habitat type



different habitats. Although the results from the haplorhine species were of the same type as those for the whole sample, no differences were found for different habitats within the strepsirhines or within any smaller taxonomic groupings. It therefore appears that, although the general trend of variation in residual r_{max} is as would be predicted by r- and K-selection theory [i.e. forest areas selecting for low r_{max} values and savannah environments for high r_{max} values] this pattern is not discernible for closely related species.

Interaction between habitat and other environmental variables

Habitat has been shown to be linked to relative r_{max} in primates, and, as previously discussed, links between habitat and other environmental variables are known to exist. It was therefore considered that the relationships between latitude and relative r_{max} could be complicated by correlations between habitat and these two variables. Similarly, the relationships between climate and relative r_{max} could be complicated by correlations between habitat and climate and between relative r_{max} and climate.

The analyses of the relationships of relative r_{max} to climate and latitude were therefore repeated for species within each habitat group. This was done for both the narrow habitat groupings and the broader habitat groupings. For example, the correlation between latitude and relative r_{max} was calculated for the eight species in the primary forest habitat group, the 30 species in the general forest group and also for the 38 species found in both primary and general forest habitats. As with the previous analyses on latitude and climate the relationships were investigated for primates of all taxonomic groups and for species within families, subfamilies and genera.

In addition, a test controlling latitude effects on habitat was also carried out. This involved splitting species into four groups according to their range limit and three groups according to their range centre; [species with a range limit 0-10°, <10-20°, <20-30°, and over 30°, and a range centre of 0-10°, <10-20°, and over 20°] and testing for differences in residual r_{max} for species in different habitats within each latitude group.

Habitat and latitude

Within the habitat groupings and within habitat and taxonomic groupings there is very little evidence of any correlation between latitude and residual r_{max}, with all correlations being insignificant. The conclusion that latitude is not strongly linked to residual r_{max} is therefore supported by this evidence.

When species were split into groups according to their range limits and range centres, three groups did not contain species in a wide range of habitats and were not expected to show differences between habitats. Of these four remaining groups, two showed significant [$p<0.05$] differences between the residual r_{max} values of habitat groups. In the 10-<20° range limit group primary forest and edge species had significantly lower residual r_{max} values than savannah species, and in the 0-10° range centre group group primary forest species had significantly lower residual r_{max} values than savannah species. This indicates that habitat can be used to predict relative r_{max}, even when the species are found in similar latitudes.

Habitat and climate

Within habitat groups, climate was found to vary with residual r_{max} in a number of cases. For all forest species there was a correlation between the variation in temperature during the year and residual r_{max}. This was found for primary forest species alone ($r=0.74$, $p<0.05$), and for all forest species together ($r=0.40$, $p<0.05$). Among the primary forest species, there was also a significant positive correlation between the variation in mean annual rainfall and residual r_{max}. In the other habitat groupings, the only significant correlation was between residual r_{max} and the mean rainfall in the driest month for the three species in savannah and open habitats [$r=-0.999$, $p<0.02$].

When subfamilies and genera within habitat groups were examined, there were several groups that showed significant correlations between residual r_{max} and climatic parameters. Some of these have already been discussed above as several taxonomic groups have species found in only one type of habitat. The significant correlations for the subfamily Lorisinae and the genera *Saguinus* [forest and edge species], *Cercocebus* [general forest species] and *Colobus* [general forest species] are listed in table 5.4. In addition, the savannah and open grassland species mentioned above are all of the subfamily Cercopithecinae. Further analyses indicated that two other taxonomic groups showed significant correlations between residual r_{max} and climate parameters within habitat groups. The general forest strepsirhine species, and the general forest Lemuridae both show negative correlations with both the variation in rainfall in the wettest month and the variation in temperature during the year.

These results indicate that climatic parameters can influence relative r_{max} independently of habitat and taxonomic group, i.e. that there are significant correlations between climate parameters and residual r_{max} even when habitat and/or taxonomic factors are controlled. In nearly all cases, the results indicate that residual r_{max} is positively correlated with climate variability and negatively correlated with the amount of rainfall and with temperature. The exceptions to this are the previously mentioned positive correlation with annual average rainfall in *Colobus* species and the negative correlations found with climate variability in the strepsirhine and lemurid forest species.

Discussion

The findings of this chapter can be split into two main parts. Firstly, there is the elucidation of the scaling of r_{max} to body weight in primates, and the comparison of this relationship to that found for other mammals. Secondly, there is the variation in residual r_{max} and the taxonomic and ecological correlates of this parameter.

The negative correlation between r_{max} and body weight was expected, both because of previous work relating r_{max} to body weight and because of the relationships found in primates between body weight and the main determinants of r_{max} [age at first reproduction and birth rate]. The finding that r_{max} in primates does not scale to the same allometric exponent as is found in other mammals indicates that the difference between primates and mammals is not simply a grade difference but also a difference in the scaling relationship. This difference is bought about by differences in the scaling relationship of the two main determinants of r_{max}, age at first reproduction and birth rate, to body weight. Although the third determinant of r_{max}, age at last reproduction [as measured by longevity], seems to scale to the same exponent in primates as it does in other mammals [see Chapter 3]. As size increases in primates, age at first reproduction increases and birth rate decreases, but they do so at a faster rate than is found for other mammals. Therefore, larger primates have a later age at first reproduction and a slower birth rate than would be found if these parameters scaled to the same value as is found for other mammals.

As has been discussed in previous chapters, the presence of grade effects can give rise to anomalous values of the allometric exponent. It was therefore considered that the lower slope value found for mammals could be due to to confusion of different grades within the mammalian group. However, when Henneman's [1984] data were reanalysed for each order separately the slopes found for all other orders were shallower than that found for primates. Similarly, Allaine *et al.* [1987] found that primates showed a steeper slope than any other mammalian order for log birth rate *versus* log body weight. It was also considered that the high slope value for the logarithmic plot of r_{max} against body weight in primates could be due to grade confusion <u>within</u> the primate order.

As previous work on other parameters indicated that a grade difference could exist between strepsirhines and haplorhines [Leutennegger, 1973; this study, Chapters 3 & 4], it was thought that differences between these two groups might be responsible for an elevation of the allometric exponent. There is some indication that the r_{max} of strepsirhine species may scale differently than in haplorhines. Some indication that the difference is a "real" one is found in the significant differences found between the age at first reproduction of strepsirhines and haplorhines [see Chapter 4]. Despite this, there is no significant difference between the relative birth rates or the relative r_{max} values of the two groups, with the smaller haplorhine species, the tarsiers and the marmosets and tamarins having similar rates of increase to strepsirhine species of the same size. Hence, it does not appear that one can regard the strepsirhines as being selected for a higher rate of increase than the haplorhines.

As age at first reproduction is the major determinant of r_{max}, it seems somewhat anomalous that strepsirhines and haplorhines can be shown to have significantly different relative values for this parameter, but not for r_{max}. One possible explanation for this is found when one considers the partial correlations, removing body weight effects, found between r_{max} and other life-history parameters in the two groups. In the haplorhine species, age at first reproduction is highly correlated with r_{max} even after the effects of body weight are removed, whereas in the strepsirhines no such correlation is found. Partial correlations indicate that the most important factor determining relative r_{max} in strepsirhines is relative birth rate. The reason for the lack of correlation between relative age at first reproduction and relative r_{max} in strepsirhine species may be the fact that many live in seasonal climates. If seasonality confines a species to breeding at yearly intervals, it is less easy for selection to vary the age at first reproduction and it is more likely that selection for a higher or lower r_{max} will operate through the selection of a smaller or larger litter size.

The residual variation in r_{max} was found to be connected with some aspects of ecology but not others. In direct contradiction to the hypothesis of McNab [1980], which suggests that diet and r_{max} will be correlated via a link with metabolic rate, the diet of primates was not found to be linked to their capacity for population increase. Further confirmation of the lack of an association between metabolic rate, diet and r_{max} comes from the lack of correlation between relative r_{max} and relative basal metabolic rate [BMR]. It appears that primate species with a relatively low BMR can maintain a relatively high r_{max}. It is suggested that this may be because such species are able to elevate their BMRs during reproduction, and therefore increase reproductive output [as discussed in Thompson and Nicoll, 1987]. Further discussion of the relationship between growth rates and relative BMR can be found in Chapter 6.

Although diet and BMR were not found to correlate with relative r_{max}, other factors, notably phylogeny [as measured by taxonomy] and environmental variability [as measured by habitat and climatic variables] were found to correlate with relative r_{max}. Within the major groupings of primates clear taxonomic divisions appear to occur between species with a low relative r_{max} and those with a high relative r_{max}. In the New World the cebid monkeys [family, Cebidae] generally have a very low relative r_{max} as compared to the marmosets and tamarins and Geoldi's monkey [family, Callitrichidae]. In the Old World haplorhine primates it is the apes [greater and lesser] that show a low $r_{max}$for their size, with all species except for the gorilla having a negative residual r_{max}. Although the gorilla does have a low r_{max} its very large size means that an even smaller rate of increase would be predicted. In particular, the lar gibbon, the siamang and the orangutan show very low rates of increase for their size. In contrast to the apes, the Old World monkeys, show high rates of increase for their size. Generally speaking, this taxonomic division of species into those with a high relative r_{max} and those with a low relative r_{max} reflects ecological divisions between the groups.

In the New World, the marmosets, tamarins and Geoldi's monkey are frequently found in secondary forest and nearly all have a relatively high r_{max}. Looking at the cebid species in more detail, the spider monkeys [*Ateles* spp. and *Lagothrix lagotricha*] are found almost entirely in primary and undisturbed forest and the three *Ateles* species are found to have a particularly low r_{max}. [Although the woolly monkey, *Lagothrix lagotricha*, has a higher relative r_{max} this could be due to the data for this species being from captive animals.] Other cebid species that are found in a wider variety of forest habitats have higher relative r_{max} values than the *Ateles* species but still have low relative r_{max} values as compared to other primates. These include *Saimiri sciureus*, the *Cebus* species, *Callicebus moloch and Pithecia pithecia*. The species that are found in the widest variety of habitats are the howler monkeys [*Alouatta* species] and the owl monkey, *Aotus trivirgatus*, and these species have high relative r_{max} values for cebid monkeys [or about the expected value for a "typical" primate]. In the Old World, it is interesting to note that the monkeys are found in a far wider variety of habitats than are the apes, which tend to be restricted to forest.

It therefore appears that in the two major groups of haplorhine primates there is a group that has evolved a low rate of reproductive increase, the cebids in the New World and the apes in the Old World. When seen in the context of mammalian reproduction, rather than only primate reproduction, it becomes clear that the apes and cebids have an extremely slow breeding strategy as all primates have a low reproductive output for their size. Both groups consist of basically arboreal, forest-living, mainly tropical species that feed predominantly on fruit and it is therefore possible that their similar ecologies have selected for similarly low rates of increase. Another interesting convergence between the two groups is seen in the exceptions to the rule of a negative residual r_{max}. In the cebid monkeys the exceptions are seen in the howler monkeys [*Alouatta* species] which are found in secondary forest and woodland to a greater extent than other cebid species and among the apes the gorilla is found in secondary forest and also in mountainous areas. Both howlers and gorillas are also more folivorous than are their respective relatives. As no clear links between r_{max} and diet could be found in primates it is probable that it is the occupation of secondary forest and more marginal habitats that has selected for higher relative r_{max} values in these species. It can therefore be postulated that both howler monkeys and gorillas have evolved different life-history characteristics from those of their relatives so as to enable them to cope with more marginal habitats. Both the occupation of such habitats and the increased proportion of leaves in the diet allow howler monkeys and gorillas to occupy forest niches that are not exploited by their own close relatives and thus avoid competition with them, [although the gorillas could be competing with another large group of forest-living, folivorous primate, the colobine monkeys].

In West Africa some chimpanzees are found in habitats that include areas of savannah [Nishida and Hiraiwa-Hasegawa, 1986] and these animals might therefore be expected to have a higher relative r_{max} than those in the forested areas for which data are available. Similarly, *Pan paniscus* [the bonobo or pygmy chimpanzee] appears to be restricted to forest [Nishida and Hiraiwa-Hasegawa, 1986] and therefore might be predicted to have a particularly low relative r_{max}. We must wait for further information on the life-histories of these species to test these predictions.

A comparison of the fast-breeding Old World and New World haplorhine groups [the cercopithecines and the callitrichids] is not appropriate. Although both groups have adapted to living outside of primary forest areas, their ways of doing this have been very different. The callitrichid monkeys are small species tending to live mainly in edge forest, where they feed on insects, fruit and exudates, whereas the cercopithecine monkeys are characterised by their large size, adaptation to ground-living habitats and a diet of a varying proportion of leaves and fruit. The convergences between these two groups are therefore not as striking as those found between the cebid monkeys and the apes.

A better Old World "equivalent" to the marmosets and tamarins may be the small strepsirhine species [bushbabies, lorises and pottos] which occupy a similar ecological niche to that of the callitrichids and also tend to have a high relatively r_{max}. In both groups there are species that can produce up to four young a year, and both have species that can start breeding at a very early age. However, there are some interesting differences between Old World strepsirhines and the New World marmosets and tamarins in their apparent response to more stable habitats.

Given the apparent link between a relatively low r_{max} and living in primary forest [see below] it is perhaps surprising that some of the marmosets and tamarins species living in more stable habitats do not have lower r_{max} values. For example, the golden lion tamarin [*Leontopithecus rosalia*] is confined to the Atlantic rainforest of Brazil and is not a secondary forest species, but its r_{max} is no lower than other marmosets and tamarins. One possible explanation for this apparent anomaly is that the life-history data used to determine r_{max} in the callitrichids is all from captive animals. In captivity, female marmosets and tamarins start to breed at about 18 months of age unless they are kept in family groups. Young females kept with their mothers or an older reproductive female do not become reproductively active until the older female stops reproducing or they are removed from her group. This inhibition of reproductive activity is due to the hormonal influence of the older female on the younger female. This generates a hormonal effect that prevents her from ovulating [Abbott, 1984].

Marmosets and tamarins in the wild generally live in groups containing only one reproductively active female [Goldizen, 1986; Ferrari, 1988], which suggests that the suppression of reproduction of younger females also occurs naturally. If this is the case, wild animals will have a later age at first reproduction than is found in most captive animals that are usually housed in breeding pairs. This would mean that the r_{max} of some marmosets and tamarins would be lower than that used in this study. There is some evidence that suggests that marmosets live in larger and more stable groups than do tamarins [Ferrari, 1988]. It therefore seems likely that marmosets would be more likely to have groups containing more than one adult female and hence that the age at first reproduction of the younger marmoset females will be delayed for longer than in tamarins. Marmosets also differ from tamarins in being better adapted to eat plant exudates, a characteristic that ensures a more stable food supply than for the tamarins. The combination of a stable food supply and a delayed first age at reproduction [and hence a lowered r_{max}] is precisely what would be predicted by the theory of r- and K-selection and, indeed, by this study. It can therefore be predicted that further studies of marmosets and tamarins will find that populations that live in areas where they can be assured of a stable food supply, and that therefore live in larger and more stable group, will delay first reproduction to a later age than will populations that do not have access to a stable food supply.

A particularly interesting feature of the marmosets and tamarins is that all species so far studied appear to have retained the capacity to breed at a young age when removed from the influence of older females. Hence, although wild populations in stable areas will presumably show delayed reproduction, the younger females will be able to start breeding immediately if the reproductive female in the group dies. The marmosets and tamarins can therefore be viewed as being primarily r-selected, in that they have been selected to be fast breeding and retain the capacity for a high rate of increase in colonizing situations, but secondarily K-selected, in that they will delay reproduction in times of stability. Ford [1980], suggests that many of the features of marmosets and tamarins can be explained by their being "phyletic dwarfs", i.e. being derived from a larger ancestor by selection for a small size. Ford considers that a possible explanation for dwarfing could be that marmosets and tamarins have been selected for maximum efficiency in a competitive environment, with the small size increasing carrying capacity [i.e. K-selection]. However, this scenario does not take the relatively high r_{max} of the marmosets and tamarins into account, as selection for increased efficiency would also be expected to select for slower rates of breeding, whereas the reverse which has apparently occurred. It therefore appears more likely that the reason for the small size of marmosets and tamarins is r-selection rather than K-selection. The question of the life-history strategy of marmosets and tamarins will be discussed further in the last chapter of this thesis.

There is no evidence to suggest that a similarly flexible response to environment is found in the African and Asian strepsirhines; instead the species are divided into those with a high r_{max} and those with a low r_{max} for their size. The bushbaby species that are typical of edge habitats, woodland and savannah [*Galago moholi*, *G. senegalensis*, *G. crassicaudatus* and *G. garnetti*] have high r_{max} values for their size whereas a species that is commonly found in primary forest [*Galago demidovii*] has a relatively low r_{max}. Another forest species [*G. zanzibaricus*] has a r_{max} that is only very slightly above that that would be predicted for a typical primate of that body size. Similarly, a loris species found mainly in forest clearings [*Arctocebus calabarensis*] has a relatively high r_{max}. The one surprising finding is that two other lorisid species, the loris [*Loris tardigradus*] and the potto [*Perodicticus potto*] have relatively low r_{max} values despite their living predominantly in secondary forest.

The second Old World group which tends to have a relatively high r_{max} contains the Old World monkeys. This group also has a considerable amount of variation in relative r_{max} within the family. The more arboreal, forest adapted guenons tend to have a lower relative r_{max} than do the macaques, langurs and baboons which are found in a wider number of habitats. This group is discussed in some detail in Chapter 7 and therefore will not be discussed further here.

These links between environmental predictability and relative r_{max} are largely borne out by the more detailed analyses of habitat and climate. Species in primary rainforest have low residual r_{max} values, whereas those in open country habitats have high residual r_{max} values. This trend was found for both the primates as a whole and for haplorhines separately but it was not obvious in the strepsirhines alone. It should be noted that, when looking at species within smaller taxonomic groups [i.e. families, subfamilies, genera] there was no clear correlation between environmental predictability and relative r_{max}. This may indicate that the division of species into those with high residual r_{max} values and those with low residual r_{max} values occurred far back in the evolutionary past. Some groups' ancestors being selected to be forest-living and having low residual r_{max} values and others being selected to live in open country [or other unpredictable habitats] and having high residual r_{max} values. To some extent this interpretation is borne out by the previously discussed taxonomic divisions of species into those with relatively high and those with relatively low r_{max} values.

However, the idea that groups are uniformly selected for a high or low residual r_{max} is not supported by the nested analysis of variance, which shows that over 60% of the residual variation in r_{max} is accounted for by variation of species within genera. The lack of significant differences in residual r_{max} between habitat types for closely related species may be explained by the rather crude measures of habitat used and the severe reduction in sample number that is incurred by looking at species within a single subfamily or genera. Some indication that environmental variation can be linked to the evolution of relative r_{max} within small taxa is found by looking at the relationship found between relative r_{max} and climatic variables. In several cases there are significant correlations between climatic variables and residual r_{max} for species within genera and species within subfamilies. These correlations are also found when all species are within the same general habitat type. This evidence all suggests that closely related species that are found in areas of differing environmental variability will be selected to have different relative r_{max} values. Although these results are based on very small sample sizes, and must therefore be viewed as preliminary, it is striking that nearly all of the correlations that are found indicate that a high climatic variability is linked to a high relative r_{max}. In addition to this, there is evidence to suggest that habitats thought of as predictable and stable are associated with species with a low relative r_{max} whereas those considered to be unpredictable are associated with species with a high relative r_{max}. The results of this chapter are therefore broadly in agreement with the idea that primary forests and predictable and/or stable climates select for a relatively low r_{max}, whereas more open habitats and unpredictable and/or variable climates select for a relatively high r_{max}.

A link between environmental predictability and a low r_{max} is predicted by both r- and K-selection [r/K] theory and by bet-hedging theory. A link between environmental unpredictability and a high r_{max} is also predicted by both r/K theory and by bet-hedging theory, but in the latter the link is conditional on the majority of mortality, caused by the unpredictable environment, being in the adults of the population. Although there are few data on mortality patterns in primates, what there is suggests that there are higher mortality rates in young animals [e.g. Altmann, 1980; Dunbar, 1984]. The results of this study therefore seem to support r/K theory rather than bet-hedging theory.

However, it should be noted that the results only support r/K theory if one looks at relative r_{max} rather than the actual r_{max}, i.e. if one assumes that body weight effects should be removed from the r_{max} data. The removal of body weight effects can be justified on the grounds that an animal's body size will effect its response to the environment. As discussed in Chapter 1, larger animals can be expected to experience a given environment as being more stable than smaller animals, and one might therefore predict that larger animals will tend to have lower r_{max} values. By removing body weight effects one is therefore controlling for the differential responses of large and small animals to the same environmental changes.

There is, however, one notable area where the results of this, and the previous, chapter do not appear to be in agreement with r/K theory. The theory of r- and K-selection predicts that unpredictable environments will select for a high r_{max} and also select for high reproductive effort. The results of Chapter 4 indicate that several life-history parameters that are associated with reproductive effort [e.g. neonatal weight, gestation length, weaning age] do not vary predictably with habitat type. Additionally the partial correlations indicate that, although weaning age is found to be negatively correlated with r_{max} in the haplorhines, indicating that a long maternal investment during lactation is linked to a low rate of population increase, no other measures of reproductive effort were found to correlate with r_{max}. The indication that reproductive effort in primates does not vary as is predicted by theories of life-history evolution, led to a more detailed investigation of the variation of various measures of reproductive effort. These investigations are reported in the next chapter.

Chapter 5

Summary

The scaling relationship of r_{max} to body weight in primates is found to be described by the equation: $r_{max}= 4.9M^{-0.38}$ [where M= average adult body weight]. This relationship differs from that found in other mammals, in having a higher allometric exponent [the slope value of the logarithmic best-fit line] and a markedly lower allometric coefficient [the intercept value of the logarithmic best-fit line]. These characteristics mean that primates have a lower rate of population increase than other mammals over the whole primate size range. These relationships are discussed in some detail.

The variation in relative or residual r_{max}, [i.e. the variation not accounted for by variation in body size] is examined and found to be largely correlated with taxonomy and with environmental factors. Relative r_{max} is not found to correlate with the latitude, the diet or the relative basal metabolic rate of the species. Some groups of haplorhine primates [the cebid monkeys, the lesser and greater apes] have low relative r_{max} values as compared to other primate groups, whereas other [the Old World monkeys, the marmosets and tamarins] have low relative r_{max} values. The strepsirhine primates include species with both high and low relative r_{max} values, but are not found to have consistently higher relative r_{max} values than haplorhines.

Relative r_{max} is found to be generally high in species living in more open habitats and low in species found in primary rainforest. Although there are few correlations between relative r_{max} and climate parameters, those that are found suggest that variable climates, dry climates and hot climates will select for a high relative r_{max}. It is suggested that these results indicate that primates can be thought of as fitting either an r- and K-selection model or a bet-hedging model where density independent mortality mainly effects adult animals. In either case, however, the results only fit the models when relative r_{max} rather than the actual r_{max} is used.

Chapter 6

Reproductive effort

This chapter is concerned with reproductive effort in primates. Possible correlates of the observed variation in reproductive effort are investigated, with particular emphasis on testing the prediction that reproductive effort will be linked to environmental variability. The chapter is introduced by a general discussion of the concept of reproductive effort, particularly in relation to life-histories in mammals. These ideas are used to explain the measures of reproductive effort used in this study. There then follows a discussion of factors that have been previously suggested to affect the reproductive effort of mammals. These factors are investigated in an attempt to determine their relevance to primate reproduction.

As has been discussed in previous chapters, the reproductive effort of a species has been suggested to be related to its ecology in two important theories of life-history evolution. However, in some circumstances, bet-hedging theory and r- and K-selection theory will predict that different relationships between reproductive effort [RE] and environmental predictability will be found. The theory of r- and K-selection [r/K theory] predicts that species in an unpredictable environment will have a high reproductive effort, whereas bet-hedging theory predicts that unpredictable environments may select for a high RE if adult mortality is affected but for for a low RE if juvenile mortality is affected. This two hypothesis are therefore tested with an examination of the variation of RE with several measures of environmental variability.

Other variables that have been suggested to be correlates of reproductive effort, or at least of the measures of reproductive effort used here, are also discussed, these include body weight, basal metabolic rate, diet and certain life-history variables.

A definition of reproductive effort

The following discussion of reproductive effort draws largely on the seminal paper by Trivers [1972]. Reproductive effort is a term commonly used in sociobiology to describe the proportion of an organism's available resources that it expends on reproduction. The reproductive effort of an organism will therefore include all effort expended in order to produce offspring. The reproductive effort of a sexually reproducing individual can be split into two basic components.

1) The proportion of available resources expended in order to find a mate and to successfully copulate with that mate, using the terminology of Trivers [1972] this will be referred to as

nonparental reproductive effort.

2) The proportion of available resources expended in the raising of the offspring. This will be referred to as parental investment

As has been noted by Bell [1980], for reproductive effort [RE] to have evolutionary significance it is necessary to assume that the measures of RE used can be taken as being a measure of the cost to the organism. If there were no cost of reproducing, the amount of resources that could be expended on reproduction would be infinite. If organisms lived in a world with unlimited resources, and the amount of reproductive effort expended on one litter did not alter an organism's capacity to produce later litters, one would predict that natural selection would continuously select for a higher and higher reproductive effort. However, it is clear that such a situation does not occur, and hence an organism may be selected to expend resources on reproduction or on other things such a maintaining itself, and competing with other organisms.

An animal that spends a large proportion of its available resources on reproduction might therefore be expected to have less available energy to put into surviving. In general terms, one can therefore say that an increased reproductive effort will be predicted to be associated with an increased risk of mortality, and this has been shown to be true for some organisms [Stearns, 1976]. Similarly, it would be expected that, on average, the greater input an organism puts into one litter the less will be the organism's input into future litters. This appears to be a logical assumption to make, as it can be assumed that an organism that puts a large proportion of its available resources into reproduction will have less resources available for future reproductive attempts. Reproduction is therefore considered to have costs, in terms of cost to fecundity and cost to survival.

Nonparental reproductive effort

Several activities might be classified as nonparental reproductive effort. These include; searching for a mate, defending a territory containing several possible mates or defence of a mate against conspecifics or predators. The type of nonparental reproductive effort that is expended varies with several factors, such as the physiological constraints on the animal, the social structure of the species and on the individual's sex.

For animals that do not live with adults of the opposite sex [or that do not mate within their own social group] mates must be located for each breeding attempt and this will require the expenditure of energy that should be included in the calculation of reproductive effort. In some species [e.g. some bushbabies] the male may maintain a territory that includes one or more females, such activity might therefore be included as reproductive effort. For many species the process of finding a mate is facilitated by adults living in groups containing adult members of both sexes. In primates such groups are generally breeding groups [i.e. they do not seek mates from another social group] and the adults will not have to expend energy in searching for a mate.

However, it could also be argued that the commonly observed phenomena of adults of one or both sexes leaving their natal group to join a new group at puberty is carried out for the purpose of finding a mate, and therefore the energy expenditure incurred in this process should be included in the calculation of reproductive effort. In groups where one male has access to several females [e.g. *Theropithecus gelada, Papio hamadryas*] the male must expend energy to exclude rival males, and to prevent the females from straying or deliberately seeking out other males. In some multi-male groups [e.g. some Old World monkey species] more dominant males may father a larger proportion of infants and hence energy expenditure spent maintaining a high rank would be considered as a part of reproductive effort in such species. Similarly, in monogamous species both the male and female may expend energy in preventing competitors of their sex from gaining access to their mate.

This brief description includes just some of the possible causes of variation in nonparental reproductive effort that may arise from differences in social structure. It can be seen from this that many other possible causes of variation could be discussed [e.g. number of females in group, female ranking, sex ratios], but it is felt that this topic is outside the scope of this study.

Parental investment

Trivers [1972] defines parental investment as:

> "....any investment by the parent in an individual offspring that increases the offspring's chance of surviving [and hence reproductive success] at the cost of the parent's ability to invest in other offspring."
>
> [Trivers, 1972; p.55].

Using this definition, it can be seen that parental investment will include both the direct channelling of resources to the young [both *in utero* and *via* lactation in mammals] and the more indirect investment of resources to promote the offspring's welfare through such activities as carrying them and protecting them from predators. Although only the mother can contribute resources through gestation and by lactation, both parents can contribute to the more indirect forms of investment. The father may also be able to help by provisioning both the mother and the infant. As discussed below, the measures of parental investment used here are measures of the amount of resources put into the young. Among mammals, such investment is often entirely maternal investment but, in some cases, the father may also contribute and the term parental investment is therefore used.

Measures of reproductive effort used in this study

The quality and the quantity of both parental and nonparental reproductive effort vary depending on the species and the sex of the individual concerned. The accurate testing of hypotheses on reproductive effort would ideally require knowledge of the total reproductive effort of an individual over its lifetime, relative to the total resources available to it, and its apportioning between separate reproductive attempts. As such information is not available for primate species [and indeed is almost impossible to measure in any species] the data used is based on measures of the reproductive effort for the production of a single litter.

As discussed above, both parental investment and nonparental investment should properly be measured by their effects on the future reproductive output of the animal concerned, i.e. by measuring the "cost" to the adult. Some studies have tried to quantify the costs of infant production. For example, Altmann *et al.* [1978] looked at the effect of infant survival on interbirth intervals in savannah baboons. However, such a measure cannot account for many factors: for example, it does not account for the costs of undetected pregnancies. In the absence of controlled conditions and studies lasting several generations, it will therefore be almost impossible to calculate the true costs of reproduction in primates. It was decided that it would not be practicable to measure reproductive effort in terms of the cost to the breeding adult. Instead the less "correct", but more readily quantifiable, measure of gain to the offspring was employed. Parental investment is quantifiable by measurement of its effects on the infants' size and growth, whereas nonparental investment can only be measured by the cost incurred to the parent. Using a measure of gain to the infant means that all of the measures of reproductive effort used in this study are measures of parental investment, and no attempt is made to quantify a measure of nonparental investment.

Parental investment in mammals can be separated into investment made before birth, i.e. during gestation, and that made after birth, i.e. during parental care of infants. Two possible measures of the parental investment can be considered. The first takes parental investment as the total amount of energy invested in the young during the gestation period and lactation period combined, a measure of this being the total litter weight at weaning. The second deals with the energy investment <u>per day</u> of the mother, as measured by growth rates of the young during the gestation period and the lactation period.

The use of total litter weight as a measure of total investment has the problem that animals may increase their total investment by increasing the period of parental care, while the amount of resources that they put into the litter per day may be the same, or even lower, than for another species with a different period of parental care. Using growth rate as a measure of parental investment therefore allows the comparison of species with different periods of parental care.

An outcome of using growth rates as a measure of parental investment is that, for example, this study would classify an species that produces a total litter mass of 2000 grams in six months as having a higher parental investment than a species producing a litter of 3000 grams in a year. Although the former species would have lower total litter weight at weaning its average growth rate would be about 11 grams/day, whereas the latter would have an average growth rate of just over 8 grams/day. It is therefore assumed that an animal that puts a large amount of resources into its young per day, albeit for a short period of time, will probably be incurring a higher cost, in terms of its future reproductive output, than an animal that invests the same amount of total resources over a longer period of time. Although this may be true, in that it is likely that a high reproductive effort per day will increase the chance of death by predation or disease, it should be noted that a long period of parental care can be costly to future reproductive output by delaying the time of the next litter. For these reasons reference is also made to total parental investment, as measured by litter weight at birth and weaning.

Prenatal parental investment

During gestation the mother must expend energy to maintain the foetus and allow it to grow, and she will also be putting resources into the growth and maintenance of the placenta. In addition she may have to use more energy, than when not pregnant, in order to move around searching for food, etc. Of these three parameters, it is only the first that is discussed here. The amount of investment that is put into the placenta cannot be estimated without detailed knowledge about this organ's growth and weight, and the energy content of the proportion of it that is eaten by the mother after the birth. As these are not parameters that are readily available, it is assumed that the resources put into the placenta are directly proportional to those that are put into the young during gestation. [This is a reasonable assumption to make as Rudder [1979] demonstrated that placental weight is directly proportional to neonatal weight in primates.] A similar assumption is made about the extra energy expenditure required for daily activities because of the burden of pregnancy.

The total investment in the young during gestation can be measured by the total litter weight at birth. This parameter has already been discussed in Chapter 4 and will not be discussed in detail here. The investment <u>per day</u> in the young during gestation can be measured by the growth rate of the litter from conception to birth. In most species, it appears that the growth rate of the foetus is not constant throughout gestation [Payne and Wheeler, 1967a] but is related to the weight of the foetus at any given time. It has been shown that the gestation length [G] is related to foetal weight [W_{fe}] by the equation:

$$W_{fe} = a\,(G-g')^{b}$$

[where a is a constant for a given species and b is a constant approximately equal to 3.0. The symbol g' represents the "lag phase" between conception and onset of foetal growth. The lag phase [g'] varies from species to species and is allometrically related to the gestation length [Martin and MacLarnon, 1985]. However, it is very short in proportion to total gestation length and is frequently omitted to give a simplified equation.

Given this relationship, it would be possible to calculate an instantaneous measure of the rate of foetal growth at any given point, including at birth [i.e. by substituting neonatal weight for foetal weight in the above equation and rearranging to give a measure of the growth rate]. However, for the purposes of this study the only measure of foetal growth rate used is the average rate of growth over the total gestation period. This average measure has the advantage of being easily measured and not relying on the knowledge of the parameters (a) and (b) above.

The litter growth rate was therefore calculated by dividing the total litter weight by the gestation length, giving a simple measure of the mean growth rate of the foetus throughout gestation. Similarly, the individual growth rate was calculated by dividing the individual neonatal weight by the gestation period.

Postnatal parental investment

The postnatal parental investment is the investment put into the young between birth and the time when the young become independent. It was decided to use parental investment from birth to apparent weaning age as a measure of postnatal reproductive effort. Average postnatal growth rate from birth to weaning age was the preferred measure of parental investment used. Although there is also considerable growth after weaning in primates, the pattern of growth once the young are feeding themselves is not considered here as it is assumed that the majority of growth after weaning is due to the animals' own efforts in securing food. This measure therefore ignores any parental investment made in young after they have been weaned [e.g. parents protecting older offspring from attack by predators or conspecifics], but has the advantage of being more directly measurable than a measure designed to include investment made in weaned offspring.

The estimation of weaning age is not straightforward and in some cases it has been difficult to judge the period over which growth rate should be measured. Reports of weaning age have been taken from the literature, with weaning age being defined either as the time that the young were no longer suckling or as the age at which the mother's lactation ceased. The major problem in determining a suitable measure of weaning age is that of deciding when suckling is terminated. In some species e.g. the lesser mouse lemur [*Microcebus murinus*] the young are suckled until about 1.5 months of age and are then weaned in a few days [R.D. Martin pers. comm.]. For such species, the period over which the mother is investing in the young can be reasonably assumed to be essentially complete once weaning is over. However, for other species the determination of the time of weaning is more problematic. In such species [e.g. baboons, vervet monkeys, the apes], there is a long period during which parental investment is being gradually decreased as the young become decreasingly dependent on their mother's milk [e.g. see Altmann, 1980]. In such cases the estimate of weaning age is difficult and it should be realized that this may mean that some of the weaning ages might be changed by several months if other data were used.

A second problem with the calculation of these postnatal growth rates is that such information is frequently not available for the total period between birth and weaning. With these problems in mind, the following procedure was used to calculate the postnatal growth rate.

1) For species in which weaning age does not appear to be ambiguous, and data are available both for birth weight in grams [W_n] and for weight at weaning in grams [W_w], growth rate to weaning [G_{0-w}] is calculated by:

$$G_{0-w} = (W_w - W_n)/\text{weaning age [days]}$$

2) For species in which weaning age does not appear to be ambiguous, but data are available for only a part of the growth period between birth and weaning, the average growth rate over this period is used as a substitute for G_{0-w}.

3. In some species, weaning age is difficult to estimate because there is a period of time where it is not clear if the infant is still dependent in the mother for sustenance. In such cases the growth rate used has been based on what appears to be the best estimate of time to weaning.

The figures used for the calculations are given in detail in Appendix III. As can be seen, this appendix includes details of growth rate data of hand-reared young. In the majority of analyses it was felt that the growth rates of hand-reared infants could not be used to estimate parental investment, as hand-reared infants may have elevated or depressed growth rates. Under ideal conditions, hand-reared infants may be fed more than a mother might be able to give them, and such infants would be able to grow faster than those that are mother-reared. Some indication that this may occur, comes from studies comparing the growth rates of hand-reared and mother-reared baboons. Wild savannah baboons grow at about 5 grams per day in their first year of life [Altmann and Alberts, 1987], whereas hand-reared baboons can grow at over eight grams per day in their first year [Coelho, 1985]. In contrast, a further problem with data from hand-reared animals is that such infants are frequently hand-reared because they have been deserted by their mother or are sick. In these cases, the infant cannot be regarded as normal and may have low growth rates and/or abnormal growth patterns. For these reasons it was decided to include only data from mother-reared infants in the majority of the analyses, this restricted data set contained 35 species. However, previous studies on growth rates have included data from both mother-reared and hand-reared infants [e.g. Case, 1978; Kirkwood, 1985]. The full data set [59 species] has therefore been used as well to calculate best-fit lines for as many species as possible, permitting comparison with these studies.

Total reproductive effort

This study makes no attempt to use a measure of total reproductive effort throughout the whole period of parental care, i.e. mean growth rate from conception to weaning age. This was because it was felt that, for a given rate of infant growth, there would be very great differences in energy demand on a pregnant female and a lactating female. In pregnancy, there is a direct transfer of nutrients from the mother to the foetus via the placenta and the foetus is protected from variation in temperature by the mothers body. During lactation nutrients are transferred less directly and the energy requirements of the young are increased as they must maintain a constant body temperature. This combination of less efficient energy transfer from mother to young and higher maintenance costs for young after birth means that a growth rate of [say] one gram per day during gestation cannot be considered as being equivalent to one gram per day during lactation. Hence, a species that produced an infant of 2kg after 2 months of gestation and 6 months of lactation cannot be considered to have made the same reproductive effort as a species that produced an infant of the same weight after 4 months of gestation and 4 months of lactation. By keeping the two measures of growth rates separate, it was considered that the comparisons of species were of "like with like" and hence more useful information would be yielded.

As mentioned above, the total reproductive effort can be considered to be represented by the weight of the infant at the time when investment is terminated, i.e. at weaning. The scaling of this weaning weight to adult body weight and the residual variation in this measure are discussed Chapter 4.

Factors influencing the amount of reproductive effort

Several parameters have been suggested to be important in determining the proportion of resources an animal allocates to reproduction. Some of these factors are not relevant to a discussion of mammalian evolution and will not be dealt with here. For example, the "choice" of either male and/or female care of eggs and babies is open to birds, whereas in mammals the male is unable to either carry unborn infants or to lactate. Unlike a female bird which can desert her eggs to the male immediately they are laid, a female mammal must therefore be a direct participant in at least the early development of her young. Factors that may influence the reproductive effort of mammals include body size, metabolic rate, and ecological and environmental influences. These factors will be discussed in turn for both prenatal and postnatal parental investment [as measured by average growth rates].

Chapter 6

Allometric analysis of growth rates

The scaling of foetal growth rate to body weight

There have been several previous studies of the allometry of foetal growth rate in all mammals and in primates [e.g. Martin and MacLarnon, 1988; Ross, 1988; Rudder,1979]. Although it is the growth rate of the litter that is of primary interest for this study [as it represents the total reproductive effort of the mother during gestation], the scaling of individual foetal growth rates to body weight is also briefly discussed, as it was felt that an understanding of the growth rate of the individual foetus would be of interest to a study of the growth rate of the total litter. [As the plot of $\log_{10}$ litter growth rate to $\log_{10}$ body weight is very similar to the plot of $\log_{10}$ individual growth rate to $\log_{10}$ body weight, only the former is shown here.]

Figure 6.1 and tables 6.1 and 6.2 show the scaling relationship of foetal growth rate to body weight. It can be seen that there is some indication that the strepsirhine and haplorhine primates should be considered separately, with the strepsirhines appearing to have lower foetal growth rates than haplorhines of the same size. The slopes of the strepsirhine and haplorhine lines are not significantly different, with their 95% confidence limits overlapping [tables 6.1 and 6.2].

Taking individual growth rate first; to test for grade differences between the two lines a line of slope 0.665 [i.e. the average of the two species lines] was drawn through the mean of the total sample and an ANOVA test [as described Chapter 2] was carried out on the residuals. This test indicated that the strepsirhines have a significantly lower relative foetal growth rate than the haplorhines [$p<0.001$]. Many strepsirhines typically produce more than one offspring, whereas the majority of haplorhines only produce singletons. It was therefore considered that the reason for the slower growth rate of the strepsirhine foetus [relative to body weight] could be due to the apportioning of resources between two offspring. Figure 6.2 shows the difference between those primates producing several offspring [an average of 1.2 offspring or more per litter] and those that typically produce singletons [i.e. with an average of less than 1.2 offspring per litter]. There is no indication, from this plot, that species producing multiple offspring have a lower individual foetal growth rate than do those producing single offspring. This is borne out by the results of ANOVAs, carried out on both the whole sample and on the two suborders separately, which found no significant difference between the relative foetal growth rates of the singleton and multiple offspring group [$p>0.05$].

Further evidence that the difference between the relative foetal growth rates of the haplorhine and strepsirhine species is not due to the former group's tendency to produce smaller litters than does the latter group, comes from the analyses of the scaling of the total foetal growth rate of litter. Figure 6.1 and table 6.2 show the scaling of the foetal growth rate of the

Table 6.1

Major axis statistics for $\log_{10}$ individual foetal growth rate vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	59	0.96	0.74	-2.54	0.69	0.80
	genera	40	0.96	0.72	-2.46	0.65	0.79
	subfamily	16	0.97	0.70	-2.38	0.61	0.81
Strepsirhines:	species	23	0.91	0.67	-2.42	0.54	0.81
	genera	13	0.88	0.71	-2.55	0.48	0.88
	subfamily	5	0.92	0.64	-2.30	0.22	1.31
Haplorhines:	species	36	0.98	0.66	-2.17	0.61	0.71
	genera	27	0.98	0.66	-2.18	0.60	0.71
	subfamily	11	0.98	0.66	-2.20	0.57	0.76

Table 6.2

Major axis statistics for $\log_{10}$ litter foetal growth rate vs. $\log_{10}$ body weight

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	59	0.95	0.67	-2.24	0.61	0.73
	genera	40	0.94	0.64	-2.13	0.57	0.72
	subfamily	16	0.96	0.64	-2.13	0.54	0.76
Strepsirhines:	species	23	0.84	0.61	-2.15	0.44	0.80
	genera	13	0.78	0.66	-2.28	0.35	1.08
	subfamily	5	0.81	0.53	-1.88	-0.10	1.81
Haplorhines:	species	36	0.97	0.58	-1.84	0.53	0.62
	genera	27	0.98	0.58	-1.84	0.52	0.63
	subfamily	11	0.98	0.63	-2.03	0.53	0.73

Figure 6.1

Log_{10} litter foetal growth rate versus log_{10} body weight for 59 primate species

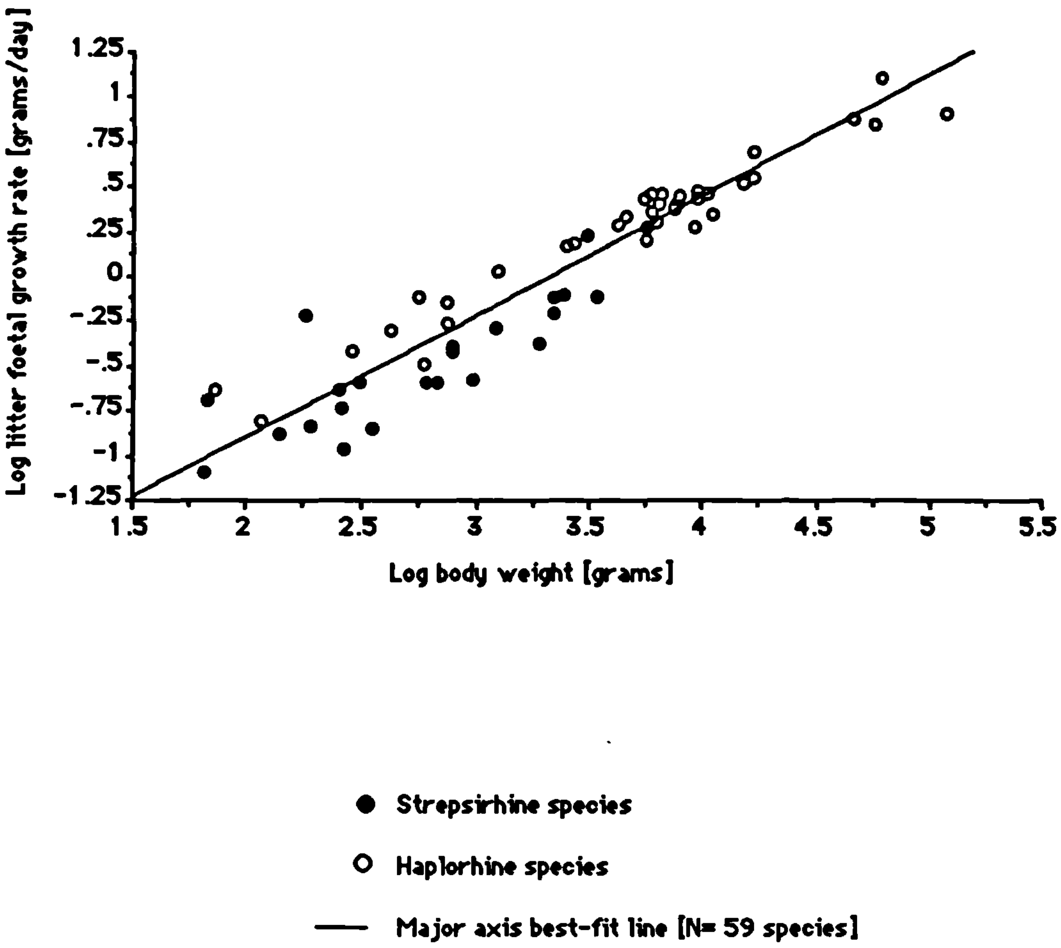
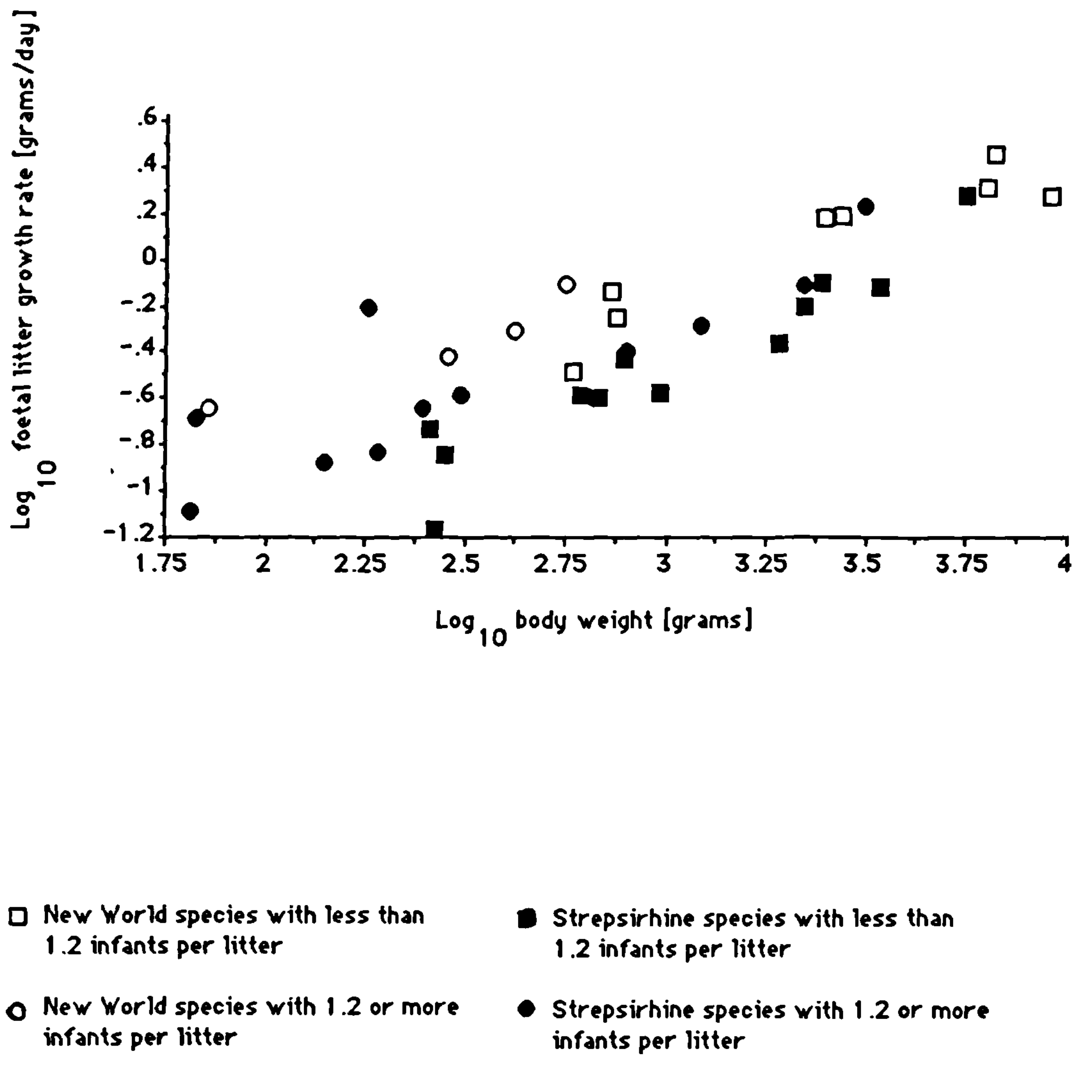


Figure 6.2

Log_{10} foetal litter growth rate versus *$\log_{10}$ body weight for strepsirhine and New World primate species, showing litter size*



litter to body weight. As with individual foetal growth rate, there is evidence that the strepsirhine species have a lower litter foetal growth rate than do the haplorhines. This is confirmed by an analysis of variance on the residual values, taken from a line of the species average slope [0.60], where it was found that the strepsirhines had significantly lower residual values than the haplorhines [ANOVA, $p<0.001$].

Species with more than one offspring per litter do not have significantly lower individual foetal growth rates than do species, of the same size, with a single infant per litter [see above]. It might be expected that the foetal growth rates of the litters of species producing several infants per litter would be relatively higher. This is indeed found to be the case. In both haplorhine and strepsirhines groups, litter foetal growth rates are significantly higher, relative to body size, in species that produce an average of 1.2 or more offspring per litter [$p<0.05$]. This suggests that the parental investment per day during gestation is higher for species with larger litters.

It was considered that taxonomic differences in foetal growth rate of individual young or of the total litter might also be apparent within the two suborders. However, there are no haplorhine groups that are characterised by particularly high or particularly low foetal growth rates. Within the strepsirhine group the Cheirogaleinae [dwarf and mouse lemurs] show a relatively high foetal growth rate [both of individual young and of the total litter], which brings their level of parental investment during pregnancy into the range of the haplorhine group. The only other strepsirhine species with a comparably high foetal growth rate is *Varecia variegatus*, the ruffed lemur. The high litter growth rate is bought about by both a relatively short gestation and a relatively high litter weight in *Varecia variegatus* and *Cheirogaleus medius*, but is mainly due to a short gestation length in the *Microcebus* species.

The results of these analyses are in agreement with the relationships between neonatal weight, gestation length and adult body weight, previously discussed in Chapter 4. Strepsirhine species have significantly smaller neonates than do haplorhines, but the relative gestation lengths of the two groups are generally similar. The combination of these two factors means that one would expect that strepsirhines would have a lower foetal growth rate than haplorhines. Exceptions are found in the dwarf and mouse lemurs and the ruffed lemur, which all have relatively short gestation lengths but normal or slightly high litter weights, and therefore have very high foetal litter growth rates for their size.

The scaling parameters for both individual foetal growth rate and litter foetal growth rate could have been predicted from the scaling parameters given for neonatal weight, litter weight and gestation length in Chapter 4. For example, for haplorhine species:

$$\text{Litter weight } (L) = k_1 M^{(0.67)}$$
$$\text{Gestation length } (G) = k_2 M^{(0.07)}$$

$$\therefore \quad \text{Litter foetal growth rate} \; = k_3\{L/G\} = k_3\{\underline{M}^{(0.67)}/M^{(0.07)}\} = k_3 M^{(0.60)}$$

The scaling parameter that would be predicted, 0.60, therefore agrees with the value of 0.58 that is actually found [the small difference can be explained by the slightly different set of species used in each case, as some species have data for litter weight and not gestation length and *vice versa*]. The scaling exponents found therefore need to be explained with reference to the scaling exponents for birth weight and gestation length. The scaling relationships found and the differences between haplorhines and strepsirhines are discussed at the end of this chapter.

The scaling of postnatal growth rate to body weight

As with foetal growth rate, both individual and litter postnatal growth rates are discussed here but only the plot of $\log_{10}$ postnatal litter growth rate to $\log_{10}$ body weight is shown. The relationships between individual postnatal growth rate and body weight and litter postnatal growth rate and body weight are shown in tables 6.3 and 6.4 and figure 6.3. These tables include results from both hand-reared and mother-reared animals and can be compared with other studies carried out on mammals generally. The statistics from mother-reared animals alone are also given, and all further discussion is confined to these species unless otherwise stated.

Two comparable studies on postnatal growth rate have previously been carried out, one dealing with terrestrial vertebrates [Case, 1978] and one with primates [Kirkwood, 1985]. Case's study looked at the mammals as a single group and also at the primates separately. In addition to looking at primates as a single group, both of these studies divided the primates into prosimian and anthropoid primates, with Kirkwood [1985] making further divisions within the anthropoid primates [see below]. It should be noted that, as neither of these studies include data for any tarsier species, the use of the taxonomic groupings of prosimian and anthropoid primates that they use are no different, in practice, from the divisions strepsirhine and haplorhine that are used in this study. For reasons of clarity, I have therefore used the terms strepsirhine and haplorhine throughout the following discussion.

Case [1978] looked at the variation in postnatal growth rate of individual young for a large number of species of terrestrial vertebrates. In particular, his paper looks at the relationship between postnatal growth rate, body weight and taxonomy. Case also investigated the possibility that other factors might influence growth rates in animals and this second aspect of his study will be considered to later in this chapter.

Case examined rate of growth [g/day] for the early period of the animal's life, this period varying with taxonomic group. In mammals, Case states [p.244] that the rates were "....calculated over the relatively linear phase of growth from the time when 5 per cent of

Figure 6.3

Log_{10} litter postnatal growth rate versus log_{10} body weight

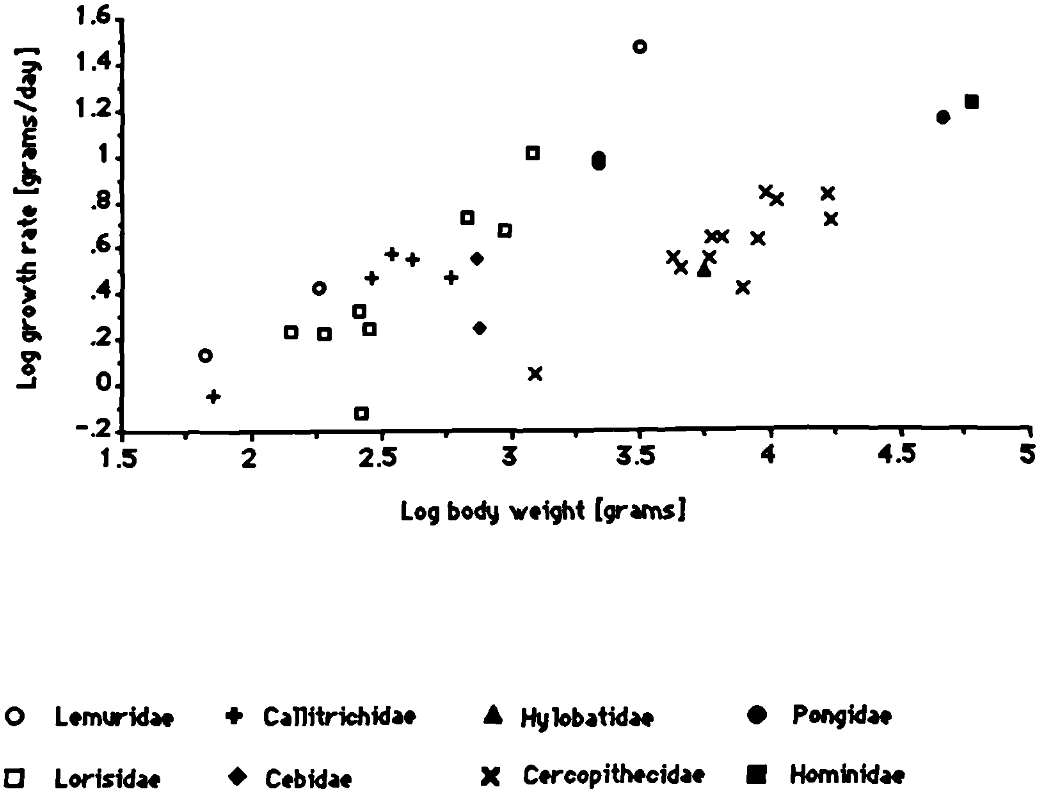


Table 6.3

Major axis statistics for $\log_{10}$ individual postnatal growth rate versus $\log_{10}$ body weight

a) Mother-reared infants only

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	35	0.80	0.42	-0.86	0.31	0.54
	genera	24	0.83	0.45	-0.94	0.32	0.60
	subfamily	12	0.89	0.43	-0.82	0.28	0.59
Strepsirhines:	species	13	0.95	0.85	-1.83	0.68	1.05
	genera	9	0.94	0.87	-1.87	0.62	1.19
	subfamily	4	0.99	0.79	-1.67	0.79	0.79
Haplorhines:	species	22	0.90	0.43	-0.98	0.33	0.53
	genera	15	0.92	0.45	-1.04	0.34	0.58
	subfamily	8	0.93	0.42	-0.87	0.26	0.60

b) Hand-reared and mother-reared infants

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	59	0.82	0.40	-0.83	0.33	0.48
	genera	36	0.81	0.40	-0.80	0.31	0.51
	subfamily	17	0.86	0.40	-0.75	0.26	0.51
Strepsirhines:	species	16	0.95	0.81	-1.71	0.66	0.98
	genera	10	0.77	0.95	-2.00	0.44	1.96
	subfamily	4	0.99	0.84	-1.77	0.84	0.84
Haplorhines:	species	43	0.90	0.44	-1.05	0.38	0.51
	genera	26	0.93	0.45	-1.03	0.38	0.56
	subfamily	13	0.87	0.40	-0.77	0.26	0.55

Table 6.4

Major axis statistics for $\log_{10}$ litter postnatal growth rate versus *$\log_{10}$ body weight,*

a) Mother-reared infants only

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	35	0.67	0.33	-0.49	0.21	0.47
	genera	24	0.72	0.38	-0.63	0.22	0.55
	subfamily	12	0.80	0.35	-0.49	0.25	1.18
Strepsirhines:	species	13	0.90	0.84	-1.68	0.59	1.16
	genera	9	0.86	0.91	-1.89	0.51	1.57
	subfamily	4	0.95	0.75	-1.38	0.25	1.18
Haplorhines:	species	22	0.78	0.31	-0.52	0.20	0.44
	genera	15	0.83	0.35	-0.62	0.22	0.49
	subfamily	8	0.90	0.34	-0.62	0.19	0.55

b) Hand-reared and mother-reared infants

Sample	Taxonomic level	N	r	Slope	Intercept	Slope 95% C.L.'s	
All species:	species	59	0.72	0.32	-0.52	0.24	0.41
	genera	36	0.72	0.33	-0.50	0.22	0.45
	subfamily	17	0.82	0.33	-0.50	0.21	0.47
Strepsirhines:	species	16	0.90	0.81	-1.60	0.60	1.06
	genera	10	0.73	0.96	-1.92	0.39	2.28
	subfamily	4	0.93	0.61	-1.05	0.61	0.61
Haplorhines:	species	43	0.79	0.33	-0.62	0.25	0.42
	genera	26	0.88	0.37	-0.71	0.29	0.46
	subfamily	13	0.86	0.36	-0.62	0.22	0.51

growth had been completed until the time when 30 to 50 per cent of adult body weight had been reached." The regression analyses of his data showed that postnatal growth rate was strongly linked to both body size and taxonomy of the animal. When considering the elevation of the best-fit lines [i.e. the "grades" of organization], the results showed that homoiotherms show a relatively higher growth rate than do poikilotherms. In the former group atricial birds grow relatively faster than do precocial birds and mammals. Precocial birds and mammals grow at about the same rate, when the influence of body size is accounted for, but the marsupials and the haplorhine primates tend to be significantly slower growing than are other mammals of the same adult size.

Despite these differences in grade, Case found that the slopes of most best-fit lines were approximately equal. Taking the classes of fish, reptiles, eutherian mammals and marsupial mammals separately, Case obtained regression lines with slopes of between 0.61 and 0.82. Looking at smaller taxonomic groups [orders and sub-orders] of mammals, the slope values are mostly within this range. The notable exception is that obtained for all primates, where the slope is only 0.37 [Sciuromorphs are the only other exception of single order outside of this range, with a slope value of 0.87]. Although the slope for the strepsirhines alone was 0.62, that found for the haplorhines was only 0.35. Hence, Case found that the haplorhine primates differed from other mammals in their scaling of of postnatal growth rate to adult body weight. This difference was not only a grade difference, indicating that haplorhines have a very low postnatal growth rate for their size, but also a difference in the slope of the line, i.e. an different allometric exponent. In contrast, the strepsirhine species have postnatal growth rates that have a similar relationship to body weight to those found for other mammals.

In order to directly compare the results of this study with those of Case, regression statistics were calculated for the scaling of growth rate to adult body weight. As might be expected from the high correlation found between the two parameters, the results of the regression analyses are very similar to those of the major axis analyses given in tables 6.3 and 6.4. The results of the regression analyses are basically in agreement with those found by Case. The regression best-fit slope for haplorhines in this study is 0.39 [95% confidence limits are 0.28-0.50, i.e. they include Case's value of 0.35], and 0.81 for strepsirhines alone [95% confidence limits are 0.63-0.98, i.e. they just exclude Case's value of 0.62]. It therefore appears, from this study and that of Case, that there is a fundamental difference in the relationship between postnatal growth rate and body weight in the haplorhine primates, as compared to other mammal groups. However, this interpretation was questioned by Kirkwood [1985].

The unusually low slope value found for the haplorhine primates is explained by Kirkwood [1985] as being caused by the "grade confusion" of taxa that should be considered separately. Taking information on 33 primate species, he considers the growth rates of individual young when they are 20% grown and concludes that strepsirhines, New World monkeys, Old World monkeys and apes [excluding humans] should be looked at as separate groups. This division is supported by the general appearance of the plot of log growth rate against log body weight and by the fact that the correlation coefficients are higher for the smaller groups than that found when all primates are treated together. When the subsets of the data are treated separately, the slopes of the regression lines all include 0.75 within their 95% confidence limits. Kirkwood therefore concludes that ".... growth rate is found ... to be largely a function of body size and taxonomic position ...." [*ibid*p.134].

The data from the present study also show clear, and quite striking, grade distinctions when either individual or litter postnatal growth rates are plotted against body weight in a log-log plot [figure 6.3]. The strepsirhine and New World monkeys have infants that grow relatively faster than do those of the Old World monkeys and apes. It might be predicted that species producing multiple litters would have a higher reproductive effort than species producing only a single young per litter. As taxonomic groups that include species that give birth to more than one offspring [i.e. strepsirhines and New World monkeys] have higher relative postnatal litter growth rates than do groups producing only one infant per litter [i.e. Old World haplorhines], it was thought that this might be due to the larger litter size of the former. However, it was found that these groups also have higher relative postnatal individual growth rates, indicating that this difference is *not* only due to their larger litters. Table 6.5 shows the major axis statistics for the separate groups of primates.

As noted by Kirkwood [1985], the correlation coefficients of the smaller taxonomic groupings are higher than are those for all primates together or for the haplorhines alone. However, in contrast to the work by Kirkwood [1985], the differences of scaling between strepsirhines and New World monkeys and between Old World monkeys and apes are not apparent from the present study, either from an inspection of the plots by eye or when using the ANOVA test described in Chapter 2. The analysis of variance was carried out several sets of residuals, calculated using data from individual species. One set of residuals was taken from a line of fixed average slope, with the mean value being calculated from the slopes of the groups being tested. The results were then checked by carrying out an analysis of variance on the residuals taken from the overall best-fit line for the group concerned and from a fixed slope of 0.75. For example, when testing for differences between strepsirhine and New World monkeys for total litter weight the residuals were calculated three times: 1) from a slope of 0.68, [derived from the mean values of the slope for strepsirhines (0.84) and the New World monkeys (0.52)]; 2) from the overall best-fit line [slope, 0.80] and 3) from a slope of 0.75. A similar set of analyses were carried out using the relative growth rates of individual young. In all cases the results were qualitatively the same, with the same groups being significantly different and the same groups being statistically indistinguisable.

Table 6.5

Major axis statistics for $\log_{10}$ litter postnatal growth rate versus $\log_{10}$ body weight for different taxonomic groupings of primates [mother-reared data only]

Group	N	r	Slope	Intercept	95% confidence limits of slope	
All species	35	0.67	0.33	-0.49	0.21	0.47
Strepsirhines	13	0.90	0.84	-1.68	0.59	1.16
Haplorhines	22	0.78	0.31	-0.52	0.20	0.44
New World monkeys	7	0.68	0.52	-0.94	0.01	1.60
Old World monkeys	12	0.87	0.69	-2.04	0.44	1.00
Apes and humans	3	0.99	0.70	-2.14	0.70	0.70
Strepsirhines & N.W.monkeys	20	0.86	0.80	-1.61	0.59	1.07
Old World monkeys and apes	14	0.92	0.68	-2.03	0.52	0.88
O.W. monkeys, apes & humans	15	0.94	0.68	-2.00	0.54	0.83

Table 6.6

Results of an analysis of variance on postnatal growth rate residuals [1]

Groups tested	Results of Anova
1. Strepsirhines *vs.* New World monkeys	no significant difference [$p > 0.05$]
2. Strepsirhines* *vs.* Old World monkeys	significant difference [$p < 0.01$]
3. Strepsirhines* *vs.* apes[2]	significant difference [$p < 0.01$]
4. New World monkeys* *vs.* Old World monkeys	significant difference [$p < 0.01$]
5. New World monkeys* *vs.* apes[2]	significant difference [$p < 0.01$]
6. Old World monkeys *vs.* apes[2]	no significant difference [$p > 0.05$]
7. Strepsirhines and New World monkeys* *vs.* Old World Monkeys and apes[2]	significant difference [$p < 0.01$]
8. Apes vs. humans	no significant difference [$p > 0.05$]

1. see text for details. 2. Apes were taken as including the lesser and greater apes.

Table 6.6 shows that there is no difference between the residuals for strepsirhines and New World monkeys and no significant difference between the residuals of Old World monkeys and apes [this is also true when apes and *Homo sapiens* are included in a single group and compared with Old World monkeys]. This indicates that the data are most usefully divided into two groups, with strepsirhines and New World monkeys in the first group and Old World monkeys, apes and humans in the second. This is a different result from that found by Kirkwood [1985], who considered that strepsirhines, New World monkeys, Old World monkeys, apes and humans should be treated as five separate groups.

It was considered that the differences between the results of this study and those of Kirkwood [1985] might be explained by the methodologies used in the two studies. There are two main differences between this study and that of Kirkwood. Firstly, this study tests for the difference between residuals by an analysis of variance. Secondly, Kirkwood treated the growth rates of males and females of the same species as separate data points and also treated two subspecies of gorilla separately. However, using Kirkwood's data, all five groups that he identified were found to be significantly different from one another, whether residuals were taken from the best-fit line, a line of fixed average slope or a line with fixed slope of 0.75. This was found when the data were used in the same form as in Kirkwood's analysis or when they were averaged to give only one value per species. The methods of this study therefore support Kirkwood's conclusion that his data should be split into five groups.

The differences found between the data of this study and those of Kirkwood [1985] must therefore be explained by several differences in the data sets used. Kirkwood's study contained only four strepsirhine species and, coincidentally, three of these those shown, in this study, to have the highest relative growth rates of any primate [*Microcebus murinus, Cheirogaleus medius* and *Varecia variegatus*]. When more strepsirhine species are included in the data set [there are 13 in this study] it can be seen that several of them have growth rates that are about the same as New World monkeys of the same adult size [figure 6.3]. A further difference is that the New World species for which mother-reared data are available are nearly all marmosets and tamarins. However, Kirkwood's study contained data for a several hand-reared cebid monkeys. Although this study suggest that marmosets and tamarins have a litter growth rate that is comparable to those of strepsirhine species, there is evidence that at least some cebid species have a lower relative growth rate [see below]. The inclusion of a larger proportion of cebid species might therefore increase the difference between the strepsirhines and New World monkeys in Kirkwood's study.

The second difference found between this study and that of Kirkwood [1985] is that Kirkwood considered that apes and humans should be treated separately from Old World monkeys. An analysis of variance on his data indicates that the residuals are not significantly different if taken from the best-fit line, but are significantly different if taken from a line of fixed slope of

0.75 or from a line with mean slope of 0.76 [p>0.05]. When the data from this study are examined it is found that both ape species [the lar gibbon and the chimpanzee] and humans have low relative growth rates when compared to other Old World haplorhines. A further indication that apes and humans should be treated separately comes from the fact that the correlation coefficients are higher when the groups are treated separately. However, several of the Old World monkeys [in particular the pig-tailed macaque and the savannah baboon] also have low relative growth rates and the results of the analysis of variance indicate that there is no significant difference between the relative growth rates of the mother-reared apes and Old World monkeys. A similar test that included hand-reared species also found no significant differences between the two groups. The reason for humans having a relative growth rate comparable to the apes in this study, but not in Kirkwood's, is that the growth rate for apes and humans was taken only for the first year in this study but was taken over longer period by Kirkwood [ranging from about two years in female orangutans to about six years in boys]. It is considered that the growth rate in the first year of life is the best estimate of parental investment for apes and humans, as after this age feeding on solids begins to take up an increasing proportion of the diet. The lack of significant differences in relative growth rates of apes and humans during this period is taken as sufficient evidence for treating the species together.

It appears from these results that the differences between the results of this study and those of Kirkwood [1985] are largely a result of differences in the data being used rather than in different statistical methods. It seems clear that, in this study, New World monkeys should not be separated from strepsirhines [though see below], but there is some doubt as to whether Old World monkeys and apes should be treated as separate groups. Although the results of this study do suggest that the growth rates of apes may scale differently than do those of Old World monkeys, these results are not significant and it was decided to treat the all Old World haplorhines [including humans] as one group. This approach had the advantage of not isolating the apes and humans into a separate group which would contain only three species and hence be difficult to analyse.

It should be noted here that the majority of observations that were made on mother-reared infants were also supported by the data on hand-reared infants. However, one important difference in the results that should be noted in the larger data set, is that several of the hand-reared New World monkeys did not have high relative litter growth rates. The hand-reared New World infants included several genera that were not represented in the smaller data set, including spider monkeys [*Ateles* species], capuchin monkeys [*Cebus albifrons*], a howler monkey [*Alouatta seniculus*], and a saki [*Pithecia monachus*]. Of these species, the spider and howler monkeys had litter growth rates that were comparable with those of Old World monkeys of a similar size, whereas the capuchin monkeys and the saki had relative litter growth rates that fell between those of strepsirhines and Old World monkeys. These results suggest that the New World species may not all have high relative litter growth rates. As the majority of these data are from animals that were hand-reared because of sickness or rejection by the mother, it is difficult to determine whether these lower growth rates result from problems of hand rearing. However, the results from the capuchin monkeys are based on a large sample of laboratory reared animals and their relative growth rates are similar to those found for mother-reared squirrel monkeys. It is therefore predicted that further study may well reveal further grades of organization within the New World species, with the marmosets and tamarins being shown to have higher relative growth rates than the cebids.

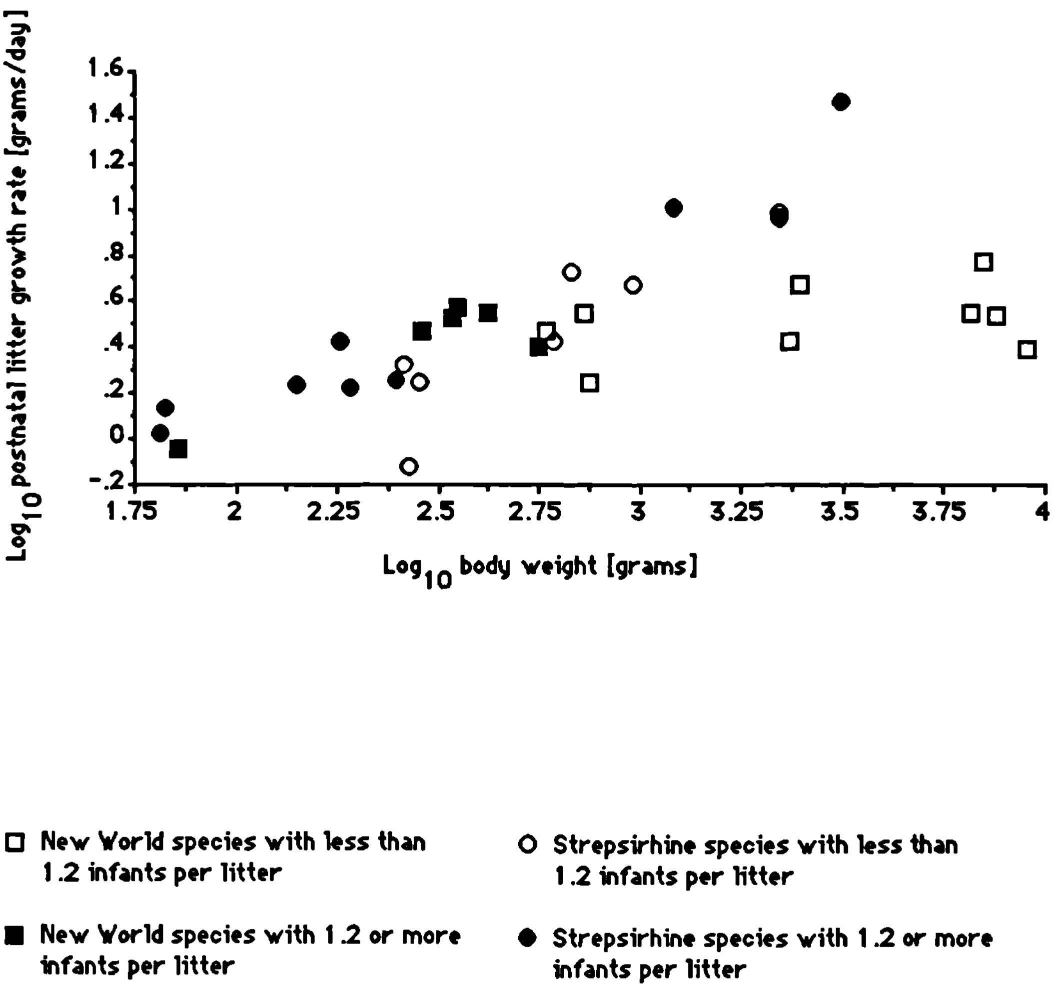
It was considered that the possible difference between relative litter growth rates of marmosets and tamarins and those of cebids could be due to litter size. The cebids usually produce only one offspring per litter, as compared to the usual production of twins by marmosets and tamarins. It was also noted that Geoldi's monkey [a species more closely related to marmosets and tamarins than to other New World monkeys (Dutrillaux *et al.*, 1988)] also had a lower relative postnatal litter growth rate than the marmosets and tamarins. Figure 6.4 shows the relationship between litter size and litter growth rate in the New World monkeys and the strepsirhine species. If one compares the residuals of species producing more than 1.2 offspring per litter with those producing 1.2 or less offspring per litter, the former are shown to have significantly higher relative litter growth rates. This result is significant whether or not hand-reared species are included and applies for strepsirhines and New World monkeys together or for the two groups separately [ANOVA, $p>0.01$ in all cases]. It therefore appears that the relatively high litter growth rates of marmoset and tamarin litters, as compared to other haplorhines, may be linked to their production of twins. Similarly, strepsirhines producing twins will be expected to have higher litter growth rates than species producing only one offspring at a time. This result is therefore similar to that found for foetal growth rates, where larger litters were also found to result in a higher parental investment per day.

It is also interesting to note that the only data for a tarsier species is from a hand-reared *Tarsius bancanus*, which has a litter growth rate that is comparable to, although very slightly below, those of strepsirhines and New World haplorhines of its size.

Whether the data from mother-reared species only, or for all possible species, are considered the major axis [MA] scaling statistics for litter postnatal growth rate are very similar. When the data are considered in the two groups discussed above [i.e. strepsirhines and New World species in one group and Old World haplorhines and humans in the second], the 95% confidence limits of the MA best-fit line include a slope of 0.75. This value is also included in the 95% confidence limits for the scaling of individual postnatal growth rate for the strepsirhine and New World group [the litter postnatal growth rate is identical to the individual postnatal growth rate for Old World haplorhines, as they have a litter size of one]. This study

Figure 6.4

Log_{10} postnatal litter growth rate versus log_{10} body weight for strepsirhine and New World primate species, showing litter size



therefore agrees with that of Kirkwood [1985] in concluding that a scaling exponent of 0.75 is possible for postnatal growth rate. This is discussed further at the end of this chapter.

Residual variation in growth rates

As has been noted above, a large percentage of variation in both prenatal and postnatal growth rates can be accounted for by body weight and taxonomy. In addition to this variation, there is also some residual variation that cannot be predicted from a knowledge of size and taxonomy, and this variation is therefore investigated here. Several factors have been predicted to be correlated with both prenatal and postnatal growth rates. These factors include other life-history variables, the degree of parental care, diet and environmental predictability. These parameters will therefore be discussed in turn.

The discussion of the relationship between relative litter growth rates and other parameters is based on partial correlation analyses and on analyses using residual values of growth rates. The residuals of prenatal growth rate were calculated from a line of fixed slope of 0.59, i.e. the mean slope value found when treating haplorhine and strepsirhine species separately. The results were checked using residuals taken from line of slope 0.75, i.e. the slope that would be predicted if prenatal growth rate scaled to the same exponent as metabolic rate. The results obtained calculating residuals from a slope of 0.75 were qualitatively the same as those found with a slope of 0.59 and are not reported here. The postnatal growth rate residuals were calculated from a fixed slope of 0.75. This is the average slope for the two grades of organization found and is also the slope that would be predicted if prenatal growth rate scaled to the same exponent as metabolic rate.

It should be noted that only variation in the relative values of litter growth rates are discussed here, as opposed to growth rates of individual young. The discussion is therefore about parental investment per litter rather than the parental investment in each individual young.

Basal metabolic rate and reproductive effort

As has been discussed in Chapter 5, the metabolic rate of an organism has been suggested to exert an influence on its rate of growth and development. Low relative metabolic rates have been suggested to be associated with low relative growth rates and high relative metabolic rates with high relative growth rates [McNab, 1980; Hennemann, 1984]. In Chapter 5 the relationship between r_{max} and basal metabolic rate [BMR] in primates was investigated and it was concluded that there was very little evidence to suggest that BMR in primates was correlated with r_{max}. However, the reason that r_{max} has been suggested to be linked to BMR is that BMR is though to influence developmental rates and this hypothesis has not been directly tested. For this reason, an investigation of the relationship between BMR and both prenatal and postnatal growth rates is carried out here.

As BMR and growth rates are both highly correlated with body weight, the correlations carried out here are all on residual values of all parameters. As in previous chapters, the BMR residuals are measured from a fixed slope of 0.75 and include only the data from the "good quality" data set [see Chapter 2]. The growth rate residuals are calculated as described above. The results of the correlations can be seen in tables 6.7 and 6.8, and the results are illustrated in figure 6.5.

The tables clearly show that there is no strong evidence for a correlation between relative basal metabolic rate and either prenatal litter growth rate or postnatal litter growth rate in primates. Significant correlations are found when the whole primate group is considered, both both of these correlations can be explained by the differences in relative growth rates and relative metabolic rates of the haplorhine and strepsirhine species. The combination of high relative BMRs and high relative prenatal growth rates in the haplorhines and low relative BMRs and low relative prenatal growth rates in the strepsirhines leads to a positive correlation between these two parameters. In contrast, haplorhines have high relative postnatal growth rates and strepsirhines have low relative postnatal growth rates, and this leads to a negative correlation between relative BMR and relative postnatal growth rate.

The correlation analyses were also carried out with species divided into groups according to the grade differences observed for prenatal growth rate [i.e. strepsirhines and haplorhines] and for postnatal growth rate [i.e. strepsirhines and New world monkeys and Old World haplorhines]. Within these groups there are no significant correlations found between relative BMR and relative postnatal growth rates. However, there is a significant positive correlation between the residual litter prenatal growth rate and residual BMR. For strepsirhines and New World species together, the correlation between residuals of litter prenatal growth rate and BMR is positive. For New World species alone there is no evidence at all of a positive correlation between these parameters, but for strepsirhines alone the positive correlation is only just insignificant. These results indicate that the links found between relative growth rates and relative BMR can be mostly explained by taxonomic differences between the strepsirhine and haplorhine species, and may not necessarily be indicative of a direct link between these parameters. However, there is some slight evidence of a positive correlation between relative BMR and relative prenatal litter growth rate in Strepsirhine species. The significance of these results is discussed in detail at the end of this chapter.

Table 6.7

Correlation statistics for prenatal growth rate residuals and basal metabolic rate residuals [1]

Species in group	N	r	Significance level
All primates	18	0.666	$p<0.010$
Strepsirhines and New World monkeys.	14	0.595	$p<0.050$
Old World monkeys, apes and humans.	4	-0.182	ns, $p>0.1$
Strepsirhines	10	0.550	$0.05<p<0.10$
Haplorhines	8	-0.436	ns, $p>0.1$

1) See text for method of calculating residuals; 2) ns= not significant

Table 6.8

Correlation statistics for postnatal growth rate residuals and basal metabolic rate residuals [1]

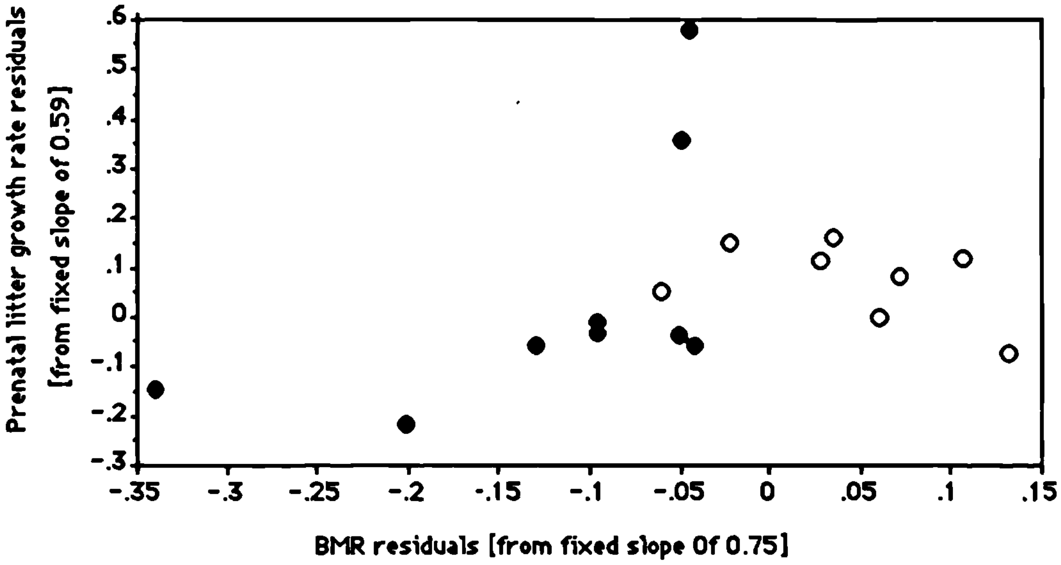
Species in group	N	r	Significance level
All primates	15	-0.529	0.050
Strepsirhines and New World monkeys.	11	-0.265	ns[2]
Old World monkeys, apes and humans.	4	-0.119	ns[2]
Strepsirhines	8	0.427	ns[2]
Haplorhines	7	-0.449	ns[2]

1) See text for method of calculating residuals; 2) ns= not significant $p>0.1$

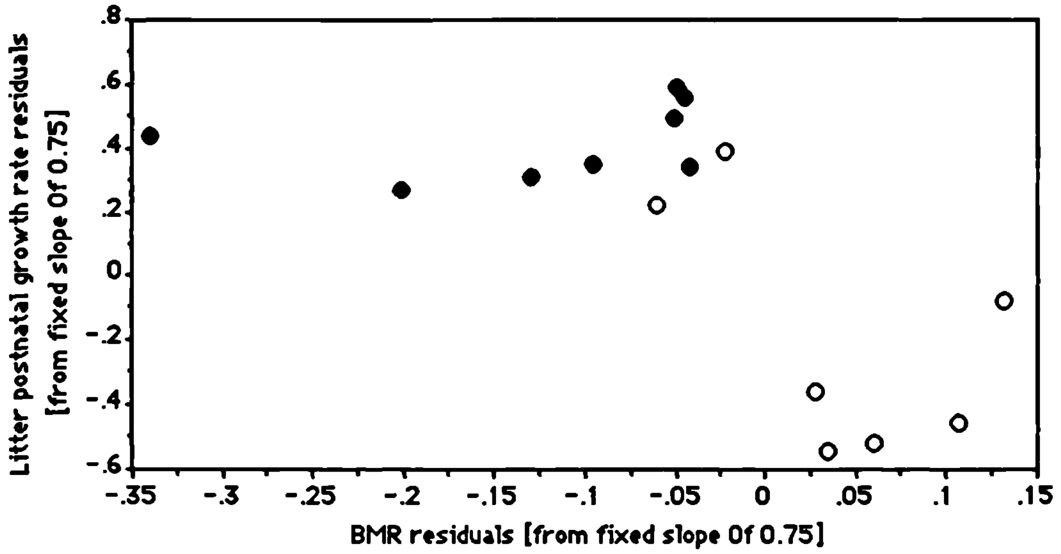
Figure 6.5

Growth rate residuals versus *basal metabolic rate residuals*

a) Litter foetal growth rate



b) Litter postnatal growth rate residuals



● **Strepsirhine species** ○ **Haplorhine species**

The relationship between relative prenatal litter growth rate and relative postnatal litter growth rate

It was felt that there were two possible ways in which relative prenatal litter growth rate and relative postnatal litter growth rate might be related. Firstly, species with a high relative prenatal growth rate might compensate for this high relative reproductive effort [RE] during gestation by having a low relative postnatal growth rate, and *vice versa*. If this were the case, the two parameters would be negatively correlated. Such a negative correlation would suggest that selection for a high relative RE during gestation would be balanced by a low relative RE during lactation. Hence, the overall relative RE might not be changed but simply redistributed between gestation and lactation by such selection.

Alternatively, species may be selected for a high reproductive effort in both gestation and after birth and the two parameters would therefore be expected to be positively correlated. The results of these analyses were therefore important in the interpretation of the selective factors influencing reproductive effort.

The correlation coefficients of relative prenatal growth rate and relative postnatal growth rate are shown in table 6.9.

Table 6.9

Correlation statistics for average prenatal litter growth rate residuals and average postnatal litter growth rate residuals[1]

Species in group	N	r	Significance level
All primates	33	-0.264	ns
Strepsirhines	13	0.836	0.001
Haplorhines	20	-0.173	ns
Strepsirhines & New World monkeys	19	0.552	0.020
Old World monkeys, apes & humans	14	-0.077	ns
New World monkeys	6	0.445	ns

(1) see text for method of calculating residuals

In the primates as a single group, we have already seen that a high relative prenatal growth rate is not always associated with a low relative postnatal growth rate and *vice versa*. Some primate species [e.g. marmosets and tamarins] have a high relative prenatal and postnatal growth rates, others have a low relative prenatal growth rate but a high relative postnatal growth rate [e.g. most strepsirhines], and others a high relative prenatal growth rate but a low relative postnatal growth rate [most Old World haplorhines]. As might be expected from this, there is no correlation between the two measures of relative growth rate when all primates are considered.

Consideration of taxonomic groups separately showed that, in the strepsirhine species, there is strong evidence that relative foetal growth rate is positively correlated with postnatal growth rate to weaning. However, no significant correlations were found for the haplorhine species. Figure 6.6 shows the relationship of the two sets of residuals for the strepsirhine group. It can be seen that there is a general trend of increasing relative postnatal growth rate with increasing relative prenatal growth rate for the whole group. This trend is also seen for three of the subfamilies for which data on both parameters are available [the bushbabies, the lorises and pottos and the lemurs], but the relative postnatal growth rate of the two Cheirogaleinae [*Microcebus murinus* and *Cheirogaleus medius*] are about the same despite *Cheirogaleus medius* having a higher relative prenatal growth rate.

It appears, then, that selection for a high relative prenatal growth rate and a high relative postnatal growth rate are combined in the strepsirhine species, but not in haplorhine species. This result is discussed in more detail below.

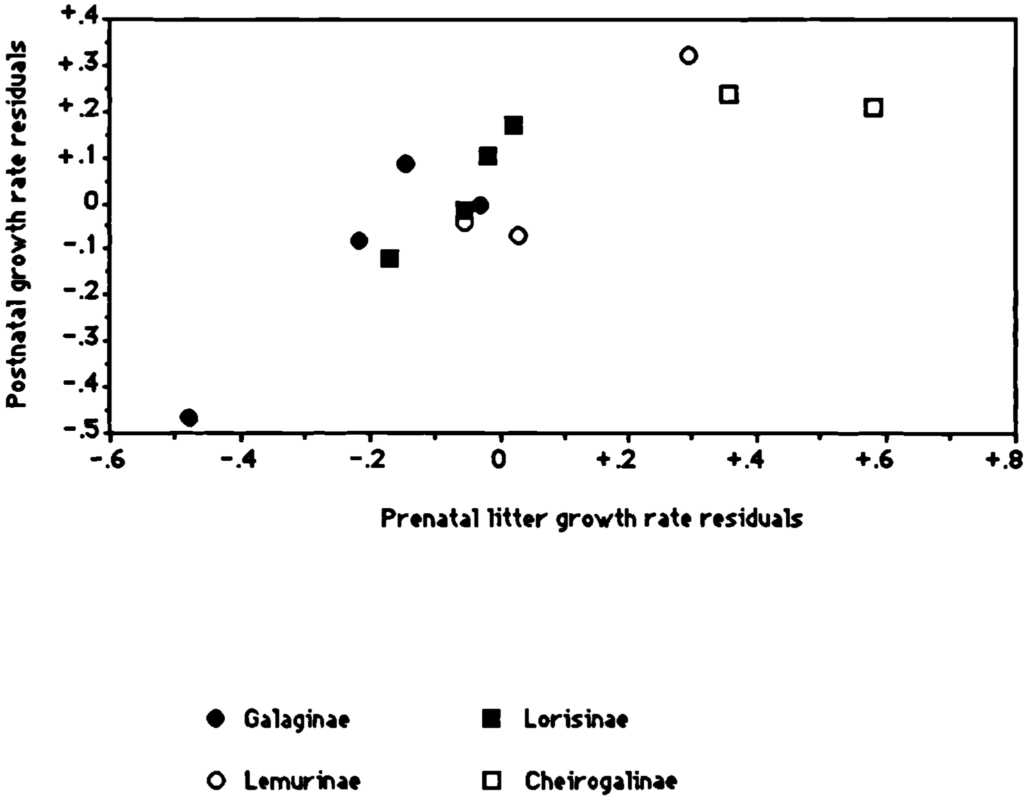
Relationships with other life-history parameters

Chapter 4 [table 4.2] summarized the partial correlations, after removing the effects of body weight, found between the life-history parameters discussed in this study. Several parameters were found to correlate with the growth rate measures, although some parameters that were predicted to be correlated with growth rate were not found to do so. However, the grade effects that are found when both prenatal and postnatal growth rates are analysed may be confusing the results of these partial correlations and it was felt that these results should be investigated more closely.

The relationships between the relative values of these life-history parameters were investigated both by the use of partial correlations and by the correlation of residuals taken from a line of fixed slope. Prenatal residuals were taken from a slope of 0.59, postnatal residuals from a slope of 0.75 [see above for derivation of these values]. Residuals of other parameters were taken from the major-axis slopes given in Chapter 4. The mean value of the strepsirhine and haplorhine slopes was used for parameters were a grade difference between the two suborders has been demonstrated. The results of the partial correlations and the correlation of residuals were qualitatively the same and only the latter results are reported here.

Figure 6.6

Postnatal litter growth rate residuals versus *prenatal litter growth rate residuals* [1] *for strepsirhine species*



[1] See text for method of calculating residuals

Correlations between relative prenatal litter growth rate and other life-history parameters

If one ignores the expected correlations with litter weight, neonatal weight and gestation length, there are very few correlations found between prenatal litter growth rate and other life-history parameters after body weight influences have been removed. The link between litter size and relative prenatal litter growth rate has already been mentioned, with larger litters being associated with higher relative prenatal litter growth rates. There is a significant correlation between relative age at first reproduction and relative litter foetal growth rate when all primates are considered [$r=0.33$, $N=54$, $p<0.02$]. However, this correlation is not found when strepsirhine and haplorhine species are considered separately [$p>0.10$ for both groups]. This suggests that the reason for this correlation are the grade differences found for strepsirhines and haplorhines for both foetal growth rate and age at first reproduction.

The only other correlations with relative foetal litter growth rate that are found to be significant are for strepsirhine species. There is a negative correlation with relative weaning age [$r=-0.54$, $N=15$, $p<0.05$] and a positive correlation with interbirth interval [$r=0.49$, $N=19$, $p<0.05$]. These correlations suggest that strepsirhine species with high foetal growth rates for their size will also have a relatively early age at weaning and relatively long interbirth intervals. The correlation with weaning age supports the earlier observation that there is a positive correlation between relative growth rates before and after birth in strepsirhine species. However, there is no correlation between relative prenatal growth rate and weight at weaning in strepsirhines. This suggests that although strepsirhine species that grow relatively rapidly during gestation also grow relatively fast during lactation, they do not continue this high postnatal growth for long enough reach an relatively large size. These species are therefore weaned earlier but at the same relative weight as species that grow relatively slowly.

Although a relatively high prenatal parental investment in strepsirhines is correlated with a relatively long interbirth interval, no significant correlation was found with relative birth rate or with relative r_{max}. This result suggests that the larger litter size of species with relatively fast growing litters compensates for their longer interbirth interval thus allowing them to have a "normal" birth rate.

Correlations between postnatal litter growth rate and other life-history parameters

There are several correlations between postnatal litter growth rate and other life-history parameters, after body size effects have been removed [see table 6.10]. These correlations suggest that primates with a relatively high postnatal litter growth rate also have a relatively large total litter weight at birth but a relatively small individual neonatal weight. This suggests that a high reproductive effort per day during lactation is preceded by a relatively high total investment in the total litter but a relatively low investment in individual young.

Table 6.10

Significant correlations between litter postnatal growth rate and other life-history parameters, after the removal of body weight effects, for all possible primate species

Parameter	N	r	significance level
Neonatal weight	34	-0.606	0.001
Litter weight	34	0.485	0.005
Age at first reproduction	32	-0.516	0.005
Birth rate	33	0.791	0.001
Weaning age	30	-0.549	0.002
r_{max}	32	0.828	0.001

The correlations for all primates further indicate that species with high relative postnatal litter growth rates also have relatively high rates of population increase [as measured by r_{max}]. The correlations indicate that this relatively high r_{max} is bought about by both a relatively high birth rate and a relatively early age at first reproduction. It can therefore be said that primates conform to the expected pattern of a relatively high r_{max} being linked to a relatively high reproductive effort, at least during lactation. These correlation with age at first reproduction would be predicted by the grade differences that are found between taxonomic groups rather than correlations within groups. The strepsirhine species have a relatively low age at first reproduction and a high relative postnatal litter growth rate, whereas the Old World haplorhine species have the opposite characteristics. Hence, when the species are split into two groups most of the correlations are lost, whether the sample is divided into haplorhines and strepsirhines or into strepsirhines with New World monkeys and Old World haplorhines.

The partial correlations of postnatal growth rate with birth rate and r_{max} are found in the haplorhine group. However, they are lost if the marmosets and tamarins [species with a high relative birth rate, high relative r_{max} and high relative postnatal growth rate] are removed. It seems, therefore, that the positive correlation between a relative postnatal reproductive effort and a relative rate of increase is found between large taxonomic groups groups but not within these groups. However, it should be noted that the cebid monkeys appear to have a high relative postnatal growth rate but a low relative r_{max}. Unfortunately, data on the growth rate of species in this group are limited, so it may be found that their growth rates are not generally as high as those found for the species in this study. As noted above some data on hand-reared species suggest that this is the case.

Two other correlations that are found when the smaller taxonomic groups are examined, are negative correlations with relative gestation length [$r=-0.566$, $N=20$, $p<0.02$] and relative weaning age in strepsirhines [$r=-0.592$, $N=18$, $p<0.01$]. These results support those found previously, which suggest that a relatively high prenatal growth rate will be linked to a relatively high postnatal growth rate, the latter resulting in a relatively early weaning age but not a relatively heavier weaning weight. In contrast, the correlation between relative weaning age and relative postnatal growth rate in the haplorhines is insignificant, suggesting that a relatively high growth rate during lactation does not lead to a reduction in the age at weaning in these species. Some evidence that relative postnatal growth rate in some haplorhines is correlated with relative weaning weight is found by the positive correlation between these parameters in the Old World haplorhines [$r=0.836$, $N=7$, $p<0.02$].

Summary of relationships between life-history variables

It appears that, once the influence of body size is accounted for, the growth rate patterns of primates fall into three main groups. Those that have a high prenatal growth rate and a low postnatal growth rate [the Old World haplorhines], those that have a low prenatal growth rate and a high postnatal growth rate [most strepsirhines] and those that have a high prenatal growth rate and a high postnatal growth rate [some New World monkeys and strepsirhines].

The differences in relative foetal growth rates found between the strepsirhines [with relatively low foetal growth rates] and the haplorhines [with relatively high foetal growth rates] cannot be explained by differences in either litter size or gestation length [see above and Chapter 4]. Instead, these two groups differ in the relative size of the individual and total neonatal weight, with the strepsirhines' neonatal weight being smaller than that of the haplorhines'. It can therefore be said that the typical haplorhine species will have a higher parental investment per day and in total during the gestation period. [Although some strepsirhine species do invest in high growth rates during gestation (i.e. the mouse lemur, the dwarf and the ruffed lemur), their gestation lengths are short and the total litter weight is no larger than for other strepsirhines.]

During the lactation period, the typical strepsirhine has a higher parental investment, per day in its young than does the typical haplorhine of the same size, as evidenced by growth rate. This high investment leads to most strepsirhines weaning their young at an earlier age than most haplorhines of the same size; but the offspring of both groups are about the same size at weaning, relative to the adult. As the strepsirhine litters are relatively lighter at birth than are haplorhine litters, one can infer that the total investment in the litter during lactation is also greater for the strepsirhine parents. It therefore appears that most strepsirhine species will have a higher parental investment per day and in total during the lactation period than will most haplorhine species. However, at least some New World haplorhine species [in particular marmosets and tamarins] are found to have a relative postnatal growth rate as high as that of strepsirhines, and these species tend to wean their young at the same age as other haplorhines. They will therefore have a higher prenatal growth rate than will most strepsirhine species and a higher postnatal growth rate than most haplorhine species. As neither gestation length nor time from birth to weaning are particularly short, this probably gives these New World species a relatively higher total parental investment than any other primate species, a feature that will be returned to later in this chapter.

Within these different groups, other correlations between life-history variables can be found. In the strepsirhines it appears that the relative reproductive effort during lactation and gestation are positively correlated. Strepsirhine species range from those with a relatively high growth rate during both lactation and gestation [e.g. the dwarf lemur and the ruffed lemur] to those with a relatively low growth rate during both lactation and gestation [e.g the slender loris]. The correlation analyses suggest that species with a high growth rate have a relatively short period of parental care, having both short gestations and a relatively early age at weaning, whereas those with a low relative growth rate have relatively long gestations and a late age at weaning. The fact that neither relative litter weight at birth nor relative litter weight at weaning correlate with relative growth rate measures, suggests that the total parental investment in young is about the same for species with high and low growth rates.

In the haplorhine species the picture is less clear. There is no evidence to suggest that RE during gestation is correlated with RE during lactation in these species, after body size effects are removed. Prenatal relative growth rate in all haplorhines and in Old World haplorhines alone is correlated with relative litter weight but not with relative gestation length, suggesting that parental investment per day is positively correlated with total parental investment in these species.

Correlations found for all haplorhine species suggest that a high relative postnatal growth rate in these species is associated with a relatively high birth rate and r_{max}, but these correlations are lost when the marmosets and tamarins are removed from the data set. It is therefore considered that the correlations occur because marmosets and tamarins have high birth rates, high rates of increase and high postnatal growth rates for their size, and Old World haplorhines have the opposite features. Similarly, the correlations found with relative gestation length and relative litter weight are lost when the marmosets and tamarins are removed from the haplorhine group. The only correlation that is found to be significant for the haplorhine species, after the removal of the marmosets and tamarins, is between relative postnatal growth rate and weaning weight. This positive correlation suggests that these Old World haplorhine species combine a relatively high parental investment per day [as measured by growth rates] with a relatively high total parental investment [as measured by weight at weaning]. This pattern differs from that found in strepsirhines, where relatively high growth rates are associated with a relatively rapid developmental time, rather than a high weight at birth and/or weaning.

The correlation analyses of the New World monkeys [either all together or split into families or subfamilies] revealed no significant correlations between relative postnatal and prenatal growth rates, and no correlations between relative growth rates and other parameters. It is possible these negative results were a result of small sample sizes and that further information will reveal patterns of covariation.

Given these varying patterns of parental investment in primates, the question of their adaptive significance remains to be answered. In the next section correlations between the growth rates of species and their social structure, ecology and environment are investigated.

Social, environmental and ecological variables and their relationship with parental investment

Parental care

Quality of parental care is a life-history variable that is not easily quantifiable but that may be important in determining the amount of parental investment made in the young. As noted by Case [1978], the participation of two parents in the raising of young should permit an increase in the amount of resources invested in the offspring. Hence one might expect increased growth rates in such species. In primates, the male does not act as provisioner to the female during pregnancy and it is difficult to imagine that his presence could have very much effect on the growth of the foetus. [Although it could perhaps be argued that his helping to defend a territory could increase the food resources available to the female.] However, once the young are born males can become more directly involved in the care of the infants, by carrying and protecting them while they are still suckling, and by feeding them as they start to eat solid foods.

In many species of New World primates [some cebid species, Geoldi's monkey and all marmoset and tamarin species studied] the father plays an important role in the care of the offspring by carrying the young for a large proportion [up to about 95%] of the time [Goldizen, 1986; Robinson *et al.*, 1986]. In marmosets and tamarins, care may also be shared with other members of the group [Goldizen, 1986; Ferrari, 1988]. In Old World primates, the father's parental role is often less obvious, although he may care for the young by protecting them both from predators and from conspecifics. This latter role may be particularly important for preventing infanticide by other males, a phenomena that has been noted in several species [e.g. see Struhsaker and Leland (1986), for colobines]. The only Old World species where the father has been observed helping to carry infants on a regular basis [albeit some considerable time after birth] is the monogamous siamang [Chivers, 1974].

It was considered possible that the growth rates of infants, in particular their postnatal growth rates, might be related to the degree of paternal care given. However, species with paternal care were not found to have significantly higher rates of growth for their size, for either prenatal or postnatal measures of relative growth rate. Similarly, no correlates of relative growth rates and social system could be found.

The reason for the lack of correlation between relative growth rates and paternal care in primates could be that prenatal and postnatal growth rates were being considered separately. As has been noted, in several primate groups a relatively high prenatal growth rate is associated with a relatively low postnatal growth rate and *vice versa*. However, this study identified a small number of species that have high litter growth rates, for their size, during both gestation and lactation. These are the marmosets and tamarins [*Callithrix* and *Saguinus* species], Geoldi's monkey [*Callimico geoldi*], the owl monkey, the lesser mouse lemur [*Microcebus murinus*], the dwarf lemur [*Cheirogaleus medius*] and the ruffed lemur [*Varecia variegatus*]. The only other species that are found to have relatively high growth rates in both gestation and lactation are some of the cebid monkeys, but it is only the owl monkey that has been demonstrated to have particularly high relative postnatal growth rate. As already discussed, other cebids have relative postnatal growth rates that are between those of the relatively very fast growing strepsirhines, marmosets and tamarins and those of the relatively slow growing Old World species.

It is noteworthy that the marmosets, tamarins, Geoldi's monkey and the owl monkey are the only haplorhine species that consistently show a high relative prenatal and postnatal growth rate. Despite having high relative growth rates, Geoldi's monkey, and marmoset and tamarin species have relatively long gestation periods and hence produce relatively large young [not only in comparison to all primates, but also in comparison to other haplorhine species]. Their high relative postnatal litter growth rates are a result of combinations of slightly increased litter weights and slightly decreased weaning ages [varying from species to species]. It is probable that the reason that these species can sustain these high rates of parental investment over gestation and lactation is that the father [and in marmosets and tamarins, other adult animals in the group] are participating in the care of the young. The owl monkey has a somewhat short gestation for a primate its size, but its high rate of growth means that it produces a litter weight at birth that is about normal for a haplorhine of its size. At weaning, the owl monkey's litter weight is about the expected size for a primate of its weight but its relatively high postnatal growth rate means that it can wean its young relatively early. Like the marmosets and tamarins, the owl monkey exhibits a high degree of paternal care, with the father carrying the young for about 70-80% of the time in the first month of life [Robinson *et al*, 1986].

Other species that show relatively high growth rate through both gestation and lactation are strepsirhine species, the dwarf and mouse lemurs [*Cheirogaleus medius* and *Microcebus murinus*] and the ruffed lemur [*Varecia variegatus*]. The dwarf and mouse lemurs are both "solitary" species [i.e. the female lives separately from the male] and, as far as is known, neither the male nor other individuals help the mother to raise her young. The social system of the wild ruffed lemur is not well understood, but captive studies suggest that the male does not directly aid the female in caring for the young, though he does help in guarding the infant [Pereira *et al*, 1987]. It is perhaps not surprising that all these strepsirhine species manage to sustain their high rates of foetal and infant growth for relatively short periods of time. All three species have very short gestations [both absolutely and relatively] and the mouse lemur and ruffed lemur also wean their young at a relatively young age. No data are available on the weaning age of dwarf lemurs.

It therefore appears that paternal care may be important in allowing some species to have a relatively high rate of growth for a long period of time. Species in which infants are cared for by only one parent appear to be constrained to growing rapidly for a short period of time, either by growing rapidly during only one phase of growth or by decreasing both the gestation and lactation periods. High growth rates for a long period suggest a high degree of total parental investment, as well as high parental investment per day. The evidence of this study therefore suggests that paternal care allows an increase in the total parental investment in the young. It is predicted that growth studies on other species with a high degree of paternal care [e.g *Callicebus* species] will reveal a similar pattern of high relative growth rates through both gestation and lactation, but without a significant decrease in the overall period of care.

Diet

It was considered that the diet of a species might effect its growth rate, either *via* an effect on metabolic rate [see previous chapters] or because other ecological factors associated with diet

Figure 6.7

Log_{10} litter foetal growth rate versus log_{10} body weight, showing diet

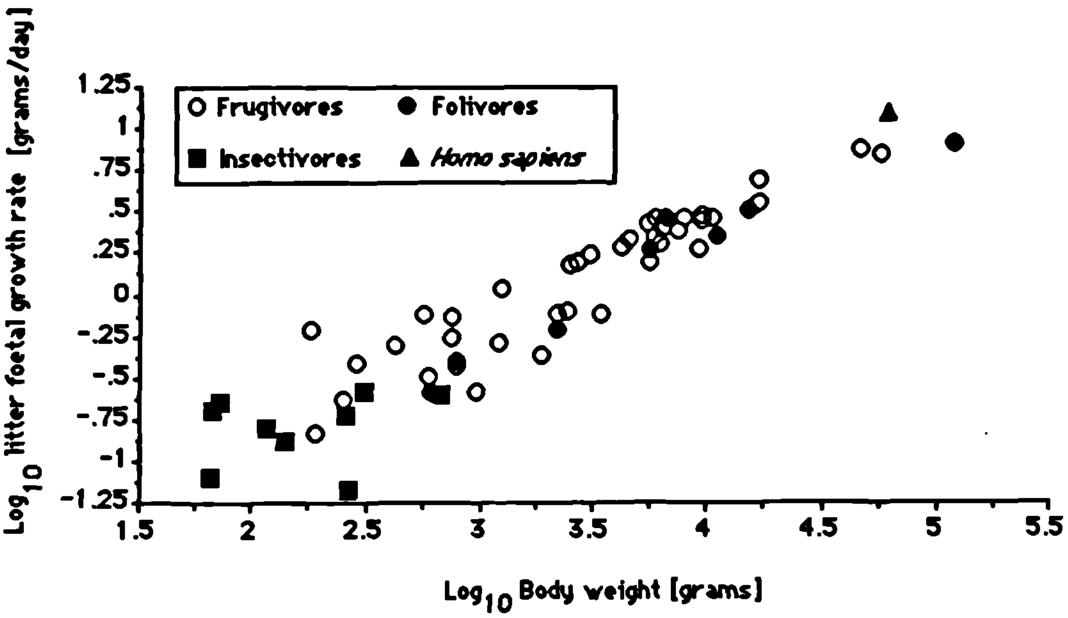
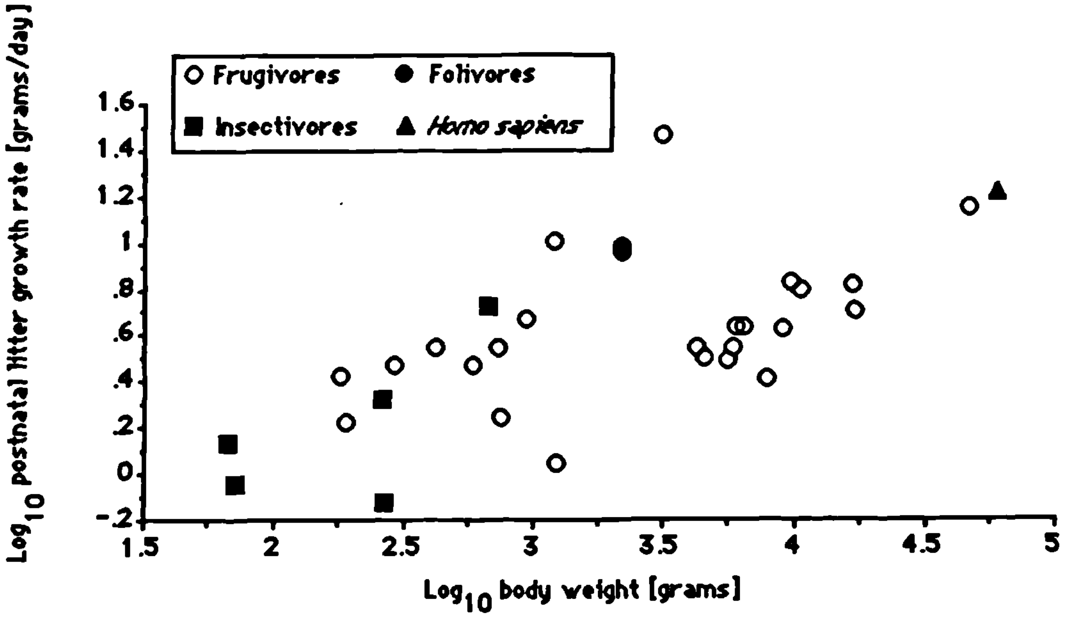


Figure 6.8

Log_{10} litter postnatal growth rate versus log_{10} body weight, showing diet



would select different growth rates. As both diet and growth rates are correlated with body weight, the relationships between diet and relative measures of litter growth rate were investigated. [See above for methods of calculating relative litter growth rates.] The procedure used for this investigation was identical to that used when investigating the relationship between r_{max} and diet, described in Chapter 5, and is not repeated here.

Figures 6.7 and 6.8 show the diets of species on plots of log growth rate *versus* log body weight. The link between taxonomy and diet is reflected in the insectivorous strepsirhine species having lower relative litter prenatal growth rates and higher relative litter postnatal growth rates than the frugivorous haplorhine species [this difference is significant, ANOVA $p<0.05$]. However, there is no obvious direct link between diet and the relative postnatal litter growth rate. Analyses of the relationships between percentages of food types in the diet and relative growth rates gave no significant correlations, [$p>0.05$]. Similarly, the results of analyses of variance showed no further significant differences between species with different diets [$p>0.05$]. These results were found for both prenatal and postnatal relative growth rates and for all taxonomic groupings [i.e. all primate species, species within suborders, species within families etc.]. Although it has been suggested that folivory might be linked to a low relative BMR in primates [see Chapter 3], there is no evidence that folivorous species have lower prenatal or postnatal growth rates than other primate species. For example, the folivorous lemur *Lemur fulvus* has a similar rate of postnatal growth to the similarly-sized, frugivorous *Lemur catta*. In conclusion, it can be stated that there is no evidence to indicate that diet is correlated either with relative prenatal growth or with relative postnatal postnatal growth in primates.

Arboreality

It was considered that the degree of arboreality might be linked to an animal's growth rate. Arboreal species could be more restricted in their movements when pregnant or when carrying young, and this could select for a higher rate of growth in such species. Using the previously discussed divisions of arboreal species, semi-terrestrial species and terrestrial species [see Chapter 2], analyses of variance were carried out to test for the hypothesis that arboreal species would have higher relative growth rates than other species. The tests were carried out on all species and on the smaller groups that have been previously used. When testing for differences in relative postnatal litter growth rate the analyses were repeated twice, firstly with all species and secondly excluding nesting species. This was done because it was considered that only species that carried their young would be selected to have high postnatal growth rates.

No links between arboreality and relative growth rates could be found in any group of primates. It is therefore concluded that arboreal species are not selected to have higher, or lower, relative growth rates than are terrestrial species. It may be that selection for increased growth rates in arboreal species is matched by higher predation rates in more terrestrial species also selecting for high growth rates in these species. Alternatively, the costs of carrying infants may not be appreciably higher for arboreal species.

Environmental predictability

There are several measures of environmental predictability used in this chapter, these being the same as those used in Chapter 5, i.e. habitat type, latitude and climate. The predictions of r- and K-selection theory and bet-hedging theory have already been discussed at some length in previous chapters and will not be repeated in detail here. Briefly, it can be said that r- and K-selection theory will predict that unpredictable environments lead to selection for rapid breeding and a high reproductive effort. Bet-hedging theory predicts that, where increased unpredictability is associated with increased adult mortality, the reproductive effort [RE] will increase with increasing environmental unpredictability. Hence, both r/K theory and, in some cases, bet-hedging theory predict that RE and therefore growth rates will increase with increasing environmental unpredictability. However, if increased unpredictability is associated with increased juvenile mortality, bet-hedging theory predicts that the reproductive effort, and hence the growth rate, will decrease with increasing environmental unpredictability.

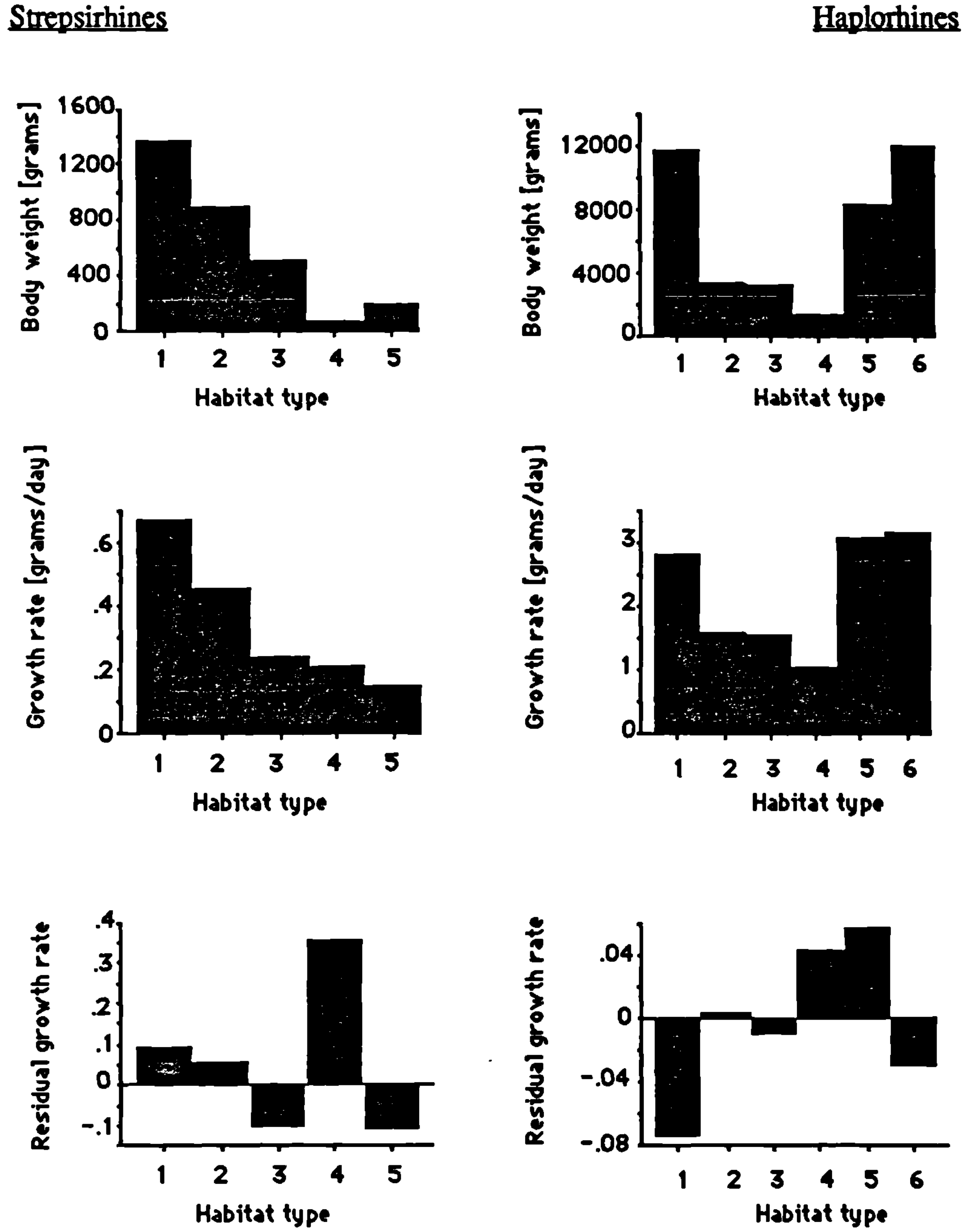
Habitat

Figures 6.9 and 6.10 show the relationship of foetal litter growth rate and postnatal growth rate to habitat type. As can be seen from these figures, body weight in this sample follows a similar pattern to that found for the larger sample of primates, with species in forest and in open country environments tending to be larger than species in edge habitats, [discussed in Chapter 3]. As one would expect from the high positive correlations that are found between growth rates and body weight, the habitats that are associated with high body weights are also associated with high prenatal and postnatal growth rates. The growth rates that are found before body weight effects are removed therefore support neither of the discussed theories of life-history evolution, as the most predictable and least predictable habitats are associated with high growth rates. However, as these patterns of variation in growth rate can be largely explained by variation in body weight the variation in the residuals is perhaps of more interest.

Although there is variation in the mean residual values from one habitat to another there is there is no clear pattern of variation of growth rates with habitat type. As might be expected from this, the analyses of variance of the residual values of both prenatal and postnatal litter growth rates revealed virtually no significant difference between species in different habitats. [The only significant difference that was found was for strepsirhines, where edge species were found to have a significantly lower relative foetal growth rate than edge and woodland species

Figure 6.9

Habitat type, mean body weight, mean prenatal litter growth rate, and mean residual prenatal litter growth rate [1]

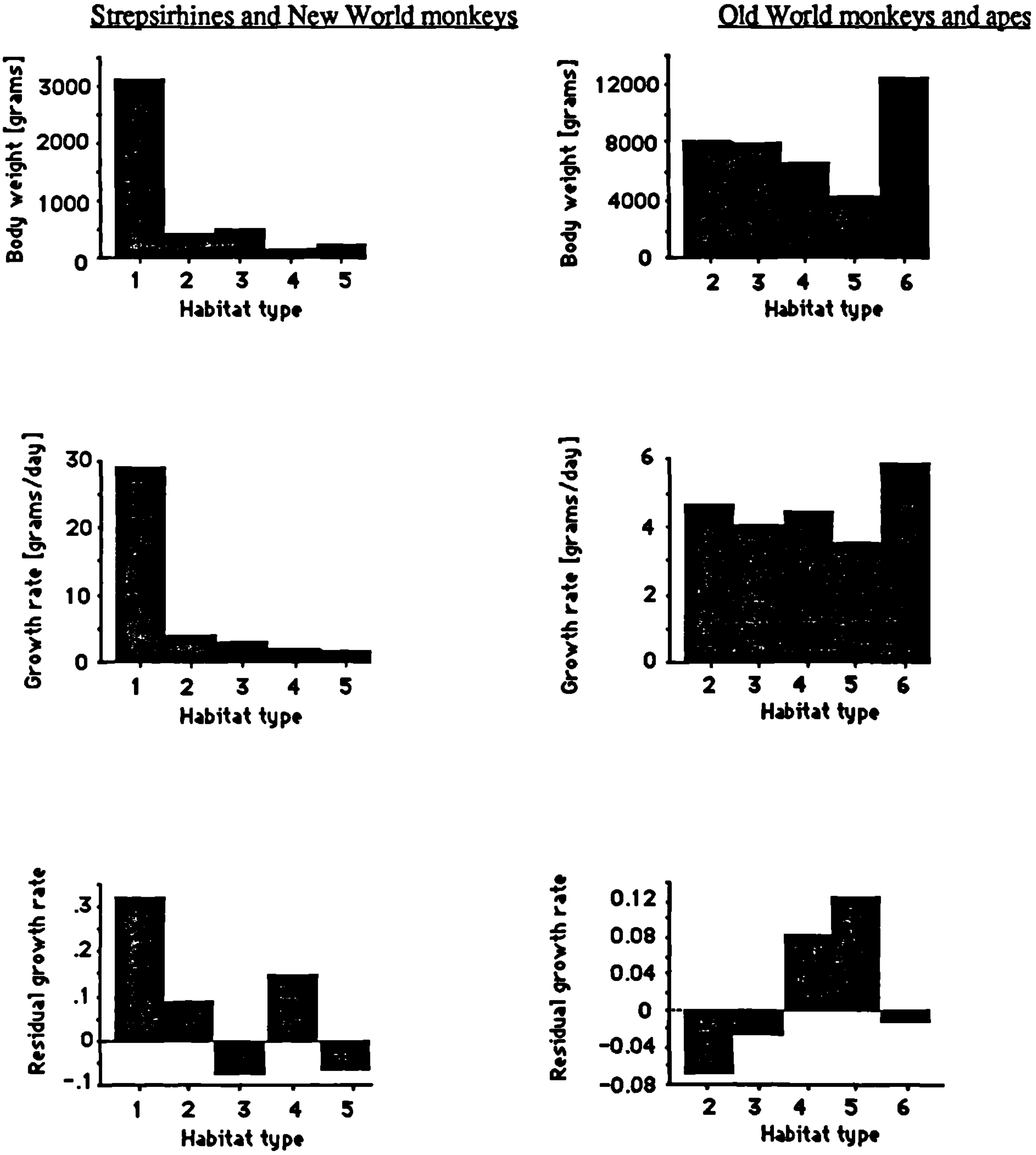


[1] Mean body weights and mean growth rates are calculated from the means of logarithmicvalues; residual means are logarithmic values.
Habitat codes: 1=primary forest; 2= general forest; 3= edge; 4= edge and woodland; 5= woodland and savannah; 6=savannah and open country.

Figure 6.10

Habitat type, mean body weight, mean postnatal litter growth rate, and m

residual postnatal litter growth rate [1]



[1] Mean body weights and mean growth rates are calculated from the means of logarithmic values; residual means are logarithmic values.

Habitat codes: 1=primary forest ; 2= general forest; 3= edge; 4= edge and woodland; 5= woodland and savannah; 6=savannah and open country.

[$p<0.05$]. However, as there is only one species in the edge and woodland species group [*Microcebus murinus*], it is not possible to draw any general conclusions from this result.

Latitude

It has been suggested [e.g. Case, 1978] that the latitude at which a species is found will influence its growth rate. As increased latitude is associated with increased seasonality, theories of life-history evolution that predict a correlation between environmental predictability and life-history will predict that latitude and growth rate will be linked [see above]. In addition to this, one might expect that species that live in seasonal environments will need to grow rapidly so that the young are large enough to survive the hardships of winter, drought or other seasonal setbacks [Case, 1978].

Case [1978] found very little evidence that postnatal growth rate was linked to latitude, although species living in very high latitudes did tend to have high relative postnatal growth rates. Case therefore concluded that it is only species whose breeding is "especially restricted by their short breeding season" that are selected to have high relative growth rates. He suggests that other species compensate for short breeding seasons by other behavioural or physiological adaptations.

To test for correlations between latitude and growth rate in primates, the relative values of prenatal and postnatal growth rates were correlated with both the species range limit and the species range centre [see Chapter 2 for an explanation of how latitude parameters were calculated]. This was done for the whole primate sample, the strepsirhines separately, the haplorhines separately, for New World species and strepsirhines together, for New World species, Old World haplorhines and for each family, subfamily and genus where there were more than three species. This procedure was then repeated for the residual values of both prenatal litter growth rate and postnatal litter growth rate.

Only two of these correlations were significant; the correlation between latitude limit and log prenatal litter growth rate for the macaques [$r=0.812$, $N=8$, $p<0.02$] and between latitude limit and residual prenatal litter growth rate in *Cercopithecus* species [$r=0.999$, $N=3$, $p<0.05$]. There are no significant correlations between latitude and log postnatal litter growth rate or residual postnatal litter growth rate.

The results of these analyses therefore show very little evidence for any link between growth rate and latitude in primates. Hence, this result offers no support for the prediction of either bet-hedging or r/K theory. As non-human primates are not found at extreme latitudes, this result supports Case's contention that it is only a very extreme shortening of the breeding season that is linked to an increase in relative, or actual, growth rate.

Climate

The analyses of climate and growth rates were carried out in the same way as were the analyses of r_{max} and climate. This was a further test of the links between environment and growth rates. Correlation coefficients were determined for the actual [logarithmic] values and for the residual values of the prenatal and postnatal litter growth rate. Those correlations that were found to be significant are shown in table 6.11.

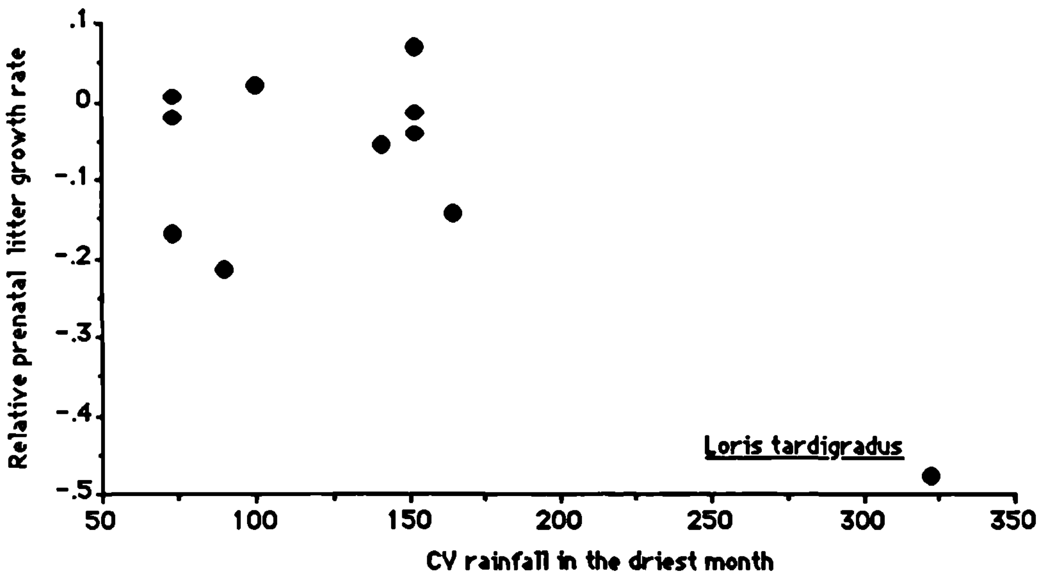
The few significant correlations that are found between climatic parameters and growth rates suggest that increasing climatic variability is associated with decreasing growth rates. Several of these correlations are found only before the effects of body weight are removed and are lost when the residual growth rates are examined or partial correlations removing body weight effects are carried out. These correlations are therefore presumed to occur because of the previously reported links between large body size and climatic variability in some groups [see Chapter 3]. There are, however, some negative correlations between residual growth rates and climatic variability.

Most significant correlations were found to involve strepsirhines, particularly the bushbabies, lorises and pottos [the family Lorisidae]. There is some evidence that climatic variability, rainfall and temperature are negatively correlated with both prenatal and postnatal growth rate in these species, with significant correlations being found for both actual and residual growth rates. However, nearly all the significant correlations involving the Lorisidae [bushbabies, lorises and pottos] or the Lorisinae [lorises and pottos] are lost if the slender loris [*Loris tardigradus*] is removed from the data set. The reason for this is that the slender loris is extremely slow-growing, both prenatally and postnatally, and lives in a climate characterized by high and variable rainfall. This combination means that this species is an outlier for many of the plots of a climatic parameter against either growth rate or residual growth rate, and its extreme position has undue influence on the correlation coefficients that are determined. An example of this effect is illustrated for dry season rainfall variability in figure 6.11. The only correlation that remains when the slender loris is removed is between residual postnatal growth rate and monthly variation in rainfall in the Lorisinae [$r=-0.998$, $N=3$, $p<0.05$]. The other strepsirhine group showing correlations between growth rates and climate contains the lemurs [including *Lemur* species only]. There is some indication that lemurs in warmer areas will have a low relative prenatal growth rate There is also a negative correlation between seasonality of rainfall and relative postnatal growth rate in three lemur species [including two *Lemur* species and the ruffed lemur, *Varecia variegatus*], but this is mainly due to the extremely high relative postnatal growth rate of the ruffed lemur, which is found in an areas with a high rainfall through the year.

Further correlations found with the haplorhine species are listed in table 6.11. No clear

Figure 6.11

Illustration of the effect of slender loris, Loris tardigradus, *on the correlations between climate and relative postnatal growth rate*



	N	r	significance
Correlation coefficient including *L. tardigradus*	11	-0.61	0.05
Correlation coefficient excluding *L. tardigradus*	10	0.20	not significant

Table 6.11

Correlations of climate parameters[1] with measures of reproductive effort

a) Correlations with log prenatal litter growth rate

Climatic variables	Groups with significant correlations	N	r	Significance level
Precipitation variables				
$\text{HI.AV}_{\text{.ppt}}$	*Lemur* spp.	4	-0.998	0.010
$\text{LO.CV}_{\text{ppt}}$	Lorisinae	4	-0.951	0.050
$\text{AN.CV}_{\text{ppt}}$	*Macaca* spp.	8	-0.767	0.050
Temperature variables				
$\text{LO.CV}_{\text{.t}}$	Lorisinae	4	-0.995	0.010

b) Correlations with residual prenatal litter growth rate

Climatic variables	Groups with significant correlations	N	r	Significance level
Precipitation variables				
$\text{HI.AV}_{\text{.ppt}}$	Lorisidae	11	-0.788	0.010
$\text{LO.CV}_{\text{.ppt}}$	Lorisidae	11	-0.613	0.050
$\text{MN.AV}_{\text{.ppt}}$	Lorisidae	11	-0.668	0.050
Temperature variables				
$\text{HI.AV}_{\text{.t}}$	Haplorhines	36	0.372	0.050
	Lemur species	4	-0.994	0.020
$\text{HI.CV}_{\text{.t}}$	*Macaca* species	8	-0.708	0.050
$\text{LO.AV}_{\text{.t}}$	Strepsirhines	22	-0.525	0.020
	Lorisidae	11	-0.650	0.050
$\text{MN.AV}_{\text{.t}}$	Strepsirhines	22	-0.437	0.050
	Lorisidae	11	-0.608	0.050

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[1] Abbreviations for climate parameters are given in table 2.1

Table 6.11 [continued]

c) Correlations with log postnatal litter growth rate

Climatic variables[1]	Groups with significant correlations	N	r	Significance level
Precipitation variables				
MN.CV$_{.ppt}$	*Galago* species	6	-0.991	0.001
MNTH.CV$_{.ppt}$	*Lemur* species	3	-0.999	0.050
Temperature variables				
LO.CV$_{.t}$	Lorisinae	4	-0.999	0.001
MN.AV$_{.t}$	Strepsirhines	13	-0.581	0.050
	Galago species	6	-0.999	0.001

d) Correlations with residual postnatal litter growth rate

Climatic variables	Groups with significant correlations	N	r	Significance level
Precipitation variables				
HI.AV$_{.ppt}$	Lorisinae	4	-0.989	0.020
	Lorisidae	10	-0.828	0.010
MN.CV$_{.ppt}$	Cercopithecinae	12	-0.617	0.050
MNTH.CV$_{.ppt}$	Lorisinae	4	-0.999	0.001
	Lemur species	3	-0.999	0.050

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1) Abbreviations for climate parameters are given in table 2.1

conclusions can be drawn from these three significant correlations. However, those found with the macaques [between temperature variability in the hottest month and relative prenatal growth rate] and for the cercopithecines as a group [between temperature variability throughout the year and relative postnatal growth rate] support the findings from the strepsirhines that climatic variability is associated with slow growth rates.

In conclusion, one can say that links between reproductive effort and climate in primates are not clear. There is some evidence that variability in climate is associated with slow growth rates. Although this correlation is tenuous and is only found in some taxonomic groups, it does appear to suggest that variable climates might select for a relatively low parental investment per day during prenatal and/or postnatal investment in the young, in at least some groups of primates.

Discussion

This chapter can be dealt with in two main sections. The first looks at parental investment in primates and the way in which it varies with body weight, metabolic rate and life-history parameters. The second section looks at possible social and environmental correlates of these patterns, with a view towards identifying adaptive reasons for the variation found in the different primate species.

The findings of the scaling analyses of measures of growth rate to body weight had been partially anticipated by the scaling analyses of other parameters in Chapter 4. For example, the way in which the scaling exponent of foetal growth rate could be predicted has already been mentioned above. Similarly, the scaling of weaning age and weaning weight to body size had suggested that the strepsirhines and the marmosets and tamarins had relatively higher postnatal growth rates than other primate species. The biological significance of the different scaling exponents is not easy to interpret for two main reasons. Firstly, the 95% confidence limits are very wide in most cases and frequently include several values that might be biologically significant [e.g the values of 0.67, 0.75 and 1.00 are all included within the confidence limits for the scaling exponent of litter postnatal growth rate for strepsirhines]. Secondly, the problem of how many grades of organization to recognize has not been completely solved [see the earlier discussion on postnatal growth rate scaling]. For these reasons I have decided not to discuss this problem at length here, but will restrict the discussion to looking at the evidence for a link between metabolic rate and growth rates in primates. This is a possibility that has been suggested by several studies, on both prenatal growth rates and postnatal growth rates [Martin and MacLarnon, 1988; Kirkwood, 1985]. However, this is the first study that looks at growth rates during both gestation and lactation. The links between growth rates and metabolic rate have been investigated in two ways. Firstly, by looking at the scaling of growth rates to body weight, as compared to the scaling of metabolic rates to body weight, and secondly, by looking at the correlations of the residuals of growth rates and metabolic rates.

Looking at the primate group as a whole, there is some evidence that a relatively low basal metabolic rate [BMR] is linked to a relatively low prenatal growth rate. However, there is no evidence that a relatively low BMR is associated with a relatively low postnatal growth rate. When compared to haplorhines of the same size, strepsirhine species have a low BMR and a low prenatal growth rate, but a high postnatal growth rate. This indicates that the strepsirhines' relatively low BMR may restrict them to having a relatively low foetal growth rate, but that it has no limiting effect on their relative postnatal growth rate.

Despite this, the evidence for a link between metabolic rate and foetal growth rate is questionable. In strepsirhine species the scaling of BMR to adult body weight BMR has an allometric exponent of 0.59. Both this value and the "Kleiber value" of 0.75 can therefore be compared with the allometric exponent found when foetal growth rates are scaled to adult body weight. It is found that both 0.59 and 0.75 are within the 95% confidence limits of the allometric exponent for foetal growth rate [for both individual and litter foetal growth rates]. This indicates that foetal growth rate may be linked to BMR in strepsirhines. However when a similar test is carried out for haplorhine species the results do not agree with this conclusion. Neither 0.75 nor the "best-fit value" [0.76] are included in the 95% confidence limits of the allometric exponent found for foetal growth rate. This suggests that relative BMR may be used to predict relative foetal growth rate in the strepsirhines, but not in the haplorhines.

This view is supported by the correlations found between residual values of BMR and litter foetal growth rate. The correlation of residuals for prenatal growth rate with BMR was positive, and almost significant [$0.1>p>0.05$] for the strepsirhine species when all possible BMR data was included. Similarly, there was a significant correlation between residual values of prenatal growth rate and BMR for the strepsirhine and New World species combined. These correlations indicate that between 30% and 35% of the residual variation in BMR can be predicted by residual variation in prenatal litter growth rate and *vice versa*. However, correlations for the haplorhine species were insignificant, and if anything negative.

Links between postnatal growth rate and metabolic rate are also doubtful. The theory that postnatal growth rate of individual young scales to the 0.75 of adult body weight, and is therefore connected to metabolic rate [cf. Kirkwood, 1985] is not disproved by this study, but the evidence for the theory is not strong. When the data are considered as representing two grades of organisation, the value of 0.75 is within the 95% confidence limits of both the Strepsirhine and New World group and the Old World haplorhine group. Similarly, the postnatal growth rate of the litter also includes 0.75 in the 95% confidence limits of its scaling exponents for the two groups. This may be interpreted as evidence for a link between postnatal growth rate and metabolic rate. However, as noted in Chapter 3, many strepsirhine species have a relatively low basal metabolic rate [BMR] when compared to other primates. In addition, the scaling of BMR to body weight in the strepsirhines is not to the power of 0.75, but to a lower exponent. These two observations would suggest that strepsirhine species would be expected to have a relatively low postnatal growth rate, and that this parameter would scale to an exponent below 0.75. Neither of these predictions is fulfilled and, in fact, the opposite is observed in both cases [i.e. the strepsirhines have a relatively high postnatal growth rate, and it scales to an exponent above 0.75]. If the scaling of postnatal growth rate to [body weight]$^{0.75}$ is to be taken as evidence that postnatal growth rate is linked to metabolic rate, it must therefore be assumed that the metabolic rate of strepsirhine species during lactation is not directly proportional to basal metabolic rate, but that it scales to [body weight]$^{0.75}$. In addition, although there is a significant correlation between logarithmic values of BMR and litter postnatal growth rate [after body weight effects have been removed] for all primates, this is a negative correlation. For smaller taxonomic groupings of primates, the partial correlation between logarithmic values of BMR and litter postnatal growth rate is not significant.

It therefore appears that the relatively low BMR of the strepsirhines may restrict them to having a relatively low prenatal litter growth rate. This effect is also apparent within the group, with strepsirhines with a particularly low relative prenatal litter growth rate also having a particularly low relative BMR. However, the strepsirhines do not appear to be restricted by their low basal metabolic rates during postnatal growth. These links between metabolic rate and growth rates in the strepsirhines can be accounted for by their ecology. It seems probable that low metabolic rates are selected as an energy saving strategy, which implies that these species are limited by their resources [see Chapter 3]. These same limiting factors could also impose restrictions on the growth rates of infants during times of food shortage.

Most strepsirhine species are pregnant during the period of annual food shortage, i.e. the dry/cold season, and give birth at about the time of increasing food abundance, i.e. the warm/wet season, [Bearder, 1986; Richard, 1986] This means that these species are pregnant during the most stressful period of the year and it is probable that resources are limiting at this time. However, after birth the increasing food abundance will allow the animals to invest more resources in their young. The relatively high postnatal growth rates of the strepsirhine young during lactation, suggests that lactation will require a rapid turnover of resources by the mother. This indicates that strepsirhine mothers might need to elevate their metabolic rate during lactation, thus allowing a higher rate of chemical synthesis. Some evidence that such a elevated metabolic rate occurred in a pregnant sifaka [has been put forward by Richard and Nicoll [1987], and has been discussed in Chapter 3. It has also been suggested that the high energy requirements of the lactating strepsirhine mother might account for the unusual phenomenon of female dominance that is found in several Malagasy primates [Richard, 1986;

Richard and Nicoll, 1987]. As the mothers need to eat a very large amount of food they will have a lot to gain by being able to displace males from good sources. In contrast, the males have little to loose by allowing the female access to food and may be helping their own offspring.

Alternatively, a raised BMR may not be needed to support the high rates of postnatal growth found in strepsirhines. If milk production were not limited by BMR, it might be expected that the relatively low BMRs found in strepsirhines will continue throughout the lactation period. This might be the case if maximum milk production was limited by a factor other than BMR [e.g. intake of a trace element, size of mammary glands] or if metabolic rate could be periodically raised to increase milk output without raising BMR. Although the work on the sifaka suggests that a raised BMR is found during pregnancy, there is no evidence on the BMR of lactating strepsirhines. More work on these species is needed to test these alternatives.

If it is assumed that BMR does limit both prenatal and postnatal growth, the general pattern of low parental investment during gestation and high parental investment during lactation in the strepsirhines can be explained by their being adapted to seasonal breeding. This theory assumes that strepsirhine species grow as fast as is possible, given the constraints of their environment. Some support for this idea is found in the few correlations between climate variability and relative growth rates, which suggest that strepsirhine species with higher residual growth rate will be those living in areas with more predictable climates, i.e. species in areas of food abundance will grow rapidly. Other evidence can be found by looking at those strepsirhine species that do not fit the general pattern of a slow prenatal growth rate, followed by a high postnatal growth rate.

Malagasy species that are found to have very high prenatal growth rates [the ruffed lemur, *Varecia variegatus*, the dwarf lemur, *Cheirogaleus medius*, and the mouse lemurs *Microcebus murinus* and *M. coquereli*] are all thought to start breeding later in the year than other Malagasy strepsirhines [Richard, 1986]. This will mean that these species are more likely be pregnant during at least a part of the rainy season, i.e. during a period when food is comparatively abundant. In addition, the dwarf and mouse lemurs are known to build up considerable fat reserves [Martin, 1972]. Unlike the ruffed lemur, these smaller species are often pregnant for at least a part of the dry season and these reserves probably help them to support high prenatal growth rates during this time. All of these species develop very rapidly and therefore manage to wean their infants before the onset of winter, hence including the whole time from birth to weaning within the wet season. Another Malagasy species that is found to have a relatively high prenatal growth rate is the indri, *Indri indri*, which gives birth in May, i.e. at the end of the rainy season [Richard, 1986]. This species has a gestation length of just over five months and is therefore pregnant during much of the wet season. As the indri is found in rainforest it will be less likely to be subject to food shortages in the winter than will species in other areas. However, it might be predicted that an effect of lactating during the dry season might be that the indri has a lower relative growth rate than some other strepsirhines. Some indication that this does occur comes from the relatively late weaning age, of about a year, that is estimated for the indri [Pollock, pers. comm. to Rudder] but confirmation of a relatively slow postnatal growth rate must await further research.

The links between growth rate and seasonality of breeding may therefore explain the patterns of development seen in the strepsirhines. However other groups of primates have very different growth rate patterns. All primate species have prenatal growth rates that are relatively low as compared to other mammals. The strepsirhine species are characterised by having particularly low prenatal growth rates for their size [Martin and MacLarnon, 1988; this study], and by having postnatal growth rates that are about the expected for mammals of their size [Case, 1978; this study]. In contrast, haplorhine species have relative prenatal growth rates that are higher than those of the strepsirhines. One group, [marmosets and tamarins and some cebid monkeys] also have relatively high rates of growth during lactation, whereas another, [Old World haplorhines and some cebids] have relatively low postnatal growth rates.

It therefore appears that the haplorhine species do not have as strong a constraint on prenatal growth as do most strepsirhines. It has been suggested [Leutenegger, 1973] that the higher prenatal growth rates of haplorhines are due to their different placentation. However, as discussed in Chapter 4, this theory does not appear to be supported by evidence from other orders of mammals [Martin and MacLarnon, 1988].

The relative basal metabolic rate of haplorhines is also typically higher than that found in the strepsirhine species. This, together with their high relative prenatal growth rate, may indicate that the haplorhines are be less restricted by resource limitations than are the strepsirhines. Although some haplorhines live in very seasonal climates those that are found in the most extreme habitats tend to be large in size [e.g. baboons, macaques and howler monkeys], with the small-bodied species, such as marmosets and tamarins, being largely tropical in their distribution. If one assumes that large animals are less subject to stress from harsh climates, it is therefore possible to explain the higher relative prenatal growth rate of haplorhines as being possible because, unlike strepsirhines, they are not severely limited by lack of resources.

The postnatal growth rates of marmosets and tamarins, and some of other New World monkeys, has already been discussed at some length above. To summarize the findings, it appears that the marmosets and tamarins, the owl monkey and possibly other cebid monkeys have a very high level of parental investment, as measured by growth rates, throughout gestation and lactation. It is suggested above that these species can support these high levels of investment because the father, and sometimes other group members, help the mother to raise the young. It is predicted from this finding that studies of mother-reared infants will find that New World species that exhibit paternal care will consistently show higher rates of postnatal growth than will species without paternal care. It is also worth noting that, in marmosets, the breeding female is dominant to males in the group and this dominance is expressed particularly during disputes over food when the female is pregnant and lactating [Ferrari, pers. comm.]. This can be compared to the system of female dominance that is found in some strepsirhine species, that may also be linked to relatively high infant growth rates.

It has already been noted in Chapter 5 that the marmosets and tamarins show relatively high r_{max} values and that the owl monkey has a high r_{max} for a cebid monkey [which generally have low r_{max} values]. The combination of a relatively high r_{max} with relatively high rates of paternal investment, suggests that these species can be seen as "r-selected", a view that is reinforced by their being found mainly in edge habitats. Whether this pattern might alternatively fit the bet-hedging model [where high variation in adult mortality selects for high breeding rates and high parental investment] is not clear, as no long term studies of mortality rates in wild populations of these species have been carried out.

The Old World [and possibly some New World] haplorhine species have relatively lower postnatal growth rates that strepsirhine species, but the relative weight of haplorhine and strepsirhine infants at weaning is the same. The relatively slow postnatal growth rates of these species therefore results in an increased period of parental care between birth and weaning. It was considered that this slow growth might be due to births occurring during the dry season, or the winter, and that the slower growth is imposed on the animals because of food shortage. However, a comparison of Old World haplorhine species that give birth at the start of the "bad" season, those that gave birth during the "good" season and those that produce infants at all times of the year showed no differences between their relative growth rates. For example, the patas monkey gives birth during the dry season but has faster-growing infants, for its size, than any other Old World haplorhine.

It seems from this that the Old World haplorhines are not constrained by their environment to have a low rate of parental investment during lactation. However, the variation of growth rates within the group gives very little indication of the type of environment that might select for a relatively low prenatal investment [either prenatally or postnatally]. Correlations between growth rates and environmental measures are practically non-existent for any grouping of primates, and the few that are found are all with climatic parameters. Within the haplorhine group there is only one such correlation with postnatal growth rate. This is negative correlation between the variation in mean annual temperature and relative litter postnatal growth rate in the Cercopithecinae [table 6.11], a correlation that throws very little light on the reasons for the slow growth rate of the Old World haplorhines.

As primitive mammals probably gave birth to large litters of small young, it would appear that the large neonatal size of haplorhines is probably a derived characteristic. Therefore, it seems probable that the high growth rate found during gestation in haplorhines is bought about by selection for a large, well-developed neonate. However, it is difficult to isolate any clear reason as to why larger infants should be adaptive in the haplorhines but not in the strepsirhines. For example, it could be argued that a large infant is more capable of clinging to its mother and can therefore be carried long distances. The large body size of most haplorhines, combined with their typically living in groups, means that they must have a large home range, a characteristic that would select for a mobile, well-developed infant. However, such an argument implies that the larger, group-living Malagasy primates should also have relatively large infants, whereas small nest-building tarsiers should have relatively small infants; neither of these predictions is true (see Chapter 4). Similar problems can be found with other possible explanations [e.g. see Harvey *et al.* [1986]. It is possible that the variation for such an adaptation may not be found in the strepsirhines.

If one assumes that the haplorhines are selected to produce large neonates, they will have made a very large investment in their young by the time it is born. It could be argued that the relatively slow postnatal growth rate of these species is therefore a necessary consequence of having a relatively high prenatal growth rate, i.e. that females are simply not capable of supporting a rapidly growing infant through gestation and lactation. However, it seems unlikely that the slow growth rate of the young after birth is simply due to female being incapable of continuing with this high level of investment. For, as already noted, species that give birth during a time of high food availability do not have high levels of postnatal growth, even though there is apparently no reason why the female's resources should be limited at this time. If a female patas monkey can give birth to a relatively large infant and then support a high infant growth rate during the dry season, another species giving birth in the rainy season could presumably support even higher relative growth rates.

It would therefore appear that the relatively slow growth rate and late weaning of the Old World haplorhines occurs as a result of selection for these characters, rather than as a consequence of selection for other characters [such as a relatively high prenatal growth rate]. Possible explanations for this character can be found in the theories of life-histories that have been previously discussed. The K-selection argument would suggest that there is a low rate of density-dependent mortality in the adult and the young of the Old World haplorhine populations. Therefore the females do not need to raise their young rapidly and risk their own lives by putting a large proportion of resources in to the young. Instead, they will be selected to produce "high quality" young that will be capable of competing with other members of the population. One way of doing this might be to take a long time to raise infants so as to spend more time teaching them about their environment. Alternatively, the bet-hedging argument would suggest that females are selected to invest only small amounts in their offspring because the infant mortality rate is high. In this situation the female that risks her own chances of breeding in the next season, runs the risk of loosing her entire investment if her infant is killed by an unpredictable change in the environment. Selection will therefore operate to reduce the levels of parental investment in these species. Whichever scenario is correct, it will be predicted that mortality rates in adult Old World haplorhines will be lower than those in adult strepsirhines and in adult marmosets and tamarins.

As already noted, there is little evidence to indicate which of these theories is closer to the truth, as the variation found between species does not seem to be related to patterns of environmental variability. The study of mortality rates and their correlates with growth rate patterns would help to answer this question, but at the time there are not enough data to do this. In particular, there are virtually no data available for strepsirhine and New World species. However, some data are available for Old World haplorhine species and these will be considered in Chapter 7.

Summary

Measures of prenatal and postnatal growth rates are used as measures of parental investment in this chapter. The allometry of growth rates in primates is discussed, and it is concluded that there are three main growth rate patterns that can be found in the primates. Most strepsirhine primates are characterized by a relatively slow prenatal growth rate, leading to a relatively low litter weight at birth, and a relatively high postnatal growth rate. This combination means that these species can be thought of as having a high postnatal parental investment and a low prenatal parental investment. It is suggested that these characteristics have evolved as a response to a seasonal environment where the animals are pregnant during times of food shortage and lactating during times of food abundance.

Old World haplorhine primates are characterized by a relatively high prenatal growth rate, leading to a relatively high litter weight at birth, and a relatively low postnatal growth rate. It is suggested that the high prenatal growth rate is has been selected to produce a large, well-developed neonate, although the reasons for this occurring in the haplorhines and not in the strepsirhines are not clear. The relatively slow postnatal growth rate can be considered to occur either because of selection for a long period of parental care or because of selection for a low parental investment. Among New World monkeys, marmosets, tamarins and the owl monkey have relatively high growth rates throughout both gestation and lactation, producing a litter of "normal" weight at weaning. It is thought that these species can support this high level of parental investment because both parents care for the young.

Chapter 7

Life-histories of the Cercopithecinae

In the previous chapters the variation of life-history parameters within the order Primates has been investigated and several conclusions have been reached regarding the correlations of these parameters with ecological variables. In some cases, it has been suggested that the correlations can be interpreted as being due to particular reproductive strategies that have evolved to deal with certain environmental conditions. However, if one is to interpret such correlations within the neo-Darwinian framework, it is not sufficient to compare only species groups that may be quite distantly related. If evolution has occurred by the gradual adaptation of species to their environment, the comparison of closely related species should yield results that are compatible with the evolutionary scenario suggested by the broader view. Analysis at a lower taxonomic level also allows a closer examination of the data being used. Such an analysis should therefore reveal more of the fine detail of relationships between reproductive strategies and the environment. It was therefore decided that a more detailed look at a closely related group was needed to elucidate the ways in which life-histories evolve.

The approach in the bulk of this work has been to compare genera and subfamilies rather than individual species. Although data for separate species have been used for most analyses the results have usually been discussed in general terms by comparing groups such as "the forest-dwelling strepsirhines" or "the semi-terrestrial colobines" rather than concentrating on the adaptations of any particular species. As discussed in Chapter 2 this approach does have advantages, in particular the reduction of the influence of variation in the data that is due to the "noise" introduced by experimental error [e.g. error resulting from sampling bias and inaccurate estimates of parameters]. The big disadvantage of such broad comparisons is that variations that are "real", and that may have important evolutionary implications, may be overlooked, or disregarded as being anomalous. Such oversights are particularly likely to occur when one is dealing with very large number of species as it is difficult for any one worker to have a detailed knowledge of the natural history of every species in a large data set. It is hoped that such problems can be overcome by focussing attention on a smaller number of species. For this reason this chapter is restricted to a discussion of one subfamily, the Cercopithecinae.

The cercopithecine monkeys [see below for a summary of the species included in this group] were chosen for this detailed examination for several reasons. The major reasons are that they constitute a large group and have been very well studied. These two factors allow comparisons to be made both between, and within, genera. In addition, they are found in a broad range of habitats and geographical locations, so that one can investigate the relationship of life-history parameters to the environment. A further interesting feature of the group is that several species are found in savannah environments and their adaptations to this environment may throw light on the evolution of early hominids. The "classical" view of human evolution is that many characteristics of modern humans evolved as adaptations to the savannah environment [see e.g. Leakey and Lewin, 1977]. However, recent studies have thrown doubt on this widely held belief, suggesting that the ancestors of humans could have been arboreal and hence living in forest [Stern and Sussman, 1983]. It was hoped that a comparison of closely related forest and savannah-living cercopithecines would help address this problem.

Evolution and ecology of the Cercopithecinae

The haplorhine subfamily Cercopithecinae contains more species than any other subfamily of primates, including about 50 species, which represent about 10 genera [the exact numbers are debatable as different authorities recognize slightly different taxonomic divisions]. The group is related to the second large group of Old World monkeys, the subfamily Colobinae, which is included with the Cercopithecinae in the family Cercopithecidae. This family is generally recognized to be derived from a single common ancestor, although the relationship of the group to the other extant group of Old World haplorhines, the apes and humans, [the hominoidea] is not clear [e.g. see Delson and Andrews, 1975].

The main ecological difference between the cercopithecine and colobine monkeys is that the former are primarily fruit-eating and omnivorous species, whereas the latter are mainly folivorous. These differences in diet are associated with differences in the dentition and digestive system between the two groups.

Most of the cercopithecine species can be described as frugivore/omnivores, with many eating a very wide range of food items. The most obvious exception to this is the gelada *Theropithecus gelada*, which feeds almost entirely on grasses, eating leaves, seeds and roots [Iwamoto and Dunbar, 1983]. The social structure of most cercopithecine species is either a multi-male/multi-female group [macaques, savannah baboons, mangabeys, vervet monkeys, talapoin monkeys] or a harem group where a single male has access to one or more females [most guenons, hamadryas baboons, geladas]. In both types of grouping, different species, and indeed different populations of the same species, may vary considerably in the precise form of social structure that exists. For example, there is evidence that in some multi-male groups the females mate promiscuously, whereas in others the dominant male(s) appear to have almost exclusive access to the female during ovulation [Andelman, 1987; Melnick and Pearl, 1986]. Similarly, harem groups may be very stable, with a single male siring all the young for several seasons or the group may have a succession of different males in a single season [Cords, 1986]. Another source of variation is found in the hamadryas baboon and the gelada [and probably in the drills and mandrills], where one -male units join together to form large feeding and sleeping groups [Dunbar, 1984; Stammbach, 1986]. Variation in social structure may have important evolutionary implications for life-history strategies, particularly in the area of parental investment. Although a detailed examination of this complex subject is beyond the scope of this work, it can be said that no clear links between social structure and any life-history parameter could be determined for the species examined in this study. For this reason, variation in social structure will not be considered further in this chapter.

The cercopithecine monkeys can be divided into two main groups or tribes; the Cercopithecini [genera; *Cercopithecus, Miopithecus, Allenopithecus* and *Erythrocebus*] and the Papionini, the baboons, macaques and mangabeys [genera; *Papio, Mandrillus, Theropithecus, Macaca, Cynopithecus,* and *Cercocebus*].

The Cercopithecini, or guenons [the term guenon will be used here to include all of the Cercopithecini, and not only the genus *Cercopithecus*], are generally small in size, with most being in the range of about 3-8kg. Exceptions are the very small talapoin monkey, which weighs about 1.25kg. and the patas monkey where the male can weigh over 12kg. Most of these species are adapted to an arboreal life and are found in secondary and primary forest. However, the vervet monkey is very terrestrial in comparison to other guenons and is found in woodland and savannah. The patas monkey is completely adapted to a terrestrial existence and is found on the savannah. Although most members of the guenon group are arboreal, it is thought that these arboreal species evolved from terrestrial ancestors, as did the rest of the Cercopithecidae family. Evidence for this idea is found in the proportions and anatomy of the limbs of this group [Aiello and Andrews, 1984].

It is generally considered that the genera *Cercopithecus, Allenopithecus* and *Miopithecus* are very closely related, and they are frequently considered as all being *Cercopithecus* species. The patas monkey has a number of unique characteristics [e.g. terrestriality] that seem to suggest that it diverged from the main guenon stock early in its evolution [Napier and Napier, 1985]. However, recent chromosomal and morphological evidence suggests that, despite their great difference in size, the patas monkey and talapoin monkey are perhaps more closely related than previously thought [Martin, pers. comm.]. As the precise evolutionary relationships between the members of the guenon group are not clear they will not be discussed further in this work.

Members of the tribe Papionini are generally more terrestrial than are the guenons and tend to be heavier and more robust. They range in size from the smaller species of macaque [about 5Kg] to the larger baboons and drills and mandrills [over 20 kg]. The macaques and mangabeys are smaller and more arboreal than are the almost completely terrestrial baboons, mandrill, drill and gelada. The mangabeys [*Cercocebus* species] are forest-living, but divide into two ecological groups. Members of the *C. torquatus* group [also containing *C. galeritus* and *C. atys*] are semi-terrestrial and often forage on the ground, whereas members of the *C. albigena* group [also containing *C. aterrimus*] are mainly arboreal and live in the canopy [Napier and Napier, 1985; Melnick and Pearl, 1986]. The macaques also vary in their degree of arboreality, with some species [e.g *M. silenus*] spending the majority of their time in the trees, but others [e.g. *M. fuscata*] being more terrestrial. Both the macaques and the baboons are found in a variety of habitats, including forest, edge habitats and woodland, and the baboons are also found in savannah. The drills and mandrills are mainly terrestrial, forest-living species. The gelada [*Theropithecus gelada*], is completely terrestrial and is found only in montane grassland in Ethiopia.

Within the Papionini, the baboons [*Papio* species], the gelada [*Theropithecus gelada*] and the macaques [*Macaca* species and *Cynopithecus nigra*] form three clear phylogenetic groups. Although the gelada is sometimes referred to as the gelada baboon, it is not a "true" baboon in the sense of being more closely related to the genera *Papio* than to any other genera. The relationships of the other genera in the Papionini to these groups is not agreed upon. The previously mentioned ecological distinction between the two mangabey groups may be associated with an evolutionary difference. Chromosomal evidence suggests that the two mangabey groups are distinct and hence they should probably be considered as separate genera [Cronon and Sarich, 1976]. However, as this problem is not resolved, this study follows most published work in placing all mangabeys in the same genus [*Cercocebus*]. Although the drills and mandrills [*Mandrillus* species] are often thought of as being closely related to "true" baboons, and are sometimes classified as *Papio* species [e.g Wolfheim, 1983], the chromosomal evidence suggests that they may be more closely related to the *C. torquatus* group of mangabeys [Martin. pers. comm.]. As the relationships of these genera to each other are not clear they will be dealt with as a single group.

Methods and data

The majority of the methods and data used in this chapter have been widely used in previous chapters and require no introduction here. As in the previous chapters the data used in this chapter come from a variety of sources. The problems of mixing data from wild and captive species have been discussed at length in Chapter 2, and it is particularly important to remember these problems when looking at a small group of closely related species. The variation that is due to data being collected under different conditions can be thought of as "noise" that obscures underlying evolutionary trends and patterns. When one is considering a large number of species from several taxa the range of variation that is due to differences in phylogeny and adaptation will be large, and the noise will be be responsible for only a relatively small part of the variation seen. However, closely related species are likely to resemble each other, and this means that the variation that is due to noise may account for a larger proportion of the total variation in parameters. For this reason particular care has been made in this chapter to identify possible influences of collecting conditions on the data type.

With one exception, all of the life-history and environmental parameters used in this chapter have been used and described previously and will not be discussed again here. The exception is that data on mortality patterns are included in this chapter. Although mortality patterns are a central parameter in theories of life-history evolution, they have not been discussed previously because data are available for only a very few species. This chapter includes data on age-specific mortality for several cercopithecine species.

As has been noted by Dunbar [1987], care should be taken when comparing mortality data from studies that have used different methods to estimate mortality rates. The literature on primates uses two basic methods to measure mortality and survival. The first method is carried out by following the lives of individual animals of known ages and recording the ages of death. By recording the fate of a single cohort [i.e. all animals born in the same year] from birth until the death of the last member of the cohort, a complete life table can be drawn up for a cohort. As primates are long-lived such data are available for very long-term studies only and several life-tables used here are taken from shorter studies where life-tables are only available for the first few years of a cohort's life. The second method of estimating age-specific mortality rates is to look at the demographic pattern of a population at a given time. The survival rate from year to year can then be inferred from the proportion of animals of different ages in the population.

Mortality data are taken from both types of estimate in this study and are used assuming that the data are comparable. It should be noted that the data from one study by Dittus [1975] on toque macaques, are considered to be "suspect" by Dunbar [1986]. This is because Dittus assumes that the population he is studying is demographically stationary in order to calculate his life-tables, and this assumption may not be correct. Other possible problems with the mortality data are discussed in the relevant part of this chapter.

Life-histories of cercopithecine monkeys, as compared to other haplorhine primates

When broad scaling analyses of life-history characters are carried out, the relative life-history parameters of the cercopithecine monkeys can be compared to those of other haplorhine primates. Such analyses have been discussed in previous chapters, where the life-histories of different primate taxa [including the cercopithecine monkeys] have been considered. The results are summarized in Table 7.1, the data for longevity being omitted as it was felt that variation in longevity is more likely to reflect the adaptability of the species towards captivity than any biologically relevant factor. Given the high degree of sexual dimorphism of many cercopithecine species, it is perhaps worth noting that all the results listed in this table are true whether one takes average adult body weight [i.e. male and female weights combined] or average female body weight as the measure of size.

One notable feature of the cercopithecines is that they tend to have relatively short gestation periods whilst retaining a "normal" relative neonatal weight, two characteristics that, combined, reflect a high foetal growth rate. The majority of the cercopithecine species for which gestation length data are available are those found in seasonal climates, and many of these species are pregnant during the season of limited resources, i.e. the dry season in tropical areas or the winter in temperate zones. These high foetal growth rates are therefore a little surprising, as one might expect that these species would have been selected to have a long gestation period and a low foetal growth rate, thus enabling them to produce a well-developed infant even when there is comparatively little food. Virtually all of the gestation period data used here are from captive animals and indicate that these species have retained at least the capacity for high foetal growth rates, though it is not known if this is always expressed in the wild.

As noted in Chapter 2, there is some evidence from Riopelle and Hale [1975] that gestation periods of rhesus monkeys may be slightly increased if nutrients are limiting. As species other than the rhesus monkey may lengthen their gestation periods in times of protein, or other nutrient, shortage it is possible that the gestation periods of wild animals will be longer than those used in this study. However, the same reasoning would suggest that the gestation periods of other wild haplorhines might be lower than the captive data used here. If this is the case, the cercopithecines could still be found to have relatively short gestation periods.

Cercopithecines also tend to breed at a younger age than do other haplorhines. Hence, this measure of developmental rate also indicates that the cercopithecines develop faster than do other haplorhines of the same size. Given this result, it perhaps surprising that the cercopithecines do not also have a high growth rate to weaning age. This implies that they achieve their early age at first reproduction either by breeding at a relatively lower weight than do other haplorhines or by growing faster to maturity after they are weaned. An analysis of the data shows that there is no evidence of female cercopithecines growing faster than other haplorhines to adult weight [this study]. By contrast, there is evidence that cercopithecines tend to breed before they reach their adult weight.

Figure 7.1 shows a plot of age at first reproduction against age at attainment of adult weight for female primates. The solid line represents the 1:1 ratio of these two measures, i.e. species that fall above the line breed before they have reached adult weight whereas those that fall below

Table 7.1

Characteristics of the Cercopithecinae as compared to other haplorhine species

1. *Neonatal weight:* In general, the Cercopithecinae have the neonatal weight that would be predicted for their body size. The baboons, macaques, guenons and mangabeys have birth weights that are either as would be predicted or that are slightly larger than would be predicted for their size. Although *Theropithecus gelada* is found to have rather small relative neonatal weight this is based on a small sample of only three neonates, one of which was considerably larger than the value used here.
2. *Gestation length:* Cercopithecinae have short gestation lengths for their body sizes. This is true for 24 of the 25 species for which gestation data are available, the exception being *Miopithecus talapoin* which has a gestation very slightly longer than one would predict from its size.
3. *Age at first reproduction:* Relative age at first reproduction in the Cercopithecinae is generally earlier than in other haplorhines, two very obvious exceptions being *Cercopithecus ascanius* and *C. mitis,* which start to breed at a relatively late age.
4. *Birth rate:* The majority of the group have higher birth rates than one would predict for a haplorhine of their body size. However there are some exceptions which are discussed below.
5. *Age at weaning:* The age at weaning of most cercopithecine species is about that that would be expected for species of their size, with the majority of variation being traceable to different definitions of when an animal is weaned.
6. *Foetal growth rate:* Most of the Cercopithecinae have relative foetal growth rates that are as would be expected for a haplorhine, although a few species do deviate from the expected rate, as discussed below.
7. *Postnatal growth rate:* In the majority of cases the relative postnatal growth rate of Cercopithecinae is below that that would be expected for a haplorhine. However it should be remembered that the Old World monkeys and apes generally have a relative postnatal growth rate that is below that of the New World monkeys. When compared only with other Old World haplorhines there is no difference observed in the growth rate to weaning.
8. r_{max}: Of the 25 cercopithecine species for which r_{max} can be calculated 14 have rates of increase above that that would be predicted for a haplorhine of their size, eight have approximately the expected r_{max} and three have a low relative r_{max}.

the line breed after they have reached adult weight. Most of the cercopithecine species can be seen to breed before they reach adult weight. The only cercopithecine species that appear to delay reproduction until some time after they have reached adult weight are three forest-living guenon species, *Miopithecus talapoin*, *Cercopithecus neglectus* and *Cercopithecus cephus* and a forest-living mangabey, *Cercocebus galeritus*.

Rudder [1979] suggests that it is only larger species that can breed before the attainment of adult weight. He argues that because the neonates of smaller species are proportionately larger, relative to adult size, the stresses of pregnancy and lactation are greater for small species, and therefore, females cannot cope with producing young before they reach adult size. The data used here also suggests that small species are unlikely to breed before the attainment of adult weight. Rudder suggests that the reason for small species not breeding earlier is because of the allometric scaling of neonatal weight. If this is the case, one might expect that this effect would operate uniformly with increasing body size. However, there is not a gradual increase in the time lag between first reproduction and attainment of adult weight as species get larger but instead there appears to be two groups of species, those where females weigh less than about 5.5kg and those above this weight, the former do not breed until they have reached adult weight whereas the latter can produce young before they are full sized [figures 7.1. & 7.2].

The reasons for this discontinuous distribution in the relative breeding weight are unclear. It is possible that the dichotomy may be one of taxonomy rather than size, as virtually all of the large-bodied species are cercopithecines and apes, whereas nearly all of the smaller species are strepsirhines and callitrichids. In the wild, female great apes do not breed until they have reached adult weight, although they may do in captivity. This suggests that these species have the capacity to breed before reaching adult weight, but that this capacity is not expressed in the wild, or at least not in the populations studied.

As might be expected from their generally short gestation periods, high birth rates and early age at first reproduction, the figures for r_{max} suggest that most cercopithecines have a greater rate of increase than do other haplorhines of the same size. The relatively high r_{max} is due to both an early age at first reproduction and a short interbirth interval compared to other haplorhines of the same body size [this being true for both wild and captive animals]. Exceptions to the general tendency to have a high relative r_{max} are three forest-living guenon species [*Cercopithecus ascanius, C. mitis* and *Miopithecus talapoin*] which are found to have a low r_{max} for their body size. These species are discussed below.

In conclusion, it can be said that, as a subfamily, the cercopithecine monkeys have a short gestation period, a high foetal growth rate, an early age at first reproduction and a high birth rate in relation to their size. These characteristics give rise to a relatively high r_{max} as

Figure 7.1

Age at attainment of adult weight versus *age at first reproduction for primates*

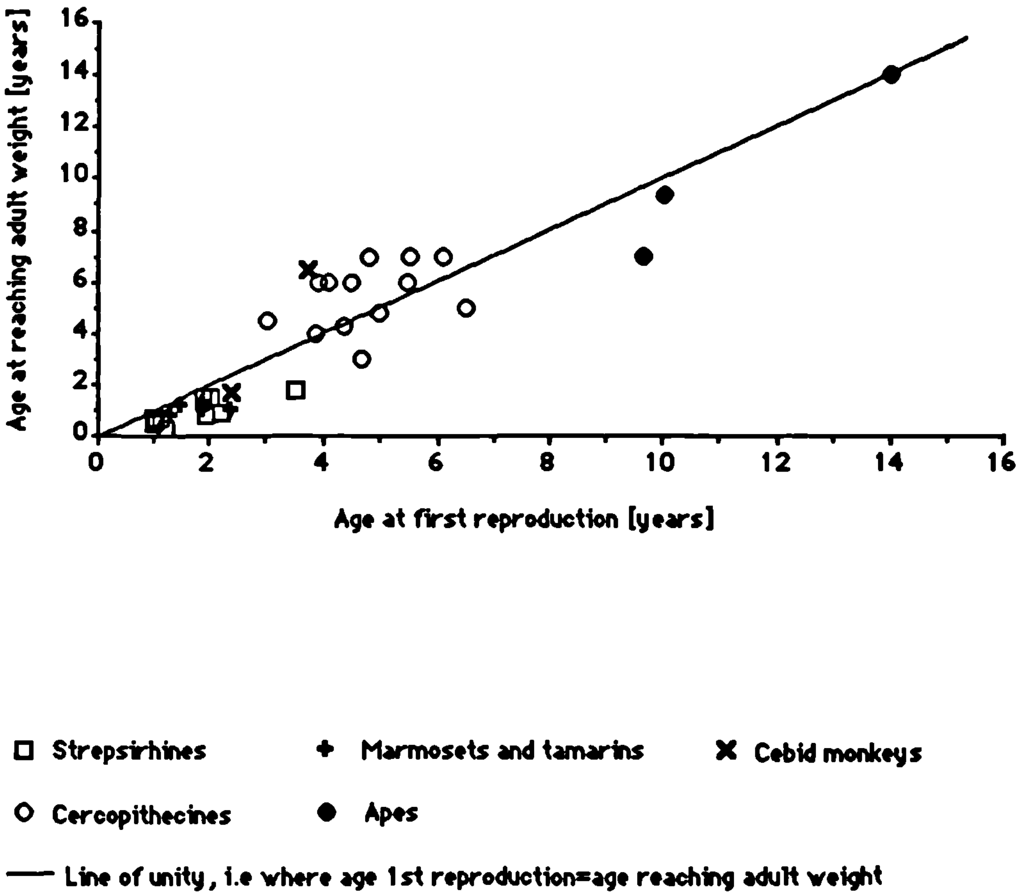
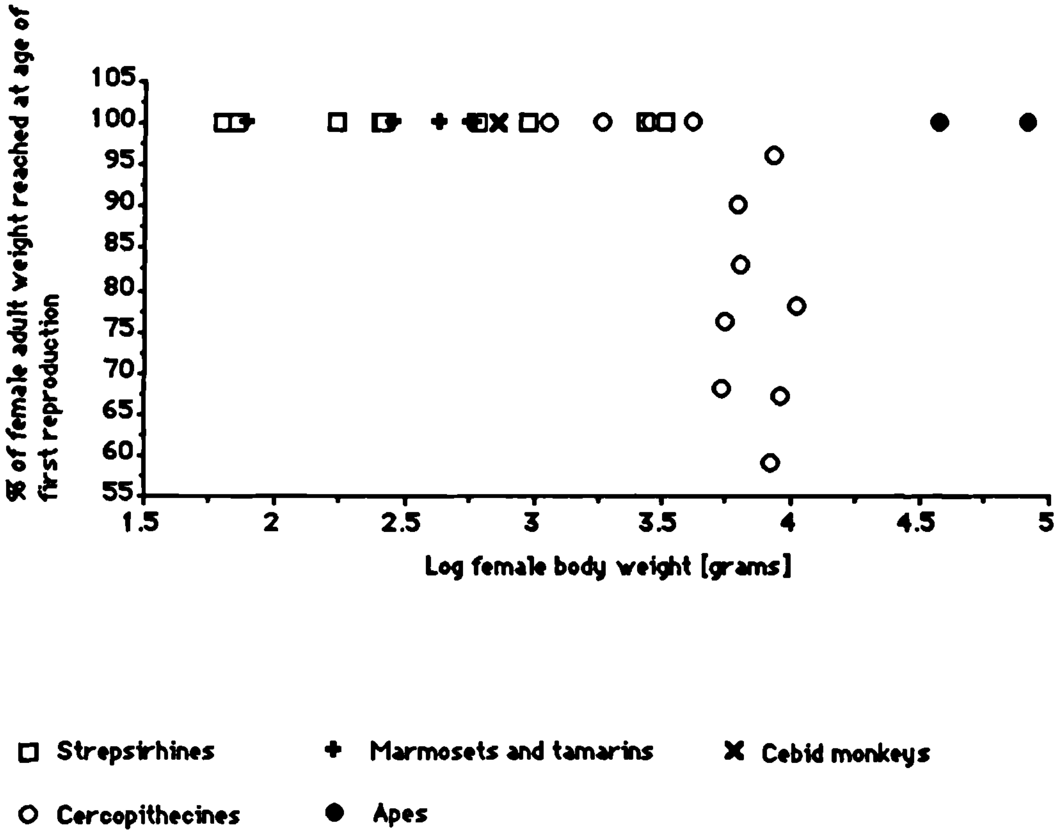


Figure 7.2

Percentage of adult weight reached at age of first reproduction versus *body weight for primates.*



compared to other haplorhine species. The relatively early age at first reproduction in the cercopithecines seems to be due to their beginning to breed before they have reached the full adult weight.

Variation within the Cercopithecinae

Body size

Cercopithecine species range in size from the small talapoin monkey weighing about 1.3kg to the baboons, which weigh from about 15 to over 25kg [depending on sex and species]. However, the next smallest species to the talapoin monkey are some of the guenons, the smallest of which are about 3kg. The talapoin is therefore unusually small.

The correlation between environmental variables and body size in the cercopithecines reflects the general pattern of correlations reported for all primates in Chapter 3. Generally speaking, savannah and open-country species are larger than forest-living species. As would be expected from this, terrestrial species are larger than semi-terrestrial species, which are in turn larger than completely arboreal species.

As expected from the comparative study of all primates, correlations are found between body size and diet. There is a weak significant correlation with the amount of foliage eaten [$r=0.45$, $N=19$, $p<0.5$], and a significant negative correlation with the amount of animal food eaten [$r=-0.71$, $N=18$, $p<0.01$]. As the talapoin monkey is both very small and highly insectivorous in comparison with other cercopithecines it was thought that it could have undue influence in the correlation between body size and the amount of animal food eaten. However, the correlation remains significant, although reduced, when *Miopithecus talapoin* is removed, ($r=-0.54$, $N=17$, $p<0.05$).]

Correlations between latitude and body weight and between climate and body weight, have been discussed in detail in Chapter 3. The analyses in Chapter 3 showed that, in the cercopithecine group as a whole, there is a weak positive correlation between range centre and body size [$r=0.33$], indicating that cercopithecines tend to be larger in more temperate areas. Macaques show a significant increase in size with latitude, but this is not seen within other genera.

Life-history parameters and body weight

The investigation of variation in life-history parameters within the cercopithecine group followed similar lines to the investigations of all primates discussed earlier. Firstly, major axis analyses were carried out in order to investigate the relationships of the life-history parameters with body weight. The results of the major axis analyses of the relationships of life-history parameters to body weight are summarised in table 7.2.

One striking difference between the results of the major axis analyses of the cercopithecine data and those of all primate data is that several of the life-history parameters are not significantly correlated with body weight [using logarithmic correlations]. Neither the birth rates nor the ages at first reproduction of the Cercopithecinae are correlated with body body weight. As one would expect from this, there is also no correlation found between r_{max} and body weight [table 7.2]. [Interbirth interval [IBI] need not be discussed separately for these species as they all have a litter size of one, and hence IBI is simply the reciprocal of birth rate.] The relationships of these parameters to body weight are illustrated in figures 7.3 to 7.5, where the lack of covariation between the life-history parameters and body weight can be seen clearly.

This lack of correlation between life-history parameters and body weight is surprising in the light of the strong correlations found between these parameters and body weight in the primate group as a whole. This indicates that, in the subfamily Cercopithecinae at least, there can be a decoupling of the scaling relationship found between body weight and life-history parameters. The lack of correlation means that the line of best-fit through the data is statistically indistinguishable from a line with a slope of zero, and it is therefore meaningless to calculate residual values for age at first reproduction, birth rate and r_{max} using the cercopithecine species alone. However, it is important to remember that size may still play a part in determining the values of the life-history parameters and this may be particularly important when looking at the largest species [the baboons] and the very small talapoin monkey.

The reason for the lack of correlation between body weight and birth rate is probably due to most of the cercopithecines being seasonal breeders. The majority of species therefore breed once a year or every two years, with births usually occurring in the spring or at the beginning of the rainy season. This constraint on the time of birth gives rise to interbirth intervals of one or two years for most species and allows for little "fine tuning" of birth rate to body size. A similar effect constrains the age at first reproduction to occur at yearly intervals, and is probably partly responsible for this parameter also not being predictable from body size. In addition, the disassociation of age at first reproduction from age at reaching adult weight may partly account for the lack of correlation between age at first reproduction and body weight.

Figure 7.5 shows that several species have either very high or very low values of r_{max}. The species with high values include the patas monkey, *Erythrocebus patas*, the talapoin monkey, *Miopithecus talapoin* and several macaque species. The sooty mangabey, *Cercocebus atys*, also has a high r_{max}, but the data used to calculate this figure are from captive animals only. All the species with a high r_{max} produce one offspring a year and start reproducing in their third or fourth year of life. Two species with particularly low r_{max} values are two forest guenon

Table 7.2

Major axis statistics for $\log_{10}$ life-history parameters versus $\log_{10}$ body weight, for Cercopithecinae species

Parameter	N	r	Slope	Intercept	95% Confidence limits of slope	
Neonatal weight	22	$0.90^{\dagger}$	0.52	0.65	0.40	0.64
Gestation length	26	$0.60^{\dagger\dagger}$	0.04	2.08	0.00	0.02
Age at 1st. reproduction	29	-0.14^{**}	-	-	-	-
Interbirth interval	27	0.02^{**}	-	-	-	-
Birth rate	27	-0.02^{**}	-	-	-	-
Longevity	33	0.40^{*}	0.21	0.61	0.04	0.40
r_{max}	25	-0.05^{**}	-	-	-	-
Age at weaning	13	0.48^{**}	-	-	-	-
Weaning weight	10	$0.94^{\dagger}$	0.77	0.23	0.56	1.04
Foetal growth rate	17	$0.90^{\dagger}$	0.51	-1.57	0.39	0.65
Postnatal growth rate [all possible species]	20	$0.86^{\dagger}$	0.71	-2.14	0.52	0.95
Postnatal growth rate [mother-reared species only]	12	$0.87^{\dagger}$	0.69	-2.04	0.44	1.00

† $p < 0.001$ †† $p < 0.002$ * $p < 0.05$

** not significant ($p > 0.05$) ∴ major axis statistics not given.

Figure 7.3

Log$_{10}$ age at first reproduction versus *log$_{10}$ body weight for Cercopithecinae*

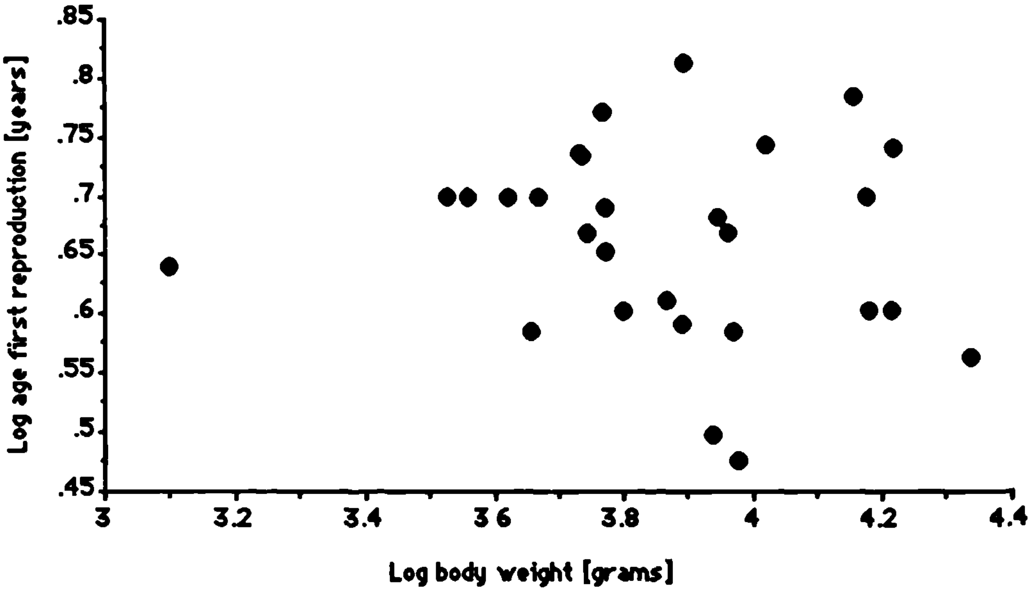


Figure 7.4

Log_{10} birth rate versus log_{10} body weight for Cercopithecinae

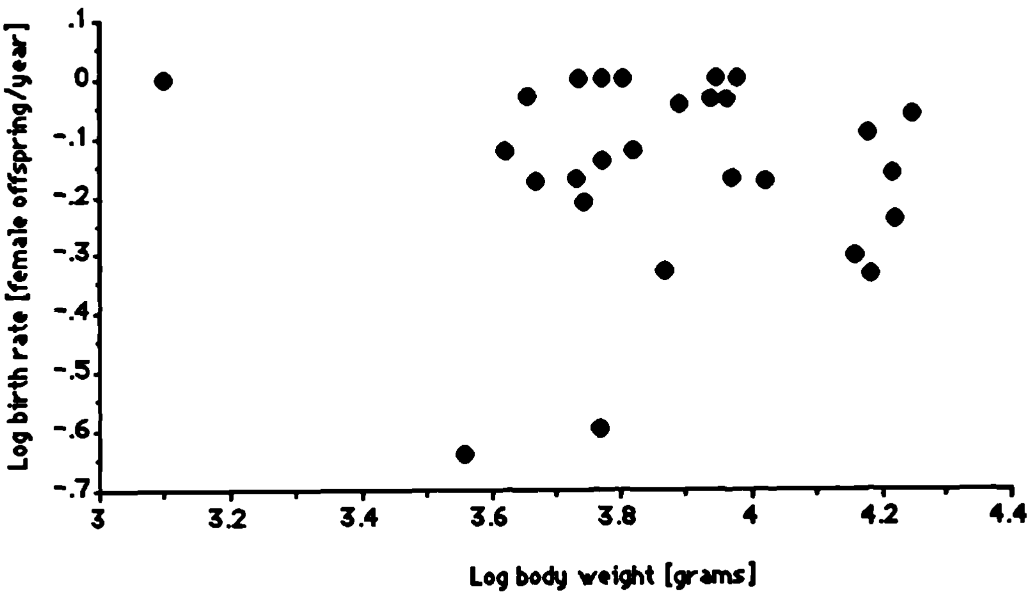


Figure 7.5

$Log_{10}\, r_{max}$ versus log_{10} body weight for Cercopithecinae

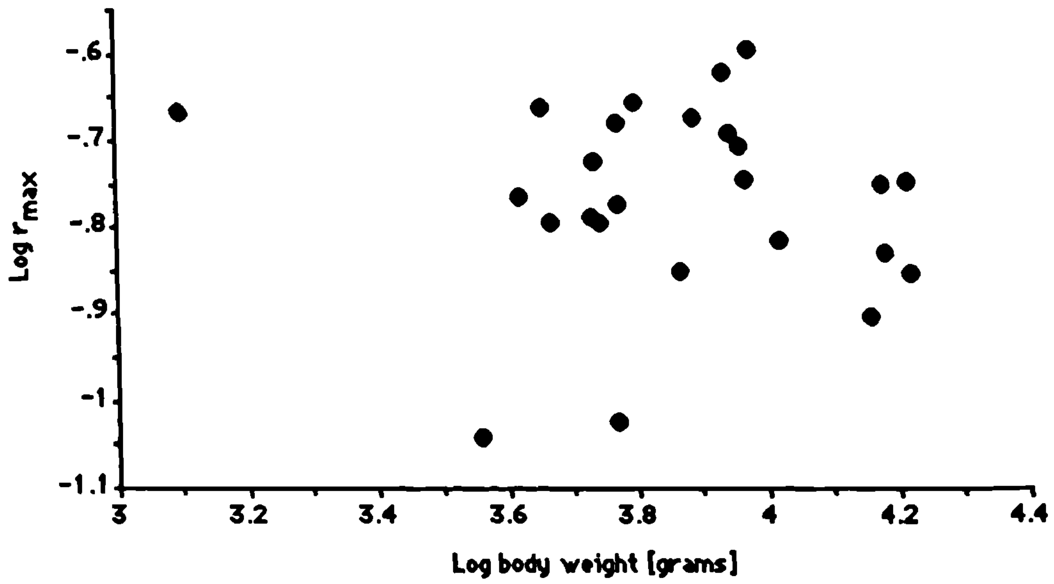


Figure 7.6

Log_{10} gestation length versus *log_{10} body weight for Cercopithecinae*

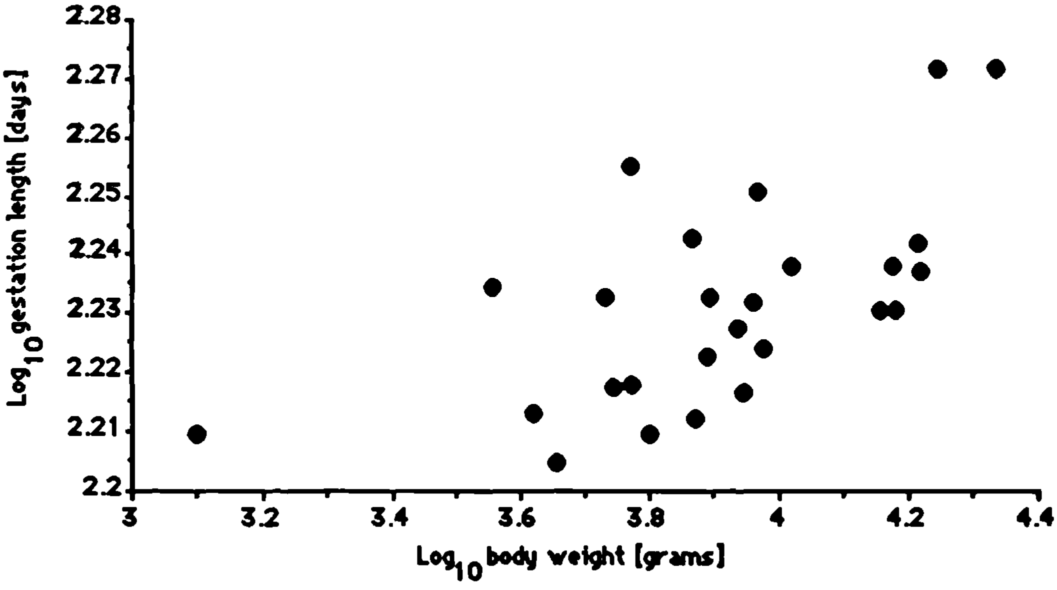


Figure 7.7

Log_{10} neonatal weight versus log_{10} body weight for Cercopithecinae

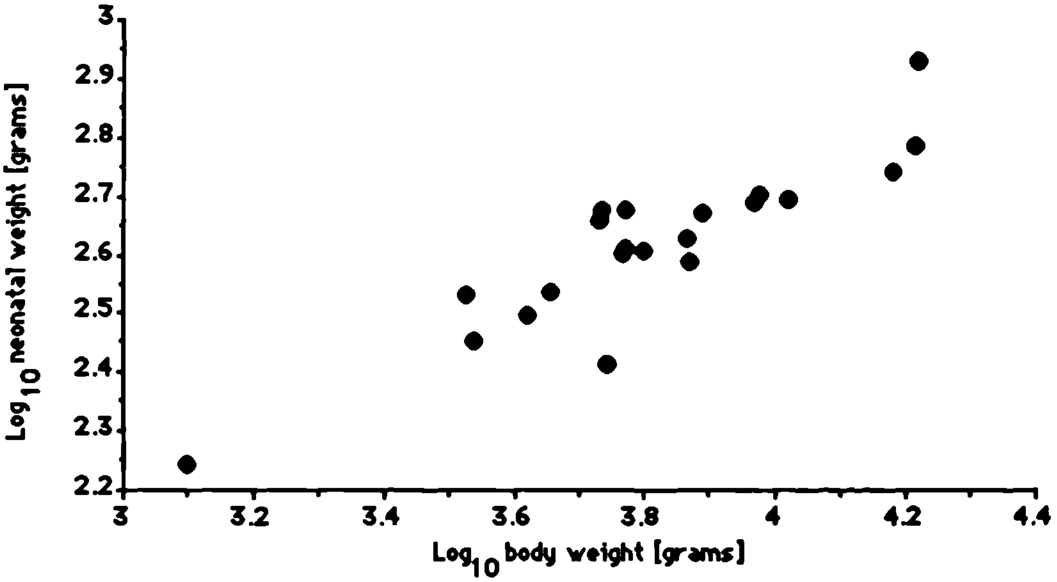


Figure 7.8

Log_{10} foetal growth rate versus *log_{10} body weight for Cercopithecinae*

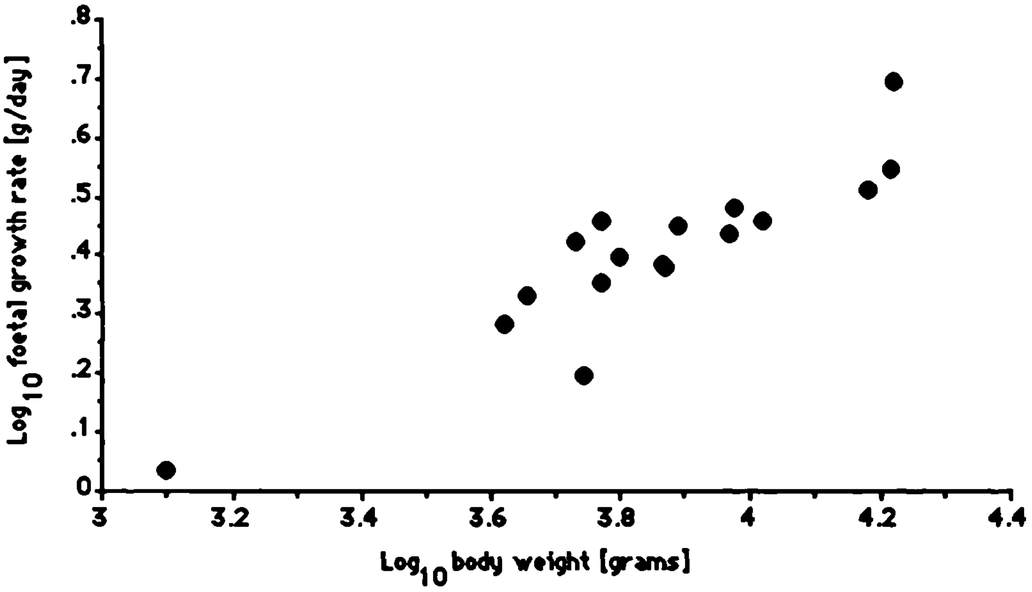
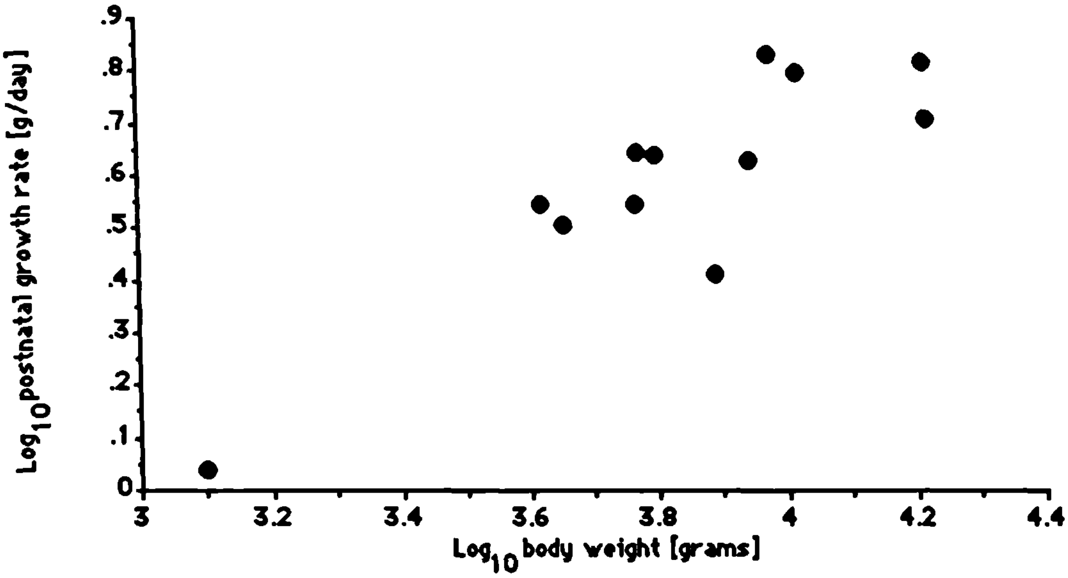


Figure 7.9

Log_{10} litter postnatal growth rate versus log_{10} body weight for Cercopithecinae



species, the red-tailed monkey, *Cercopithecus ascanius*, and the blue monkey, *C. mitis*. Both of these species have exceptionally long interbirth intervals [about four years] as compared to other cercopithecines and *C. mitis* also has a very late age at first reproduction [about 6 years].

In contrast to the parameters relating to the rate of population increase, those parameters that relate to growth rates are highly correlated with body weight. The two factors which make up foetal growth rate, gestation length and neonatal weight, are both highly correlated with body weight in the Cercopithecinae [figures 7.6 & 7.7]. As would be expected from this, foetal growth rate is also highly correlated with body weight, as can be seen in figure 7.8.

Although there is a very high correlation between logarithmic values of foetal growth rate and body weight, some species show particularly high or low residual values. *Cercopithecus neglectus* shows a marked negative deviation from the foetal growth rate predicted by its body weight; but the deviation is most probably due to an anomalous figure for neonatal weight, based on a single figure that is very low for a primate of its size. [The figure used is from a single value of 260g from Hill (1966). Further indication that it is low comes from Gautier (pers. comm. to R.D. Martin) who estimates the neonatal weight of *C. neglectus* as 350-450 grams.]

Papio cynocephalus and *Macaca mulatta* both have foetal growth rates [FGRs] that are very high for their size. In the former species this appears to be due to it having a relatively large neonate whereas the latter has both a large neonate and a short gestation period. Unlike the situation with *C. neglectus* the data for these two species are based on large sample sizes and are reliable. The remaining species show little deviation from the expected FGR.

Like foetal growth rate, postnatal growth rate to weaning age shows a high correlation with body weight [see figure 7.9]. Weaning age itself is not significantly correlated with body weight; but this lack of correlation is probably due to a combination of the small sample size for this parameter and the fact that the weaning age for several species is given as one year old. It is possible that the figure of a year is a very rough estimate of the lactation period for several species and it is predicted that further work will reveal more variation in this parameter than is evident in this study. A few species show large deviations from the expected value of postnatal growth rate. *Erythrocebus patas* has an exceptionally high postnatal growth rate for its size. In contrast, three species have a relatively low postnatal growth rate, these being *M. nemestrina*, *M. sylvanus*, and *P. cynocephalus*. As discussed below, no correlations between prenatal or postnatal relative growth rates and any other factor could be determined.

Life-history parameters, ecology and environment

As with the work on all primates, correlation analyses and analyses of variance were carried out to test for relationships between life-history parameters and diet, habitat, arboreality, climate and latitude. In cases where there was a clear correlation between the life-history parameter and body weight [where the logarithmic correlation was significant at $p<0.05$], these analyses were carried out using the residual values of the life-history parameter [i.e. after removing the effects of body weight]. In cases where the correlation between the life-history parameter and body weight was only just insignificant [$0.10>p>0.05$] the analyses were carried out on both the raw logarithmic values and residual values of the life-history parameter. In cases where there was clearly no correlation between the life-history parameter and body weight [$p>0.10$] the analyses were carried out using the raw logarithmic values of the life-history parameter only.

Diet, latitude and arboreality

No significant correlations between any life-history parameters and diet, latitude or degree of arboreality could be found.

Habitat

No correlations could be found between age at first reproduction, birth rate or r_{max} and any environmental variables for the whole cercopithecine group. This was true of both the wide and narrow habitat categories, and also when species were simply split into "forest" and "non-forest" species.

However, there are problems as the type of data available are variable and tend to be linked to the taxonomic group and the habitat [with forest groups being mainly represented by captive data]. When only the data from wild animals was examined a significant difference was found between the life-histories of species found in the forest compared with those found in other types of habitat. The forest species have longer interbirth intervals and lower rates of increase than do non-forest species [ANOVA, $p>0.05$]. No significant difference in age at first reproduction was found between the two groups.

There is no indication of either foetal or postnatal growth rates being linked to habitat. For example, although the patas monkey [*Erythrocebus patas*] has a relatively high postnatal growth rate, another savannah species, the savannah baboon [*Papio cynocephalus*] has a relatively low postnatal growth rate. Similarly, some forest species, such as the white-cheeked mangabey [*Cercocebus albigena*] have a relatively low foetal growth rate, whereas others, such as the blue monkey [*Cercopithecus mitis*], grow relatively fast during gestation. As might be expected from this, neonatal weight, gestation length, weaning weight and weaning age also show no links with habitat.

Climate

Very few correlations were found between climatic variables and life-history variables. Three of the four significant correlations that were found involve the variation of rainfall in the driest month. This parameter had a positive correlation with r_{max} [$r=0.78$, $N=13$, $p<0.002$]

and birth rate [$r=0.62$, $N=14$, $p<0.02$], and a negative correlation with age at first reproduction [$r=-0.75$, $N=13$, $p<0.005$], although all of these correlations were only significant when the data was restricted to data from wild studies. The fourth significant correlation was between relative weaning weight and average rainfall in the driest month [$r=-0.73$, $N=9$, $p<0.05$].

It can therefore be said that cercopithecine species living in areas with unpredictable drought periods tend to have high birth rates, an early age at first reproduction and high r_{max} values, with cercopithecines living in more stable areas having the opposite characteristics. As forest climates tend to be more stable than other climates, these results support those found above, that link forest-living with a low r_{max}. In addition, cercopithecines living in areas where the dry season has very little average rainfall will be expected to have a higher weight at weaning than will those where rainfall is higher. This implies that such species will have a higher total reproductive effort than species in wetter areas.

The general pattern of life-history variation in cercopithecines suggests that species that are found in forest environments and/or in areas where there is not unpredictable drought will have low rates of population increase. In contrast, species that are found in non-forest areas and/or in areas where drought unpredictably occurs will have high rates of population increase. These changes in rates of population increase are associated with changes in both age at first reproduction and birth rate, but none of these parameters is correlated with body weight. The growth rates of cercopithecines are highly correlated with body weight and the residual variation in growth rates does not appear to be correlated with ecological or environmental factors.

Although the above summarizes the general findings of this section, it should be realized that there are several species that do not have the type of life-history that one might expect. It was considered that further examination of the variation found between species would be best considered by looking at groups of closely related species. The following therefore looks at the two main groups of cercopithecines in turn. The approach of this section is slightly different to that of the rest of the thesis, being more qualitative and less quantitative in its discussion of the links between life-history parameters and other factors. For example, I have not attempted to list the correlations found between different life-history parameters and body weight for all possible genera and combinations of genera within the cercopithecines. [Generally speaking, the life-history parameters that are correlated with body weight for all cercopithecines vary in a similar way for genera and groups of genera within the cercopithecines]. Similarly, I have not given details of all correlation coefficients found between different life-history parameters and ecological factors, such as habitat, climate and latitude, as the results of such analyses have already been discussed in previous chapters. The approach of this section is to look at the general ecological position of different closely related species, and to try to link this to their life-history parameters. This was done as it was felt that the combination of very small sample sizes and a collection of data from different sources made it probable that a strictly quantitative approach would miss general trends that might be obscured by variation in the data that was due to differences in collecting conditions and the quality of data.

The Papionini

Data are available on representatives from every genus in the Papionini group, although data from some genera are restricted to data from captive animals. The macaques are dealt with separately from the other species of Papionini for two reasons. Firstly, the group is geographically separated from the other genera, with the macaques being found almost entirely in Asia [the exception being the Barbary macaque in North Africa], whereas the other genera are restricted to subsaharan Africa. Secondly, the macaques are particularly well represented in this sample and there are therefore enough data to permit meaningful comparisons within the group.

Macaques

[Including *Macaca* species and *Cynopithecus nigra*]

The high positive correlation between latitude and body size in the macaques has already been noted. This positive correlation between body size and latitude is matched by a negative correlation between several measures of mean temperature and log body weight, and a positive correlation between temperature variability in the coldest month and log body weight. It can therefore be said that macaques in more temperate areas, i.e. colder and more seasonal areas, are larger than those in tropical areas.

The continental Asian macaques can be divided into two ecological groups, those found in primary broadleaf evergreen forest and those found in other habitats [Fooden 1982]. The species in the second group are frequently found in a variety of habitats that may include highland areas, forest edge and towns. In general terms, the second group can be thought of as more opportunistic and characteristic of more disturbed habitats. In several cases there is sympatry between a species from the "forest" group and a species from the "non-forest" group [Fooden, 1982]. One would therefore predict that they might differ in life-history parameters as well as habitat for, although the climates that they are experiencing will be similar, the habitat differences will mean that their resources at any given time may be very different. Some life-history characters of the two groups are listed in table 7.3.

In three out of four cases the forest species has a lower r_{max} than does the non-forest

Table 7.3

Sympatric macaque species pairs for which r_{max} data is available

	Forest species			Non-forest species			
	AR[1]	IBI[2]	r_{max}		AR	IBI	r_{max}
A) *M. nemestrina*	3.9	1.1	0.22	*M. fascicularus*	3.9	1.1	0.22
B) *M. silenus*	4.9	1.4	0.17	*M. radiata*	4.0	1.0	0.23[3]
C) *M. arctoides*	3.8	1.5	0.18	*M. mulatta*	4.5	1.0	0.21
D) *M. arctoides*	3.8	1.5	0.18	*M. fascicularus*	3.9	1.1	0.22

1) AR= female mean age at first reproduction [years]: 2)IBI= mean interbirth interval [years]: 3) Data from *M. radiata* is based on estimates only and has not been used in the analyses in this thesis.

Table 7.4

Birth rate and age at first reproduction in Japanese macaques, for different levels of provisioning, from Mori [1979]

Provisioning	Years (N)	Birth rate[1]	Age 1st rep.	Infant mortality[2]
Low	1952-63 (12)	46%[1]	5.3 years	4%
High	1964-71 (7)	67%	6.2 years	15%
Medium	1972-77 (6)	32%	6.8 years[3]	69%

1) Where birth rate is measured as the proportion of multiparous females giving birth in a year.

2) Mortality in first year of life

3) This figure being reached by excluding older females that had not started breeding at the time of the study.

species. Pair (B) compares data from captive *M. silenus* with data from wild *M. radiata*, pair (C) compares captive *M. arctoides* with wild *M. mulatta* and pair (D) compares captive *M. arctoides* with captive *M. fascicularus* As noted before, captive animals frequently start breeding at a younger age and have shorter interbirth intervals than do wild animals. Hence, it is particularly notable in pairs (B) and (C) that the non-forest macaques appear to be breeding at a younger age and more rapidly than the forest macaques. If one uses data from captive M. mulatta the age at first reproduction is even earlier [about 3.6 years, Hadidan and Bernstein (1979)] thus increasing the difference between the two species in pair (C). The one pair where a forest species does not have a lower r_{max} than a non-forest species is pair (A), in which the two species have the same r_{max}. However the data for *M. nemestrina* are from captive animals, whereas those for *M. fascicularus* are from provisioned, free-ranging groups. Given that captive animals tend to breed earlier and faster than do free-ranging animals, this is perhaps an indication that *M. fascicularus* would have a higher breeding rate than *M. nemestrina* in the wild.

In addition to the species discussed above, life-history data are also available for four species of macaques that are not sympatric with another macaque species. These are the Barbary macaque, *M. sylvanus*, the Japanese macaque, *M. fuscata*, the toque macaque, *M. sinica* and the Celebes macaque, *Cynopithecus nigra*. The last of these species, *C. nigra*, has not been widely studied in the wild and its habitat preferences are not known. For this reason it will not be discussed further here.

Both the Barbary macaque and the Japanese macaque are found beyond the tropics and in mountainous areas that experience very harsh winters. *M. sinica* lives only on Sri Lanka, where it is found mostly in forested areas. As might be predicted from the life-history parameters of the other macaques, *M. sinica* has a low r_{max} whereas the r_{max} of *M. sylvanus* is quite high. However, the data on the Japanese macaque shows that they have a low r_{max}, in fact the lowest of any macaque species in this study. Indeed, the rate of increase in the Japanese macaque could be even lower than the figure used here, as all data is taken from populations that are provisioned to some extent.

An indication that the Japanese macaque might not be able to support such a high r_{max} in unprovisioned populations comes from Mori [1979]. Mori compares the demographic characteristics of a provisioned population where the level of provisioning was changed over time, being first very low, then very high and finally intermediate. The birth rates and age at first reproduction of this population at the different levels of provisioning were calculated by Mori [1979], and are summarized in table 7.4.

The changes in age at first reproduction are difficult to interpret, as animals giving birth for the first time in one feeding regime may have spent several years of their lives growing up in the previous regime. However, it seems clear that the birth rate increased dramatically when feeding levels were increased in 1964 and decreased again when they were reduced in 1972. Although infant mortality levels increased with time, a closer examination of the data indicates that the mortality rates during the period of high feeding were not generally higher than those during the period of low feeding. The average infant mortality rate during high provisioning is inflated by the inclusion of a single year when mortality was 100%. Notably, this high mortality was in the first year of high level provisioning which was commenced because of the poor condition of the animals. Excluding this year gives an infant mortality of just over 4%.

At first sight, the fact that the birth rate during medium provisioning is lower than that during low provisioning seems to be anomalous. The explanation for the decrease in birth rate is that the provisioning allowed the population to increase far beyond the carrying capacity of the area [the population density being about 7 times higher than a comparable wild population] and when it was decreased there simply wasn't enough food to support the number of animals present [Mori 1979].

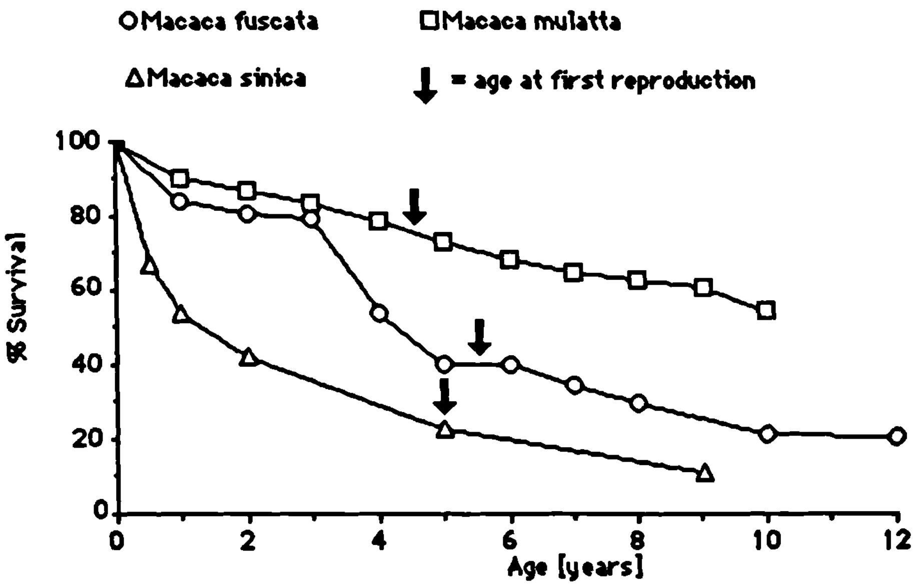
Although the potential rate of increase of the Japanese macaque may be higher when there are high resource levels, the birth rate is never as high as that found for other macaque species living in other environments, where macaques frequently breed annually. Similarly, the age at first reproduction is never as low as is found for other species. This implies that the Japanese macaque does not have the capacity to increase its population numbers as quickly as other macaque species. This is discussed below.

It therefore appears that there is some evidence to suggest that macaques that inhabit variable habitats generally have a higher r_{max} than do those that are found in forest environments. The notable exception to this rule is the Japanese macaque. Two questions therefore arise: (1) What are the immediate determinants of the variation in r_{max} in macaque species, i.e. does variation in birth rate and/or age at first reproduction cause the variation in r_{max}? and, (2) What are the factors selecting for a high or low r_{max} in these species?

An examination of the data suggests that the macaques with a high rate of increase tend to be capable of producing an infant every year. This is seen in all the non-forest Asian mainland species [see table 7.3 above] and in the Barbary macaque. In contrast, most of the other species produce an average of only two infants every three years, even in captivity. Variation in age at first reproduction is also seen, with the species with a higher r_{max} usually starting to breed at about four years of age, and the other species not producing their first infant until about five years of age. It therefore appears that selection operates on both birth rate and age at first reproduction, and that their combined effect operates to alter r_{max}. The early age at first reproduction of the non-forest species is accompanied by their breeding at weights far below the

Figure 7.10

Survivorship against age for three macaque species



full-grown adult weight. Female *M. mulatta* first give birth at about 68% of full adult weight and *M. sylvanus* at 59%, whereas two forest species *M. arctoides* and *M. nemestrina* reach 96% and 76% of full-grown weight, respectively, before breeding.

Growth rates of macaques show no clear pattern of variation with ecology, either before or after body weight effects are removed. Similarly, neonatal weights and weaning weights do not seem to vary predictably with the ecology of the species, either before or after body weight effects are removed. For example, although one forest species, *M. nemestrina*, has a very low postnatal growth rate, another forest species, *M. arctoides*, has a very high postnatal growth rate. This lack of obvious correlation between these developmental parameters and ecology suggests that this measure of reproductive effort is not closely linked to the ecology of macaques.

It was considered that mortality patterns might be linked to r_{max}, and this was therefore investigated. Figure 7.10 shows age-specific mortality rates for three species of macaques. Here, it is clear that the rhesus macaque, *M. mulatta* has a far greater survivorship to first reproduction that does the toque macaque, *M. sinica*, with the Japanese macaque, *M. fuscata*, falling between the two. The r_{max} figures calculated from the same populations [or, in the case of the Japanese macaque, an average from other provisioned populations] indicate that *M. mulatta* has an r_{max} far above that of the other two species, which have similar rates of increase. This might suggest that a high survivorship to reproductive age is linked to a high r_{max}.

However, the biological relevance of this result is unclear for several reasons. Firstly, the data from the three studies are not strictly comparable, as the conditions under which the data were collected varies and the methods of calculating mortality rates are also different. The rhesus and Japanese macaque data are from provisioned populations, whereas data for the toque macaque are from a wild population. Evidence that provisioning can affect the mortality rates of infants was presented above [from Mori, 1979]. The rhesus macaques are also living in an area [Cayo Santiago Island] where there are no natural predators, and this may partially account for their very low mortality rates. In addition to this, the demographic parameters of the toque macaques have been estimated after making several, possibly untenable, assumptions about the nature of the population [Dunbar, 1986]. Because of these problems it is impossible to draw any firm conclusions from the mortality rates of these species.

Baboons, drills, mandrills, gelada and mangabeys

There are two *Papio* species for which life-history data are available from wild populations, the yellow baboon, *P. cynocephalus*, and the hamadryas baboon, *P. hamadryas*. These species are similar in their breeding rates, with both species having an interbirth interval of about 1.5 to

2 years, and also in their age at first reproduction of 5-6 years [Altmann, 1980; Sigg *et al.*, 1982.]. The wild female gelada, *Theropithecus gelada*, reaches sexual maturity somewhat earlier, producing her first infant at about 4.5 years old, but then has a slightly slower birth rate of about one infant every 2.5 years [Dunbar, 1984]. These three species therefore have a similar r_{max}, although that of the gelada is slightly higher than that of the two *Papio* species.

These reproductive parameters mean that the baboons and gelada have very low r_{max} values as compared to most other cercopithecines. The only species with lower r_{max} values are two guenons [the blue monkey and the red-tailed monkey]. Although r_{max} was not found to be correlated with body weight in the cercopithecine species, it was considered that the very large size of the baboons and the gelada could be a partial cause of their low r_{max} values. As the baboons and the gelada are all open-country species, a comparison of their reproduction with that of the larger forest-living cercopithecines is of interest.

Unfortunately, there are no comparable data on wild populations for either of the forest-living *Mandrillus* species. Captive data suggest that they can produce their first infant at 4 to 5 years old and then give birth every 15-18 months [Carman, 1979; Hadidian and Bernstein, 1979], figures that give an r_{max} that is considerably above that of the wild-living gelada or *Papio* species. However, it is likely that wild animals will take longer to mature and have a longer interbirth interval. Indeed there is an indication [Jouventin, 1975] that *Mandrillus sphinx*, at least, is a seasonal breeder and therefore probably does not give birth more than once every two years in the wild. [If it were capable of giving birth annually one would expect the captive data to show this.] There is no evidence on the age at maturity of either the drill or the mandrill the wild. Sadly, these animals are both difficult to study [being forest-dwelling and very wary due to widespread hunting] and endangered, so it is possible that their life-histories in the natural state will ever be known.

Another large-bodied, forest-living group, related to the baboons, is the genus *Cercocebus*, the mangabeys. These are forest-living species, but all of the life-history data available is from captive animals, and it is therefore difficult to compare them with the wild baboons. One interesting aspect of the data from the *Cercocebus* species is that one species, the sooty mangabey [*C. atys*] has a high r_{max} whereas a second, the white-cheeked mangabey [*C. albigena*], has a very low r_{max}. It is possible that these differences that are found in captivity could be reflected in similar differences in wild animals. As the sooty mangabey belongs to a group of semi-terrestrial mangabey species and the white-cheeked mangabey is belongs to a second group of arboreal mangabey species, it was thought possible that differences in life-history might be correlated with differences in ecology. However, *C. galeritus*, a species that is closely related to

C. atys, has a late age at first reproduction even in captivity [about 6.5 years] and this indicates that it has r_{max} that is probably as low as that of *C. albigena*. [Although no birth rate data are available for this species, even a birth rate of one offspring per year and a lifespan of 35 years would give it a rate of population increase only slightly above that of *C. albigena*] The possibility of there being a link between the different ecologies of the two mangabey groups and their life-histories therefore remains open.

No correlations with environmental parameters and neonatal weight, gestation period, neonatal weight, weaning age weaning weight or growth rates could be distinguished. The savannah baboon has a heavy neonate for a haplorhine of its size, and this is linked to its high foetal growth rate. However, there is no data on other baboon species to determine if this is a characteristic unique to *Papio cynocephalus*.

The Guenons [Cercopithecini]

[Including the genera: *Cercopithecus*, *Erythrocebus* and *Miopithecus*].

As discussed above, the guenons are primarily a forest-living group, but two species, *Cercopithecus aethiops* and *Erythrocebus patas* are found mainly in savannah and woodland. Wild data are available for two forest species, *C. ascanius* and *C. mitis*, both of which have an r_{max} that is considerably lower than any other cercopithecine species, including the closely related woodland and savannah species *C. aethiops* [for which data from wild animals are also available]. The second savannah-living species, *Erythrocebus patas* has the highest relative r_{max} of any haplorhine species and a higher absolute value of r_{max} than any haplorhine species, apart from the callitrichids and small-bodied cebids. The patas monkey is found in the savannah to an even greater extent than the vervet monkey, and appears to be specifically adapted to a terrestrial savannah-living life. These data therefore indicate that there is a link between savannah dwelling and rapid reproduction in the guenon group.

The talapoin monkey is a forest-living species that might be expected to have a low r_{max}. However, the annual breeding of this species [Gautier-Hion, 1971] gives the talapoin a higher absolute r_{max} than many other cercopithecines. But, the talapoin monkey is considerably smaller than other cercopithecine species, being about half the size of the next largest species. It is to be expected that, despite the general lack of correspondence between r_{max} and body size in the group, this very large size difference might result in a higher r_{max}. When the data for all wild haplorhines are examined the talopoin does appear to have a low r_{max} for its body size, a feature shared with *C. ascanius* and *C. mitis*.

The remaining guenon species have r_{max} values that are calculated from captive animal data and it is therefore difficult to compare them to the species where wild data is available. Although several of these species [e.g. the diana monkey] can give birth annually in captivity, it is quite probable that their rates of reproduction are lower in the wild. Evidence that this may be the case comes from Cords and Rowell [1987], who show that wild *C. mitis* have interbirth intervals that are considerably longer than those found in captive animals [47 months in the wild as compared to about 18 months in captivity].

There are no clear links between environmental parameters and neonatal weight, gestation period, neonatal weight, weaning age weaning weight or growth rates could be distinguished. Although the patas monkey stands out as having a very high postnatal growth rate for a haplorhine of its size, the second open country species [the vervet] has a relative postnatal growth rate that is about the same as some forest guenons.

Cercopithecine monkeys in variable habitats: selection for rapid breeding?

The results from the macaque and guenon groups both indicate that there is a link between forest-living habitats and a low r_{max}, with species living in non-forest habitats having a higher rate of increase. The link between forest-living and a low r_{max} appears to be strong in the macaques, where forest species are found to have lower r_{max} values than sympatric species that are found in a greater variety of habitats. There is also evidence that forest guenons have low r_{max} values, although the talapoin may be an exception to this rule. However, the opposite connection, between non-forest habitats and high r_{max} does not seem to be as clear, with several species in very seasonal environments having a low r_{max}, notably the baboons, gelada and Japanese macaque.

When looking at baboons, one would ideally wish to compare their r_{max} with that of their forest-living relatives, either forest populations of *Papio* species or with the drill and mandrill. However, the lack of data from wild populations of these forest-living species prevents such a comparison. Despite this, the baboons and the gelada do appear to have a very low r_{max} values in comparison to most other cercopithecines, a fact that appears to need explanation. For example, the yellow baboon is sympatric with both the vervet and the patas monkey and can be thought of as being intermediate between the two species in its degree of adaptation to savannah living [Hall 1965]. It would perhaps be expected that patas would have an intermediate r_{max} value, but this is not the case [the order being *E. patas* > *C. aethiops* > *P. cynocephalus*]. Similarly, it is perhaps surprising that the hamadryas baboon and geladas have low rates of increase, when both are found in very harsh and unpredictable environments. The Japanese macaque is found further from the equator than any other primate, and can survive in extremely seasonal climates. Although most macaques that are found in variable habitats are found to have higher r_{max} values than forest species, the Japanese macaque has a low r_{max}. Some possible [and not necessarily exclusive] reasons for the low r_{max} of the all these species will now be discussed.

The low r_{max} values of these species can be explained in two basic ways. Either it must be assumed that these species are not being selected to have a high r_{max}, or, if they are being selected for a high r_{max}, one must assume that there is some kind of constraint preventing this selection from operating. To take the latter idea first, there are several reasons why these species may not be breeding as rapidly and/or as early as one might expect. The large body sizes of all of these species may mean that they are physiologically unable to support a high r_{max}. This could be due to their not being able to wean an infant within a year and hence having to breed more slowly and/or their taking longer to reach maturity. This assumes that the growth rate cannot be increased beyond a certain point because the genetic variability for increasing r_{max} does not exist.

Alternatively, environmental constraints may prevent a high breeding rate, e.g. because of a lack of adequate nutrition. This would mean that it could be physiologically and genetically possible for the baboons to have a higher breeding rate, but that the lack of available food prevents this capacity from being realised. This could be because poor nutrition prevents high growth rates, leading to a delay in age at weaning [and hence an increased interbirth interval] and a delay in attaining reproductive age. If this were the case, one might expect that the animals would increase their r_{max} when it was possible to do so and that one would see a lowering of the age at first reproduction and/or an increase in birth rate when environmental conditions permitted.

These ideas can be tested by comparing animals of the same species in different habitats or by looking at the reproduction of captive animals. There is some support for the idea that *Papio* species can increase their birth rate beyond that found in the wild populations studied. Data from captive baboon species [*Papio papio*] suggests that the interbirth interval is about 14 months [Rudder, 1979] which is lower than the 18-24 months found for related species in the wild. Similar data show that captive geladas have a mean interbirth interval of about 17 months, as compared to over 25 months in the wild [Hadidan and Bernstein, 1979; Dunbar, 1984]. It is also known that captive baboons grow faster and that age at first menarche of captive baboons can be up to two years earlier than wild animals [Altmann and Alberts, 1987]. It is therefore possible that low growth rates in the wild may also delay the age at first reproduction, perhaps because wild animals take longer to reach the body weight needed to successfully bear young. These figures suggest that the rate of increase of captive baboons and geladas may be comparable to, or even higher than those of other large bodied cercopithecines [e.g. mandrills and drills]. It is therefore possible that the apparently low r_{max} of wild baboons and gelada is similar to, or higher than, that of related forest species.

In the Japanese macaque there is little evidence to suggest that the species is capable of supporting an r_{max} that is as high as related species in seasonal climates. Even under captive conditions, the r_{max} of the Japanese macaque is lower than that of other species of macaque, including forest species measured under similar captive conditions. For example, captive Japanese macaques can breed annually, but the mean age at first reproduction is always about five years, whereas forest species such as the pigtailed macaque can also breed annually but start to breed at four years old [Scucchi, 1984; Fedigan *et al.*, 1986; Hadidan and Bernstein, 1979]. It therefore appears that environmental constraints cannot account for the low r_{max} of the Japanese macaque. It is also worth noting that, contrary to the suggestion of Wolfe [1986] it is an inability to breed at an early age and not an inability to breed rapidly that imposes the main constraint on this species. Studies of both captive and provisioned animals suggest that, when food is not limiting, the Japanese macaque can produce an offspring nearly every year [Scucchi, 1984; Mori, 1979], whereas all studies agree in showing that females do not start breeding until they are five years old [Nigi, 1976; Scucchi, 1984; Mori, 1979]. Possible reasons for this constraint are therefore discussed below.

The ideas discussed above assume that the "optimal strategy" for these species would be to have a high r_{max}, but that genetic, developmental and/or environmental constraints are preventing them from achieving an optimal breeding rate. To take the savannah and hamadryas baboons first. One possibility is that the baboons are not experiencing the savannah environment in the same way as are other savannah species, and hence that they are being selected to have a different life-history strategy. If it is assumed that it is the unpredictability of the savannah environment that selects for a high r_{max}, then one needs to look for factors that might mean that baboons do not experience their environment as unpredictable. Possible factors include their large body size acting to buffer them against environmental change and/or their eating a large number of different foods, so that they can find something to eat in every season. For example, their eating underground tubers and roots could provide them with a reliable food source in the dry season. Evidence that baboons are less affected by the seasonality of their habitat, for what ever reason, can be seen in their lack of seasonal breeding and in their mortality patterns.

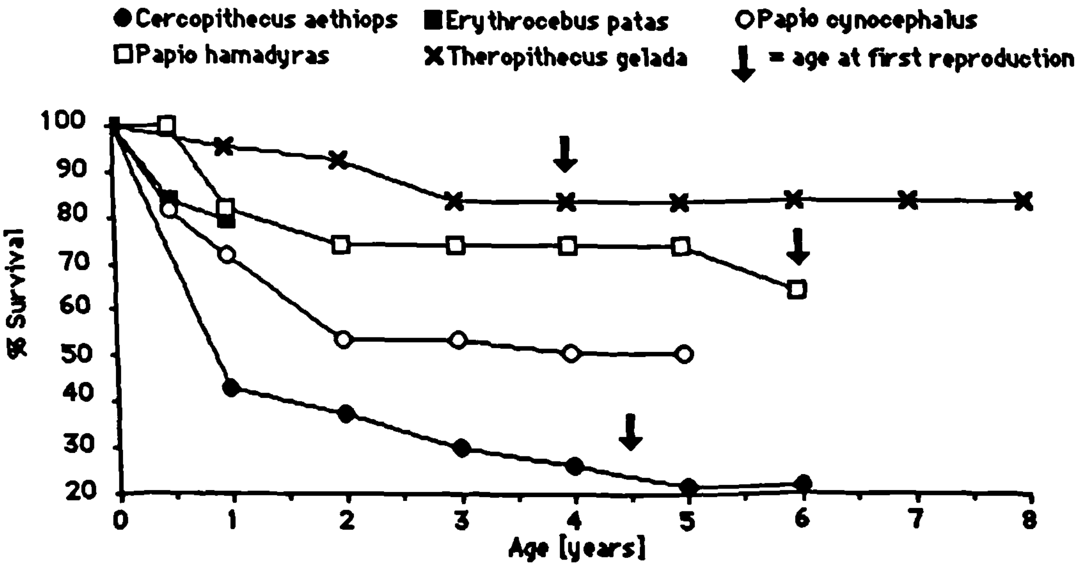
The fact that *Papio* species breed all the year round is perhaps an indication that they do not experience the seasonality of the environment as strongly as do vervet and patas monkeys which breed seasonally. There is little evidence that the mortality of yellow baboons is closely linked to the seasonality of their environment. Altmann [1980] gives details of 12 deaths that occurred in one troop over 15 months and, from the information given, there appears to be no link between these deaths and the season of their occurrence. In vervets, however, Cheney *et al.* [in press] note that there is an increase in deaths from illness during the dry season and a larger number of deaths by predation in the rainy season. Similarly, breeding female patas monkeys appear to be particularly vulnerable to periods of drought [Chism *et al.* 1984].

Another indication that baboons do not experience the savannah in the same way as the vervet monkeys comes from a comparison of the age-specific mortality patterns of the species. The, admittedly limited, data that are available on the mortality of these species suggest that vervets have a far higher probability of their offspring dying before they reach reproductive age [see figure 7.11] than do hamadryas baboons, and most probably savannah baboons. [Although the records for the savannah baboons are only available for animals up to five years old it seems likely, both from the early mortality pattern of the savannah baboon and from that up to 6 years for the hamadryas baboon, that mortality would not increase drastically between the ages of 5 and 6]. Unfortunately, data on the patas monkey are not sufficient to indicate whether this species also has a low survival to sexual maturity. Although the proportion of patas infants surviving to one year old is similar to that for the hamadryas baboon, it is possible that mortality from the ages of one to three years old may be high in the patas, as their infants are weaned at one year old and may therefore be susceptible to predation or illness at this age. It is therefore possible that these different mortality patterns may be linked to the differences observed in the life-history parameters of these savannah species.

The low r_{max} of the gelada is also associated with a very low juvenile mortality rate. However, this species does breed seasonally and there is evidence that the cold wet season is linked to increased mortality in this species [Dunbar, 1980]. It therefore appears that the gelada cannot be viewed as a non-seasonal species in the same way as can the baboons. One indication that the gelada is selected for rapid breeding is found in its early age at first reproduction. Although the adult female gelada is about the same size as the female savannah baboon [about 10-11kg], she starts to breed in her fourth or fifth year, a year or two before the baboon. The low r_{max} is therefore due to the average interbirth interval of this species being longer than that of the baboon. The reason for this is probably that geladas tend to breed seasonally [in the summer], and there must therefore be a whole number of years between births. As the infants take over a year to raise the interbirth interval must be at least two

Figure 7.11

Survivorship against age for five "open country" Cercopithecinae species



years. Although some females do breed in the winter, it would seem that this is a more risky time to give birth and selection would therefore favour delaying breeding until the summer for most animals [Dunbar, 1980]. This delay of breeding due to seasonality will be particularly favoured in this species because it has very high survival rates during adult life. The gelada can therefore be thought of as being selected for a high r_{max}, but only within the constraints of seasonality. One interesting prediction that might be made about this species, is that older females, who have higher mortality rates than younger animals, might have more to gain by risking producing infants in the winter season. As these females have a higher chance of dying, it may be better for them to risk losing an infant born in the winter than to risk waiting for six months to give birth but then dying before the infant can be raised.

The presence of links between patterns of mortality and life-history parameters cannot be conclusively demonstrated by these data. Although there is some indication that lower mortality rates are associated with lower rates of reproduction, the fact that good data are available from so few populations means that it is impossible to draw general conclusions. In addition, it appears that the situations of the baboons and the gelada are not directly comparable. The only other cercopithecine species for which mortality data and r_{max} data are available are the macaque data discussed above, where links between mortality and other population parameters could not be firmly identified. Although the data on mortality in macaques does not provide any conclusive evidence, it does appear that the mortality rate of the infant and juvenile Japanese macaque is high, with only about 40% of females surviving to reproductive age. These high rates of mortality continue for adult animals, with about 20% surviving until 10 years old [Masui *et al*,1975]. The Japanese macaques are also very seasonal breeders. For these reasons, it seems that the Japanese macaques do experience their environment as being highly seasonal and unpredictable. One indication as to why Japanese macaques do not breed at a younger age comes from Mori [1979]. Mori notes that animals that attempted to breed when small in size [below 7 kg] frequently failed to raise an infant, and in several cases the mother also died. It seems likely that the very harsh conditions experienced by the Japanese macaques does not allow mothers under a certain weight to successfully rear infants. This situation is combined with strictly seasonal breeding. Between the ages of four and five years a female might be expected to increase her weight by about 1.2kg, a size increase that takes her from about 5.8 to 7kg [Mori, 1979]. It therefore appears that females will not be large enough to breed successfully at four years old and those that attempt to do so run a very high risk of loosing both their infant and their own lives. In such a situation one would predict that there would be selection for delaying reproduction until the fifth year of life. It could be argued that if selection for early breeding were high, this could be achieved *via* selection for rapid growth. To some extent such selection does seem to occur, with Japanese macaques growing rapidly in their first year of life [both absolutely and relative to body size]. However, growth slows after weaning, and it is probable that this is due to the limitations of the harsh environmental conditions.

The results reported here therefore suggest that the factors that bring about a low r_{max} in the baboons and the gelada are probably different to those that produce the same effect in the Japanese macaque. In baboons and geladas there are two possible explanations that are compatible with the life-history data available. The first is that these species are breeding as fast as possible but that nutritional constraints are preventing then from reaching their maximum reproductive potential. Some evidence that this is the case comes from studies of captive baboons and geladas, which indicate that captive animals are capable of supporting higher birth rates [and possibly breeding at an earlier age] than are wild animals. This indicates that these species retain the genetic variability to have a higher r_{max} than is found in the wild populations studied so far. If this capacity for high rates of reproduction is retained by natural selection, it must be assumed that animals that have the capacity to have a high r_{max} must have a reproductive advantage. If this is the case, one would predict that the field studies of these species so far carried out have failed to observe a population in a time of population increase, but have only observed animals living in environments that are at carrying capacity. If the baboons and geladas are capable of supporting a high r_{max}, one would predict that a study of a population that is recovering from a reduction in numbers will find that animals in such a population will have a higher r_{max} than those so far studied. However, it should be noted that the gelada populations studied appeared to be increasing in numbers [Dunbar, 1980], but still showed a birth rate below that observed in captivity

The second possible explanation is that baboons and geladas are actually selected to have low rates of population increase. This could be for two reasons. The first is the classic K-selection argument, which would predict that low density independent mortality rates in these species allows them to reach the carrying capacity of the environment. The animals are then selected for their high competitive ability, and thus put proportionately less energy into reproduction. This results in animals postponing reproduction until they are older and putting more resources into individual young [thus increasing the time of parental care and therefore the interbirth interval]. The second reason could be that proposed by bet-hedging theory, for a situation where high infant and juvenile mortality occurs as a result of environmental fluctuations, but adult mortality is low. In this situation one would predict that the adult would be selected to "hold back" some of her resources for a later breeding attempt, rather than risk everything on an infant with a high chance of dying. If either of these reasons applies, one must assume that the capacity for higher rates of population increase expressed in captivity, is not necessarily maintained by selection.

As has been already stated, there is little evidence to suggest that baboon or gelada infants are more likely to die than are the infants of other species, and the evidence that is available suggests that they have low mortality rates when compared to other cercopithecine species with higher rates of population increase. Furthermore, there is little evidence to suggest that the mortality that does occur in baboons is due to environmental fluctuations. Two things are suggested by this evidence: firstly, high infant mortality in the cercopithecines is not linked to a low r_{max}, and, secondly, environmental unpredictability is not linked to high infant mortality in baboons. Hence, bet-hedging arguments do not seem appropriate for baboons. In gelada, there is an indication that the cold rainy season is associated with higher infant mortality [Dunbar, 1980], but the survival rate of infant and juvenile geladas is exceptionally high, with over 80% of females surviving to reproductive age [Dunbar, 1980]. These high survival rates suggest that a female runs little risk of losing her infant in the rainy season, with four out of five female offspring surviving to breed. It is therefore unlikely that gelada would have very much to gain by bet-hedging.

Conclusion

The cercopithecine species generally start to breed at an earlier age and breed more rapidly than do other haplorhine species of the same size. These are characteristics that they share with the second Old World monkey group, the colobines. It has been suggested [Aiello and Andrews, 1984] that the Old World monkeys are primarily adapted to a terrestrial or semi-terrestrial life and that the more arboreal species [e.g the forest guenons and the colobus monkeys] have become secondarily adapted to an arboreal existence. It is possible that the capacity for rapid population increase evolved alongside the increasing terrestriality of the Old World monkeys, as the expansion of savannah and open woodland habitats could be expected to select for both characteristics.

Selection for rapid breeding in the cercopithecine group appears to have been matched with selection for large body size, particularly in the open country species. These two needs, for large size and for breeding at an early age, work in opposition to each other, as selection for a large adult size will mean that the animals will take longer to reach this size. In the cercopithecines, this conflict appears to have been overcome by the disassociation of the age at reproductive maturity from the age at reaching adult weight. This characteristic explains the lack of correlation between age at first reproduction and body weight in the cercopithecine species. The cercopithecine female starts to breed at between four and six years of age but does not reach her full size until about one or two years after her first offspring is born. Although no data is available for the colobine monkeys, it seems likely that they also achieve their early breeding age by starting to reproduce before they are fully grown. In contrast, the great apes are fully grown by the time they start to produce offspring.

A second characteristic that increases the rate of population increase of cercopithecines is their high birth rate. Most species have the capacity to produce an infant every year, although in the larger species this is reduced to an infant every two years. Given the seasonal nature of many of their habitats, and their large size, this is probably the maximum birth rate that could be supported, without having multiple offspring per litter.

Some species do breed more slowly and delay reproduction to a late age. There is evidence that forest guenons do not have high rates of reproduction in the wild, with *Cercopithecus mitis* and *C. ascanius* showing long interbirth intervals and late ages at first reproduction [Cords and Rowell, 1987], and other forest species [e.g. *C. cephus, Miopithecus talapoin, Cercocebus galeritus*] showing no signs of breeding before they reach adult weight. However it appears that most of these species retain the capacity for rapid breeding and this is expressed in captivity [e.g. see Cords and Rowell, 1987]. This suggests that ancestral cercopithecines had high rates of population increase and that this character has been retained, although not always expressed, by their descendants. If the colobus monkeys are also secondarily adapted to arboreal living it can be predicted that they will be expected to share this characteristic of breeding slowly in the wild but might also retain the capacity to breed rapidly when conditions are suitable.

Species living in non-forest habitats generally have high rates of population increase, with the more opportunistic macaque species, the vervet monkey and the patas monkey all showing this characteristic. These species do not always show high rates of growth in comparison to forest species of the same size. Instead it appears that growth rates [both prenatal and postnatal] are primarily determined by adult body weight.

The question of low rates of increase in some non-forest species is discussed at length above. In short, it appears that baboons are probably selected to have a low r_{max} because they experience their environments as non-seasonal, in the sense that mortality rates are not increased because of the unpredictability of the environment. Selection has therefore operated to increase the resources put into competition as opposed to reproduction [and hence to postpone the age at first reproduction] and to producing more competitive young [thus increasing the period of parental care]. In this situation the capacity for a higher r_{max} would be seen as an relic of an ancestral adaptation that is no longer expressed in wild populations. Alternatively, this capacity might be retained by selection and be expressed at times of population growth. In the gelada, the main cause of a low r_{max} is the long interbirth interval of this species. This appears to be due to the geladas being seasonal breeders and their large size preventing year-old infants from being large enough to be weaned. In contrast, the Japanese macaque can maintain a high breeding rate but must wait until reaching a certain size before starting to reproduce, thus delaying its breeding age until it is five years old.

The case of the Japanese macaque and the gelada emphasize the importance of considering seasonal and physiological constraints when trying to understand life-history strategies. the combination of seasonal breeding and the scaling of growth rate to body size prevents the animals from increasing their rates of reproduction. In the gelada the interbirth interval appears to be "fixed" at intervals of whole years and this means that the gelada can only breed biannually. There may sometimes be an advantage in breeding at the "wrong" time and it is suggested that it might be particularly advantageous for older females to risk this. This occasional advantage appears to have helped retain the gelada capacity to breed at 18 month intervals, as is found in captivity. In the Japanese macaque their large size means that they do not reach breeding weight until after they are four years old. The seasonal breeding then means that they must delay their first birth until they are five years old. Selection for a late age at first reproduction appears to have been particularly strong, with animals in captivity and those that are provisioned still waiting until they are five years old to breed.

The results of this chapter need to be viewed in the light of the results of the analyses carried out on all primates, and compared to variation in other groups of primates. Several questions are raised about the different selective forces that might bring about high or low rates of increase in primates. In addition, the different life-history strategies of savannah-living primates can be considered with reference to human evolution. This will be done in the last chapter of this thesis, in a general overview of the results.

Chapter 7

Summary

The general pattern of variation in life-history parameters in the cercopithecines reflects those found for primates as a whole. An important difference is that, within the Cercopithecinae, parameters that influence the rate of population increase [the age at first reproduction, birth rate and longevity] do not vary predictably with body weight. As would be expected from this, r_{max} is also not correlated with body weight. Possible reasons for these differences are discussed. As compared to other Old World haplorhines, the cercopithecines are shown to be fast-breeding but having similar rates of development for their body size. It is suggested that the high breeding rates might be viewed as being a result of the adaptation of the cercopithecines to a wide variety of climates and also to ground-living.

Within the group, species that are found in more variable habitats tend to have a higher r_{max} than do closely related species in more stable, forest habitats. Exceptions to this rule are found with the baboons and the Japanese macaque. These species are found in unpredictable, seasonal habitats, but have a lower r_{max} than related species. Some suggestions are made as to why these exceptions should occur, and it is postulated that the selective forces are different in different species. Mortality data suggest that the high r_{max} of the vervet monkey [and possibly the of patas monkey] can be explained by higher mortality rates before breeding age. This would imply that the faster-breeding species can be considered as "r-selected". However, mortality data from the macaques does not support this view, and further studies of mortality rates will be needed before this question can be resolved.

Chapter 8

General conclusions

This thesis began with a general overview of previous work, both practical and theoretical, that has been carried out on life-history strategies. In this chapter I will look at the results of this study in relation to these previous studies. The chapter starts with a general discussion of the life-history strategies of different primate groups. It then looks at the original aims of this thesis, and assesses the extent to which the questions posed at the end of Chapter 1 have been answered. A discussion of human life-history characters and their implications for theories of human evolution is included. The chapter ends by suggesting some questions that have been raised by this research. The methodology used throughout the thesis is evaluated and alternative approaches are suggested. Further lines of inquiry that might prove fruitful are suggested.

Life-histories of different primate groups

In the *following* discussion relatively high *breeding rates and* relatively *high developmental* rates that are associated with unpredictable habitats are referred to as r-selected characters, whereas relatively low breeding rates and relatively low developmental rates are associated with predictable habitats are referred to as K-selected characters. Although it is possible that the r-selected characteristics might also be explicable in terms of bet-hedging, i.e. with unpredictable habitats effecting mainly adult mortality and not juvenile mortality, this is considered to be unlikely. This point is discussed further later in this chapter.

The strepsirhines

The most obvious difference found between primate groups is between the strepsirhines [lemurs and lorises] and the haplorhines [tarsiers, monkeys, apes and humans]. It is perhaps worth noting that the division into haplorhines and the strepsirhines rather than prosimians [lemurs, lorises and tarsiers] and anthropoids [monkeys, apes and humans] is supported by this study. In most cases, tarsiers appear to be more similar to other haplorhines than to the strepsirhine species. The characteristics of tarsiers are discussed more fully later in this chapter

The differences between haplorhines and strepsirhines have been discussed at length in chapters 3-6 and will not be dealt with in detail here. Briefly, it can be said that, when compared to haplorhines of the same size, strepsirhine species have a lower prenatal parental investment and a higher postnatal investment. However, for a given body size, the potential rate of population increase [as measured by r_{max}] of the two groups is about the same. It is suggested that the low prenatal parental investment of the strepsirhines is connected to their relatively low basal metabolic rate [BMR] and to a seasonal scarcity of resources. Postnatal growth rate does not appear to be linked to BMR, but the reasons for this are unclear.

The Malagasy strepsirhines

The strepsirhine species in Madagascar are as diverse in their life-histories as they are in their ecologies and social systems. The species for which good data are available are the lemurs [*Lemur* species and *Varecia variegatus*], the mouse and dwarf lemurs [*Microcebus* and *Cheirogaleus* species] and a sifaka [*Propithecus verreauxi*]. Some data are also available for sportive lemurs [*Lepilemur mustelinus*], gentle lemurs [*Hapalemur griseus*] and the indri [*Indri indri*].

The mouse and dwarf lemurs are the smallest of the Malagasy strepsirhines and are characterized by early breeding and high birth rates and by high growth rates during gestation and lactation. Although this study uses data that give these species a breeding rate of one litter per year [i.e. two offspring per year], it is possible that some species may be capable of producing two litters per year in good conditions [Martin, 1972b]. If this is the case, these species would have a relatively high r_{max}, but their small size means that only a single litter a year gives them an r_{max} that is about "normal" or slightly below the predicted for their size.

In many ways the ruffed lemur [*Varecia variegatus*] shows characteristics that are very similar to the mouse and dwarf lemurs. Despite being a fairly large animal [about 3kg] the ruffed lemur regularly gives birth to twins and, in captivity, can start breeding before it is two years old. These characteristics mean that it has a higher relative r_{max} than any other primate in this study In addition, the ruffed lemur shows extremely high rates of growth during both gestation and lactation, although both of these growth periods are very short for a primate of its body size. The exceptionally high relative r_{max} and high relative parental investment of the ruffed lemur are all the more surprising when it is realized that it is a species confined to humid rainforest. Of the species included in this study, the ruffed lemur is the only rainforest species to show a relatively high r_{max} and, as such, is a challenge to the ideas expressed above, i.e. that species in forest areas will have a low relative r_{max}. One possible explanation for this apparent anomaly is found in a study of the nesting behaviour of this species. Pereira *et al.* [1987] look at a captive group of *Varecia* living in forest enclosures in North America, and discuss nesting and parental behaviour. One striking detail of their study is that the females built and used nests on or near the ground. This differs from other nest-building primates which build nests in trees. If such behaviour occurs in the wild, it could have two important consequences for the life-history of the ruffed lemur. Firstly, the increased vulnerability of ground nests to predators would select for rapid postnatal growth, and secondly, if infant mortality is high because of increased predation the animals could become r-selected. Further studies of the ruffed lemur in the wild are now under way and it is to be hoped that the results will help us to understand their unique characteristics.

The other lemurs [*Lemur* species] and the indriids [sifakas and the indri] are slower-breeding and take longer to develop than the smaller species and the ruffed lemur. These species have a lower relative r_{max} and relatively longer gestation periods. In the lemurs and the sifaka, the relatively longer gestation result in a neonate that has about the same relative size as those of the mouse lemurs, whereas the indri produces a relatively large neonate. This means that the lemurs and the sifaka have a relatively lower daily parental investment during pregnancy than do the other species mentioned. This relatively low foetal growth rate is also found in the sportive lemur and in the gentle lemur. Few data are available for postnatal growth rates in these strepsirhines, but it appears that at least two species of lemur [*L. catta*and *L. fulvus*] have relatively low postnatal growth rates as well as their relatively low foetal growth rate.s Data from a hand-reared sportive lemur suggest that this species also has a relatively low postnatal growth rate.

It therefore appears that the different life-histories of these species can be split into two groups; the relatively fast-breeding, fast-developing species [mouse lemurs, dwarf lemurs and the ruffed lemur] and the relatively slow-breeding, slow-developing species [the "true" lemurs, the sifaka and possibly the sportive lemur and gentle lemur]. [The indri appears to be intermediate between these groups as it has a relatively low r_{max}, but appears to have a high foetal growth rate for a strepsirhine. More work is needed to understand the life-history of this species.] The dichotomy found between most lemurs cannot be explained by differences in ecology alone. The mouse lemurs and dwarf lemurs are characteristic of edge habitats and secondary forest, and the ruffed lemur may be constrained to rapid breeding by a habit of ground nesting. Hence, the r-selected characters of these species can be explained. However, it is notable that several members of the slow-breeding group are also found in very seasonal and unstable habitats. The ring-tailed lemur, *Lemur catta*, in particular, is found in the dry seasonal forest and woodland of South and Southwestern Madagascar, but shows no evidence of being more r-selected than the similar sized brown lemur, *Lemur fulvus*, which characteristically inhabits more forested and less seasonal areas. Both species breed for the first time at about two years old, both produce about one infant every two years, both have a foetal growth rate of just over 0.6 grams per day and a relatively low postnatal growth rates [with that of the smaller *L. fulvus* being slightly higher]. Similarly, Rasmussen [1985] noted that species of *Lemur* and *Varecia* from more tropical areas have larger litter-sizes than those from more seasonal areas, i.e. the opposite pattern to that predicted by r/K theory.

It is possible that the reason for the apparent lack of strong correlation between life-history characters and ecology in these species is that they have not yet had time to adapt to their environment. It is believed that many species [at least 14] of Malagasy primates have become extinct since the arrival of humans on the island, about 2000 years ago, and this is presumably due to the effects of hunting and competition for resources by humans [Richard, 1985]. As these extinctions are recent in terms of evolutionary change, it is probable that species may be found in areas for which they are not completely adapted, and where they would have once been excluded by other, now extinct species. Sadly, many of these species may themselves become extinct before natural selection can act to adapt them slowly to their new habitats.

The Lorisids

The lorisids contain two groups, the slow-moving lorises and pottos [lorisines] and the faster-moving bushbabies [galagines] [e.g see Bearder, 1986]. The differences in locomotion probably reflect differences in relative metabolic rate, with this study indicating that three out of four of the lorisine species have basal metabolic rates [BMRs] that are below 50% of the expected "Kleiber" value, whereas most of the galagine species have BMRs that are from 63 to 78% of the expected "Kleiber" value. [*Euoticus elegantulus* is reported to have a BMR of 88% of the expected "Kleiber" value (Hildwein, 1972), but this may be an overestimate due to young animals being used]. The fourth lorisine species [*Arctocebus calabarensis*] has a BMR just under 65% of the expected "Kleiber" value.

The generally lower relative BMRs of the lorisine species may be linked to their particularly low relative growth rates. The slender loris, *Loris tardigradus*, and the potto, *Perodicticus potto*, both have very low prenatal and postnatal growth rates for their size, with their postnatal growth rates being as low as those of Old World haplorhines of the same size. However, the slow loris [*Nycticebus coucang*] and the angwantibo [*Arctocebus calabarensis*] have only relatively low prenatal growth rates and their postnatal growth rates are about normal for strepsirhines [i.e. relatively higher than the Old World haplorhines]. This pattern of growth rates suggest that the slender loris and the potto, alone of the primates discussed in this study, are not capable of [or not selected for] raising their metabolic rates during either gestation or lactation. The reasons why these two species should be restricted to low growth rates during both gestation and lactation is not clear from the present knowledge of their diets and general ecology. It is particularly surprising to find a very low growth rate in the potto, as this is a forest species feeding mainly on fruit and gum, two foods that are not usually considered to be either difficult to digest, or particularly limited in distribution. The reasons for these differences between the lorisine species may be explicable when more is known about their ecology and metabolism. Despite their relatively low rates of postnatal growth, it is worth noting that neither the slender loris nor the potto have very low rates of population increase for their size, with both species starting to reproduce at the expected age and having "normal" birth rates. This supports the idea, suggested in Chapter 6, that low growth rates and low metabolic rates may not be a disadvantage in terms of reproductive output.

All four of the lorisine species looked at in this study are typically found in tropical forest, but only the slow loris is restricted to continuous canopy forest. Of the other three species, the potto is found in both primary and secondary forest, the slender loris occurs in rain forest and woodland and the angwantibo is restricted to edge forest and tree fall zones [Bearder, 1986; Wolfheim, 1983]. It might therefore be predicted that if one was to arrange these species from the relatively slowest-breeding and relatively latest-maturing to the relatively fastest-breeding and relatively earliest-maturing, the order would be: the slow loris, the potto, the slender loris and the angwantibo [with the potto and the slender loris being relatively close to one another].

Both of the smaller species, the angwantibo and the slender loris produce an infant every six months and become sexually mature in the first year of life [Bearder, 1986; Neischalk and Maier, 1984]. This means that, when compared with other strepsirhines species, the angwantibo does appear to have a high birth rate for its size, as does the similarly-sized slender loris. The angwantibo has a slightly early age at first reproduction for its size and the slender loris a slightly late age at first reproduction for its size. These characters give the slender loris a "normal" relative r_{max} for a strepsirhine and the angwantibo a slightly high relative r_{max} for a strepsirhine. The two larger species, the potto and the slow loris both produce one infant a year [Bearder, 1986], giving the potto a "normal" birth rate for a strepsirhine of its size and the smaller slow loris a relatively low birth rate for a strepsirhine. The potto first breeds in its second year, giving it a "normal" age at first reproduction and slightly low relative r_{max} for a strepsirhine of its size. It therefore appears that the relative r_{max} values of the two lorisines in less predictable habitats are higher than that of the potto. There are no data available for the age at first reproduction of the slow loris. It will be interesting to see if further study of this species will reveal that it does have the late age at first reproduction predicted for a primary forest species, and hence a relatively low r_{max}.

The second group of lorisids, the bushbabies, are generally found to have relatively high metabolic rates and high prenatal growth rates when compared to the lorisine species. These species are particularly interesting because they are found in habitats ranging from tropical

Table 8.1

Reproductive parameters of bushbabies

Species and habitat	Life-history parameters [1]			
	M	AR	BR	r_{max}
West Africa - rainforest				
G. alleni	250	1.0 (-)	1.3*(-)	0.49*(-)
G. demidovii	65	1.0 (+)	1.2 (-)	0.48 (-)
E. elegantulus	290	-	1.0*(-)	-
East Africa- forest				
G. garnetti	780	1.6 (-)	1.8 (+)	0.51 (+)
G. zanzibaricus	140	1.0 (-)	2.4 (+)	0.79 (+)
G. braccatus	285	2.0 (+)	2.2 (+)	0.50 (-)
G. senegalensis	215	-	2.0(+)	-
South Africa- variety habitats, including woodland				
G. crassicaudatus	1205	2.2 (+)	1.6 (+)	.40 (+)
G. moholi	190	1.0 (-)	3.2 (+)	.96 (+)

1) M=average adult body weight [to nearest 5 grams];AR =Age at first reproduction [years]; BR =Birth rate [no.young/year]; (-) or (+) indicates whether the residual value is positive or negative, relative to the major axis best-fit line for strepsirhines.

*) Estimated figures, not used in other analyses in this thesis.

rainforest [e.g. *Galago alleni*] to woodland [e.g. *G. senegalensis*]. The work of Nash [1983] was mentioned in Chapter 1. Nash discusses the birth rates of nine taxa of bushbabies, found in three areas of Africa [these taxa represent nine species if Nash's three subspecies of *G. senegalensis* are regarded as full species (*G. senegalenis, G. braccatus and G. moholi*) and the two *G. crassicaudatus* subspecies are also treated as distinct (*G. crassicaudatus* and *G. garnettii*)]. Table 8.1 summarizes the work of Nash on birth rates, with additional data on age at first reproduction and r_{max} added from this study. The West African species are found in rainforest, where the climate is stable and where there is a low probability of periods of drought or extreme temperature variations. The other two areas are more variable, with the East African area being the most liable to drought and the South African climate having more extreme temperatures and also suffering from periodic drought. It can be seen from table 8.1 that the South African species have relatively high r_{max} values, as do two of the East African species. Two species from West Africa have relatively low r_{max} values and it is probable that the third [*E. elegantulus*] will also be found to have a relatively low r_{max}, as its birth rate is probably low. Even if it started breeding at one year of age, its r_{max} would still be low for a primate of its body size. The results therefore seem to indicate that the bushbabies can be broadly separated into r-selected species in the more seasonal areas and K-selected species in rainforest. However, the delayed reproduction of *G. braccatus* appears to deserve further investigation.

The tarsiers

As previously noted, tarsiers have been included in a group with the monkeys and apes rather than with the Malagasy lemurs, lorises, pottos and bushbabies. As expected from the work of Leutenegger (1973) and Martin [1975], the tarsiers are found to have the neonatal weight one would predict for a monkey or ape of their size, rather than the relatively smaller neonate found in other primates. The grade difference between haplorhines and strepsirhines is also found with total litter weight. However, the production of one offspring per litter by the tarsiers, as compared to the twinning found with other small haplorhine species [i.e. marmosets and tamarins], means that the relative weight of a tarsier litter falls between that of other haplorhines and that of strepsirhines. This effect was also noted by Leutenegger [1973].

Other parameters that were found to show clear grade distinctions were age at first reproduction and growth rates. Data for age at first reproduction were available for only one species [*T. spectrum*], which falls with other haplorhine species. The growth rate data were for a second species [*T. bancanus*], with the postnatal growth rate data being for a hand-reared individual. Despite having a very long gestation length for its weight the relative foetal growth rate of *T. bancanus* is clearly higher than that of most strepsirhine species and falls along the same line as that of other haplorhines. The relative postnatal growth rate falls between that of the fast-growing strepsirhines and New World monkeys and the slower-growing Old World monkeys and apes. If tarsiers do have a relatively low basal metabolic rate [BMR], [as suggested in Chapter 3] these relative growth rates suggest that the BMR might be raised during gestation, and possibly slightly raised during lactation.

These results indicate that the life-histories of tarsiers are fully in accordance with their being grouped with monkeys and apes, rather than with strepsirhine primates. Unfortunately, there is not enough data to make a comparison of the life-histories of the three species of tarsier, although their very similar ecologies and sizes suggest that most life-history parameters will be similar as well. As noted by Bearder [1986] the infants of *T. bancanus* are better developed at birth than are the infants of the other species, and this may be linked to the relatively long gestation of this species. It might be expected that the gestation periods of *T. spectrum* and *T. syrichta* will be shorter, but there are no good data on the gestation periods of these species, as yet.

New World Monkeys

The marmosets and tamarins

This group of New World primates is particularly interesting as these species show several reproductive and social characteristics that set them apart from other primate species. Several of these features have been discussed in previous chapters, and therefore will be listed only briefly here. Marmosets and tamarins are characterized by a very high birth rate [up to four young a year], an early age at first reproduction [about 18 months-2 years] and high growth rates during gestation and lactation, which result in high litter weight. Even if their small body size is taken into account, these species develop and breed rapidly when compared to most other primates. These characteristics are therefore precisely those that would be predicted for an r-selected species. As marmosets and tamarins are primarily inhabitants of secondary forest and edge species, the interpretation of their life-history parameters as being r-selected is in accordance with their ecology.

However, although the situation appears, at first sight to be clear cut , a closer look at the social structure of the marmosets and tamarins shows that they have several characteristics that are usually regarded as being typical of K-selected animals. These characteristics include a high degree of paternal care and a social system that appears to result in adult females delaying reproduction until they become dominant in the group [Goldizen, 1986]. The first of these characteristics, paternal care, can be seen as an adaptation that allows the production of two fast-growing infants. The relative litter weight of the marmosets and tamarins is high and it is probable that a female could not cope with the demands of both lactation and the carrying of infants. Only by the male carrying the infants can the female supply them with enough milk to grow rapidly, thus allowing her to wean the infants quickly and produce two litters a year.

However, the delayed breeding of these species is not so easily explained. It was suggested in Chapter 5 that this characteristic could be due to the gum-eating behaviour of some species.This could give them a stable diet, despite their apparently unstable habitats, and thus allow them to be secondarily K-selected. It is therefore assumed that these species were originally selected to breed and develop rapidly, both through selection for small size and selection for relatively rapid breeding and development. This view that marmosets and tamarins have been selected to be small [the "dwarfing hypothesis"] is supported by evidence that several characters of the marmosets and tamarins indicate that they were originally derived from a larger ancestor, that did not produce twins [Ford,1980]. As twinning does not necessarily occur because of the small body size of these animals [see Chapter 4, this study] and they also have the capacity to breed at a relatively early age, the evidence also suggests further selection for a high rate of population increase.

Once these species had become adapted for colonizing areas of edge and secondary forest, it is possible that there was increased selection for feeding on gum sources, a food source that can be reliably found even in periods when fruit and insects are scarce [Ferrari, 1988]. In the marmosets [including the pygmy marmoset] the lower front teeth are adapted for gouging trees in order to procure gum [Coimbra-Filho and Mittermeier, 1978]. The claws of both marmosets and tamarins have also been suggested to be an adaptation to gum-feeding [Garber, 1980]. The ability to feed on gum may give all these species, and particularly the marmosets, a stable food supply, thus effectively altering their experience of their edge forest environment from that of an unpredictable habitat to that of a more predictable one.

It might therefore be predicted that a group of marmosets colonizing an area of secondary forest would rapidly expand their population numbers to reach the carrying capacity of the environment. Despite the possibilities of fluctuations in food supply, both due to seasonality and to spatial changes in areas of secondary forest, these animals could use the predictable gum supplies to support them and would therefore suffer relatively little mortality through food limitation. Once the population has reached carrying capacity, it can be seen that two strategies are open to the young adult marmoset reaching breeding age. The animal can remain in its natal area, where the food supply is known and reliable, or it can leave its natal group and attempt to colonize a new area of secondary forest. If a female remains in her natal group she is unlikely to gain by breeding at an early age. If resources are limiting, it is probable that older and more dominant females will have prior access to them and will therefore be more successful in raising young. The female will therefore do better to delay breeding until she is able to be certain of having a high enough rank to secure adequate resources for her young. Similarly, a young adult male might be prevented from breeding by older and more dominant males. This "staying at home" strategy therefore carries the cost of delayed breeding, but has the advantages of not risking the dangers of unknown territories. In addition, the young adults [of both sexes] can increase their fitness in their natal group by helping to raise their own siblings. However, if an animal is born into a large group it is likely that there will be several older adults dominant to it and the costs of delaying breeding until all of these adults have died or lost their high rank may outweigh the advantages of staying at home. In this situation, young adults may do better if they risk "leaving home" and therefore have the advantage of being able to breed at an early age.

It can be seen that this situation would select for females that would not waste resources on an unsuccessful breeding attempt. In the marmosets it appears that this prevention of breeding is achieved by young females responding to the presence of an older female by suppressing fertility [Abbott, 1984]. However, once the dominant females influence is removed the younger animal will begin to breed. As these species are primarily colonizing animals, the ability to breed at an early age has been retained and will be expected to be expressed in the wild when it is advantageous for young animals to leave their natal groups and colonize a new area. This scenario gives scope for several interesting predictions regarding the sociobiology of marmosets and tamarins, many of which could be tested in the field or laboratory. Some suggestions for future research on these animals are therefore made at the end of this chapter.

Geoldi's monkey

The relationship of Geoldi's monkey, *Callimico geoldii*, has been disputed. It has been suggested that it is closely related to marmosets and tamarins, that it is better thought of as a cebid monkey and that it is better dealt with as a member of a separate monospecific group [e.g. see Sussman and Kinzey, 1984]. However, recent evidence suggests that *Callimico geoldii* shares derived chromosomal features with the marmoset and tamarin group but that it branched from this group before the split between marmosets and tamarins [Dutrillaux *et al.*, 1988]. Geoldi's monkey has about the same body size as the larger tamarins and, like these species, it lives in secondary and edge forest and feeds mainly on fruit and insects.

Geoldi's monkey differs from the marmosets and tamarins in giving birth to single young, but it shares their ability to produce two litters a year and in having the capacity to breed at an early age. These characteristics Geoldi's monkey a relatively high birth rate, a relatively early age at first reproduction and a relatively high r_{max} value. A relatively high foetal and postnatal growth rate is also found in *Callimico*, and, as in other New World species with these characteristics, this species also exhibits a high degree of paternal care.

The life-history characteristics of Geoldi's monkey are therefore very similar to that of the marmosets and tamarins, but it should be noted that they are also the characteristics of a cebid monkey, the owl monkey, that is similarly found in secondary and edge forest. This supports the idea that secondary habitats will select for rapid breeding and that paternal care can lead to high levels of paternal investment, but clues to its taxonomic position cannot be found in this analysis of its life-history characters.

The cebid monkeys

It was shown in Chapter 5 that many of the cebid monkeys are characterized by having a relatively low rate of population increase. Several groups have this character, including spider monkeys, capuchin monkeys, the squirrel monkey, the dusky titi and the white-faced saki. Relatively low r_{max} values are found with these species, because they have having both a relatively low birth rate and a relatively late age at first reproduction. For example, the relatively small capuchin monkeys give birth for the first time at 4 or 5 years of age and breed about about once every 18 months, as compared to the annual breeding, starting at about two years old seen in some similarly sized lemurs. Spider monkeys first give birth at 5 or 6 years and give birth about once every 2.5-3 years, whereas cercopithecine monkeys of a similar size can breed at 4 or 5 years of age, and then give birth annually or biannually.

The degree of parental investment of cebid species with a relatively low r_{max} is not completely understood. They appear to have relative foetal growth rates and neonatal weights that are similar to those of other haplorhine species. However, in some species the postnatal growth rate may be higher than is found in most other haplorhine species of the same size. This is not certain, as there is a lack of data from mother-reared infants of cebid species and it is not clear as to whether a relatively high postnatal growth rate is found only in species which have paternal care, or whether it is a common trait in all New World species.

Although most cebid monkeys have a relatively low breeding rate and a late age at first reproduction there are some exceptions, notably the owl monkey and the howler monkeys. It is these exceptions that suggest that the low breeding rates and late age at first reproduction of the remaining species can best be explained by their living in stable forest habitats. The species that have relatively high r_{max} values for cebid monkeys [although not for haplorhines generally] are also found in some of the most varied and harsh habitats occupied by any cebid.

The howler monkeys are interesting in that they are probably the nearest available equivalent to the opportunistic Old World monkeys. In a similar way to the Old World monkeys, female howlers breed at a early age, at about 3.5-5 years old [Crockett and Eisenberg, 1986] and probably before they reach adult weight. [This is based on an estimate of 6.5 years for age at reaching adult weight from Rudder (1979).] Breeding rates are also similar to many Old World monkeys, in that howlers can give birth annually in captivity [Shoemaker, 1979] and probably breed annually or biannually in the wild [Glander, 1980; Crockett and Eisenberg, 1986]. The other cebid that has a high relative r_{max}, the owl monkey, does not breed before it reaches adult weight. Instead it has a high postnatal growth rate and a relatively early age at first breeding [for a cebid of its size] of about 2.5 years as well as the capacity [at least in captivity] to produce three young every two years. Given the recent suggestion that the owl monkey is in a fact a group of several species [Hershkovitz, 1983], it will be interesting to see if owl monkeys from different areas and/or habitats also differ in life-histories.

If the differences in strategy among the cebid monkeys can be explained by the classical distinction between r- and K-selected species, one might expect that owl and howler monkeys would have higher mortality rates than other cebid species. There are no data on mortality rates of owl monkeys, but some data are available for mantled howler monkeys. These can be compared to mortality data from another large-bodied cebid species, black spider monkeys. These data suggest that infant mortality rates, in the first year of life, are similar for both species, with 33% and 38% mortality respectively [Symington, 1988; Glander, 1980]. Similarly the mortality rates of the adult howlers [age 4-15 years] were similar to those estimated for adult spider monkeys [about 3% for both species]. However, there are no records of mortality rates for howler monkeys aged between 1 and 4 years old, as it was not known if animals had left the group to join another or whether they had died. In the species studied, both male and female howler monkeys left their natal groups before breeding, whereas only male spider monkeys did so. It might therefore be expected that female howlers will suffer a higher rate of mortality than will female spider monkeys. If the howler monkeys can be considered as being more r-selected than spider monkeys one would expect that further research should show a higher mortality rate in young adults of the former species. Conformation of this view awaits data on mortality rates from both groups.

Old World haplorhines

Old World monkeys

Chapter 7 has discussed the the life-histories of one of the two Old World monkey subfamilies, the Cercopithecinae, in some detail. The points made in that chapter will not be reiterated here and the reader is referred to the summary of Chapter 7 for a brief description of the life-histories of the cercopithecine monkeys.

The second subfamily of Old World monkeys, the Colobinae, are not as well represented in this study as the cercopithecine monkeys. Data on demography are available for only a few species. Like the cercopithecine monkeys, the colobine monkey species have high rates of population increase for haplorhines of their size, this being due to both a relatively early age at first reproduction and a relatively high birth rate. As nearly all the data for these species are from captive animals, it is difficult to determine whether forest species [e.g. *Colobus* species] have more r-selected characters than do species found in more severe habitats [e.g. *Presbytis entellus*].

Growth rate data are virtually non-existent for the colobines, with no foetal growth rates being available and postnatal growth rate data being available for only one species, a hand-reared black and white colobus monkey [*C. polykomos*]. This species has about the postnatal growth rate expected for an Old World monkey. Given the relatively low BMR found for one colobus species and the link found between relative postnatal growth rate and relative BMR in strepsirhine species, it will be interesting to see whether a similar link can be found in colobines.

The apes

Data on the apes comes mainly from two lesser apes, [the lar gibbon, *Hylobates lar*, and the siamang, *Symphalangus syndactylus*] and three great apes [the gorilla, *Gorilla gorilla*, the chimpanzee, *Pan troglodytes*, and the orangutan, *Pongo pygmaeus*]. Most of these species have a low birth rate and a late age at first reproduction for their body size. However, the gorilla does not share these characteristics, and it has a slightly higher birth rate and earlier age at first reproduction than would be expected for a haplorhine of its size, and hence has a high relative r_{max}. [Given the large sexual dimorphism of the gorilla, it is worth noting that this is also true if female body weights are used in place of average adult body weights].

All of the demographic data from wild populations is taken from mountain gorillas in Rwanda and Zaire. The high relative r_{max} of the gorilla might be explained by its preference for edge and secondary forests and occurrence in mountainous areas, habitats that would be expected to select for a large body size but relatively rapid breeding. It might therefore be predicted that the lowland gorilla will have a lower relative r_{max}, as it is found in a less harsh environment than the mountain gorilla. Confirmation of this awaits further study.

Although gibbons, siamangs and orangutans are restricted to rainforest and would therefore be expected to have relatively low r_{max} values it is perhaps surprising that the more ecologically opportunistic chimpanzee also has a relatively low r_{max}. However, the demographic data used here come from the forest population at Gombe in Tanzania, and it is possible that further studies on populations found in more open areas of woodland and savannah may show different results.

As noted in Chapter 6, the apes tend to have a lower relative postnatal growth rate than other Old World haplorhines. It seems likely that this is associated with their late maturation and is another feature of their K-selection.

Chapter 8

Discussion

At the end of Chapter 1, some questions were listed that I considered were raised by previous studies on life-histories and that were relevant to primate evolution. The foregoing summaries of the different strategies of each primate group allow us to address these questions in some depth. Here I repeat those questions and give the answers suggested by this study.

1) How much of the variation in primate life-history parameters can be explained by body size?

A very large amount of the variation in most life-history parameters can be explained by variation in body size, as measured by body weight. The precise amount varies from about 48% for gestation length to over 92% for litter weight and foetal growth rate. This means that, as in other animals, it is extremely important to take body size into account when looking at primate life-history parameters.

2) Do primate life-history parameters vary with body weight, and with each other, in the same way as in other mammals? If not, what is the pattern [if any] of their covariation?

In chapters 4 to 7, we considered the way in which several life-history parameters varied with body weight, with metabolic rate and with one another. In a broad sense it can be said that the patterns of covariation in primates are similar to those found in other mammals. As expected from previous studies, it was found that primates, of all body sizes, are usually slower-developing and slower-breeding than other mammals of the same size. However, larger primates develop and breed more slowly than do smaller primates, in the same way as other larger mammals generally develop and breed more slowly. These patterns are shown in bivariate plots as grade differences between primates and mammals, with the primates scaling to about the same exponent as other mammals, but with their best-fit line lying above or below that of the mammals, depending on the parameter concerned.

Despite this general similarity in scaling parameters, it was noted in Chapter 4 that there was some indication that the primates differed from other mammals by more than grade differences. Several measures of "physiological time" were taken and compared to equivalent measures from other organisms. In particular the finding of Lindstedt and Calder [1981], that all animals tend to have the same number of physiological events in their lives, was considered for primates. It was found that the primates differed from other mammals in that larger primates will be expected to spend a greater proportion of their lives growing to maturity and will give birth to a smaller number of offspring. This appears to be mainly due to the larger monkeys, especially baboons and spider monkeys, and the apes being particularly K-selected and having a very slow maturation.

3) Can the variation in primate life-history parameters be explained by environmental predictability and/or variation and, if so, how?

The measures of environmental predictability that were used revealed several links with primate life-history parameters. These links are found at two levels, the first follows from a correlation between environmental predictability and body weight, and the second is a correlation between environmental predictability and relative values of life-history parameters.

Species that are found in rainforests and in savannah habitats tend to be large in size. As developmental and breeding rate variables are strongly correlated with body weight, the rainforest and savannah species are generally slow to develop and breed. In contrast, species that are found in secondary forest, edge habitats and woodland are smaller, faster-breeding and develop more rapidly. Overlaying this pattern of variation is the covariation with environment that cannot be explained by body weight, referred to as the residual variation. The measure of population increase used, r_{max}, has residual variation that can be partly predicted from a knowledge of environmental variability. Generally speaking, species that are found in less predictable habitats have a higher residual r_{max} , this being caused by a lower residual age at first reproduction and/or a higher relative birth rate, although there are exceptions such as the cercopithecine monkey species discussed in Chapter 7. In contrast to these correlations, between residual r_{max} and environment, there is no strong evidence that residual parental investment is correlated with any measure of environmental variability used here.

4) Do patterns in life-history variation vary within and between primate groups? Similarly, do the apparent causes of variation vary from group to group?

The short answer to the first of these questions is yes. In some groups, such as the strepsirhines and the marmosets and tamarins, individuals appear to achieve a relatively early age at first reproduction by growing rapidly to adult weight. In others, such as the Old World monkeys and howler monkeys, an early age at first reproduction is associated with breeding before adult weight is reached. In the smaller species the breeding rate can be increased by producing more than one offspring per litter, whereas in larger species it appears that the only way breeding rates can be raised is to decrease the interbirth interval. Differences in the growth rate patterns of different taxonomic groups are also found, and these were discussed in Chapter 6.

The answer to the second part of this question is less unequivocal. This study suggests that the basic causes of high or low rate of population increase are very similar in all primate groups. Other things being equal, species that are large-bodied have lower rates of population increase than species that are small-bodied. Species that experience unstable environments will have higher residual rates of population increase than species that experience more stable environments. However, other things may be different. For example, the relatively low basal metabolic rates of the strepsirhine species may effect their growth rates, paternal care in some New World monkeys may allow them to have relatively high growth rates and large litters, and the highly seasonal environments of some cercopithecine monkey species may impose restraints on when and how often they can breed.

5) Is there any difference in the patterns of variation seen at different taxonomic levels?

It appears that the basic patterns of variation are similar when small groups of closely related species are examined and when a broader approach is used. Although some differences are apparent, these most probably occur as a result of the methodology used rather than being a reflection of "real" differences. For example, it was noted in earlier chapters that correlations of relative r_{max} with climate were apparent at lower taxonomic levels but not when larger groups were considered, whereas the opposite was found when looking for links between habitat and relative r_{max}. In the case of the correlations with climate, the comparison being made is between a measure of the environment and a reproductive parameter. It is unlikely that a low rainfall will effect a small bushbaby in the same way as it would a large baboon. It will therefore be expected that when comparing "like with like", e.g. a bushbaby with a bushbaby, the effects of differing climate conditions will be more apparent than when comparing very different species. It seems probable that the loss of correlations between habitat and relative r_{max}, when moving from a higher to a lower taxonomic level, is probably due closely related species being found in similar habitats that are not separated in the habitat categories used in this work. For example, three closely related species of lorisids [the potto, the slender loris and the slow loris] are all classified as being "general forest" species, despite their occupying secondary forest and woodland to different degrees.

6) What are the implications of these results, as regards theories of life-history evolution?

In the introduction to this thesis several different theories of life-history evolution were discussed. Two of these, r/K selection theory and bet-hedging theory, explained different strategies as being a result of environmental variability. A third explained delayed reproduction as being due to the influence of age-specific fecundity, with reproduction being delayed because the advantages of increased fecundity when older outweighed the advantages of producing when young, with its increasing of mortality. Finally, we looked at non-adaptive reasons for variation in life-histories, such as the constraints of body size and lack of genetic variation.

To take the last idea first. This study gives a great deal of support for the idea that the evolution of primate life-histories are constrained by a number of factors. Perhaps the most important of these is body weight, which explains between about 50% and 95% of the variation in all life-history parameters discussed in this study. In particular the growth rates of young [both before and after birth] appear to be tightly constrained by adult size, i.e. either by the weight of the mother or by the eventual full-grown weight of the infant. There is also some evidence that growth rates may be constrained by the mother's basal metabolic rate [BMR], which is, in turn, constrained by limited resources. However, the evidence for this is tenuous, as the capacity of some species to raise their BMRs during reproduction may mean that the growth rate appears not to be correlated with the BMR when the latter is measured in non-reproductive animals.

Another important constraint on life-history parameters is that of seasonality. Animals in seasonal environments are frequently found to produce their young at one season of the year only. This is particularly true of smaller animals that are more effected by fluctuations in climates and resources. The effect of a restricted breeding season on life-history evolution may be to prevent small adjustments in parameters such as the age at first reproduction and the birth rate, as these are constrained to be in units of 12 months. In the absence of small adjustments, selection for change in reproductive output must either operate to give very large alterations, [e.g by selecting for animals that breed a year later or a year earlier than "normal"] or it must act on the birth rate via the size of the litter.

The effects of seasonality were in some cases thought to remove the high correlations seen between life-history parameters and body size. For example, in the the cercopithecine monkeys correlations between age at first reproduction and body weight were insignificant as nearly all these species breed first at four or five years old. The combination of the environmental constraint of seasonal breeding and the physiological constraints of body size on life-history characters may sometimes combine to prevent an animal from reaching its "optimal strategy". For example, it was suggested in Chapter 7 that gelada baboons are selected to breed at an early age and to have a high birth rate. However, the combination of their large adult size and seasonal breeding means that they are constrained to breed only once every two years. Similarly, most Malagasy species breed only once a year and therefore usually reach reproductive age at one or two years, but their birth rate varies because of a varying propensity to produce twins.

Despite the constraints on life-history evolution, there is still evidence to suggest that at least some of the variation observed is due to adaptation. There is evidence to suggest that age-specific fecundity, combined with the effects of seasonality, acts to delay reproduction in the Japanese macaque. It is probable that similar effects will be found in other species where environmental conditions will mean that a young adult female breeding too soon runs a high risk of loosing her offspring and/or her own life.

Further variation is correlated with the predictability of the environment. This variation cannot be explained in a simplistic way with one type of habitat selecting for rapid breeding and/or rapid development whilst another type selects for the opposite characters. Instead one must consider the way in which an animal experiences its environment. This means that one must look at factors such as size, diet, and social structure before one can understand how the environment effects an animal. This reiterates the point made at the beginning of this thesis, i.e. that an organism's environment cannot be considered as being separate from the organism. The organism's "environment" includes its own characteristics. This principle was illustrated in Chapter 7, where the different effects of savannah living on three cercopithecine monkey species were discussed.

Only when these factors have been taken into account can one discern a link between environmental variability and life-history parameters. There is a general trend for species that experience their environments as being more stable to have lower rates of population increase than do those that experience environments as less stable. This is precisely the correlation that would be predicted by r- and K-selection theory, when unpredictable environments are linked with a high degree of density-independent mortality affecting both adults and infants. Bet-hedging theory also predicts this correlation when density-independent mortality due to unpredictable environments is mainly inflicted on adults of the population. However, in all primate species studied to date, mortality is markedly higher in infants than in adults, and there is no evidence to suggest that unpredictable environments have a disproportionate effect on adult mortality. Therefore, primates can be best thought of as being either r- or K-selected. However, it should be realized that there are several reasons why one might disagree with this interpretation of the results.

Firstly, there are several exceptions to the general rule that may not be explicable by the r/K theory. The most obvious examples are the Malagasy strepsirhines, but other examples can be found above. In some cases apparent anomalies have been resolved by close study of the ecologies of these species. For example, it appears that the rapid breeding rate of the rainforest-dwelling ruffed lemur could be linked to its building nests on the ground, while the slow-breeding of the savannah-dwelling baboons may occur as a result of the opportunistic use of food resources. In the case of the Japanese macaque selection for a large body size and seasonal breeding has resulted in the animals being forced to delay breeding until they are five years old. It remains to be seen whether other species' life-histories that do not seem to fit the pattern can also be explained. If not the conclusions of this thesis will have to be revised.

A second, and perhaps more significant, objection to the use of the terms "r- and K-selected" when discussing primates is that reproductive effort does not seem to vary in a predictable way with the environment. Body size, phylogeny and possibly metabolic rate seem to account for almost all of the variation in the measures of reproductive effort used in this study. Paternal care was the only other factor that was correlated with reproductive effort. The link between reproductive effort and environmental variability is one of the cornerstones of r- and K-selection theory, and the absence of any such demonstrable link being found in this study suggests that r- and K-selection theory cannot be used to explain variation in reproductive effort in primates. It is possible that one reason for this result was the use of parental investment as a measure of reproductive effort. A more complete measure of reproductive effort might give results that would be more compatible with r/K theory. For example, one could include some measure of the costs of reproduction by comparing mortality in reproducing and non-reproducing animals in a given year. Whatever the results of further studies on reproductive effort, it seems clear that growth rates of primates are primarily linked by to their adult size and their taxonomic group.

If the level of environmental predictability does select a particular life-history strategy, there must be a mechanism through which selection operates. The alteration of birth rates and the age at first reproduction are both dependent on changing the rates of an animal's development. A faster-developing animal can be weaned earlier, hence decreasing the interbirth interval and increasing the birth rate and it will also reach sexual maturity earlier. Gould [1977] discusses ontogeny and the ways in which evolution can ocur by changes in the timing of the development of an organism's characteristics in relation to one another. Gould suggests that the following processes may be important in r- and K-selection., the words in italics being Gould's terms for these processes.

1) Sexual maturation is accelerated so that the animal becomes reproductively active before it reaches the ancestor's fully grown condition. This results in a truncation of development hence the adult animal will then appear to be similar to a juvenile stage of its ancestor. This is *progenesis*.

2) Sexual maturation is retarded, so that the animal becomes reproductively active at a later age than the ancestor. If the development of complexity of form and size continues at the same rate as in the ancestor, the adult animal will be larger and/or more complex than the ancestor. This is known as *hypermorphosis*. However, if the development of complexity of form is also retarded the animal will reach maturity before it reaches the complexity of the ancestor, and will animal appear to be similar to a juvenile stage of its ancestor. This is known as *neoteny*.

Gould suggests that the first of these processes will occur under r-selection, whereas the second will occur under K-selection. He also presents extensive evidence that suggests that the K-selection of humans can be explained by neoteny, together with increased an increase in size. However, this is outside of the scope of this study and will not be discussed further here.

Some evidence that r-selection of the cercopithecine monkeys and the of the howler monkeys is linked to an acceleration of sexual maturation is shown by their initial breeding before the attainment reach adult size. However, the process is different from Gould's idea of progenesis in that the animals continue to grow after reaching sexual maturity and therefore the adults do not resemble a juvenile form of the adult. These species therefore show a dissociation of rates of somatic and sexual development, presumably in response to conflicting selection pressures for both large size and early breeding.

In smaller species, sexual maturation does not occur until adult weight is reached. The marmosets and tamarins have been suggested to be both dwarf forms and r-selected [see above], a combination that could be reached by the process of progenesis. However, it is debatable whether these species can be considered to be juvenile forms of their ancestors. For example, Sussman and Kinzey [1984] suggest that such dwarfing would be accompanied by an increase in relative brain size, as the brain size of juvenile primates is relatively greater than is found in adult primates. However, marmosets and tamarins do not have relatively large brains, as compared to other simian primates [Sussman and Kinzey, 1984]. If the dwarfing hypothesis is accepted, it must be assumed that the dwarfing of marmosets and tamarins was linked to a slowing of brain growth in these animals.

If r-selected species are found to have relatively larger brains, this could indicate that progenesis has occurred. However, the question is complicated by the varying degrees of sexual dimorphism [Leslie Willner, pers. comm.], and by the fact that both progenesis and neoteny will be expected to lead to ancestral juvenile characteristics in adults. Similarly, where species have relatively small brains and are larger than the ancestral form, one might argue that hypermorphosis has occurred, and could be acting as a mechanism for K-selection.

Although this subject is beyond the scope of this thesis, a preliminary investigation suggests that there is a negative correlation between relative brain size and relative r_{max} [$r=-0.412$, $n=42$, $p>0.01$] and a positive correlation between relative brain size and relative age at first reproduction [$r=0.554$, $n=44$, $p>0.001$] in primates. This suggests that primates that mature relatively early and have a relatively high $\overline{r}_{max}$ also have relatively small brains. This suggests that r-selection is not commonly linked to progenesis and juvenilization in primates, but that K-selection might be linked to neoteny.

Humans and human evolution

An important difference between humans and other haplorhine primates is that human babies are relatively very large at birth, a characteristic that arises because of a high relative foetal growth rate combined with a fairly "normal" gestation length. This high foetal growth rate is continued after birth, to give humans a higher relative postnatal growth rate in the first year of life than in other Old World haplorhines. However, if a longer growth period is considered humans have a relatively low postnatal growth rate [Kirkwood, 1985]. The reasons for these differences in growth rates have been discussed at length by Martin [1983] and will not be dealt with in detail here. Briefly, it can be said that adult brain size in most primates is directly proportional to neonatal brain size. In most primates, the growth rate of the brain [as measured by weight] slows after birth. Selection for a large brain size in humans has probably led to selection for a neonate of with a brain of maximum size, and therefore a large neonate. "Design constraints" acting on pelvis size mean that there is a limit to the size of head that can be passed through the birth canal. Further selection for increased brain size in humans has acted to increase the time of rapid brain growth to include about the first year of postnatal growth. Humans therefore have both a relatively high prenatal brain growth rate and, initially, a relatively high postnatal brain growth rate, and this is linked to their relatively high body growth rates.

Anther aspect of human life-histories, is that humans have a relatively low rate of population increase as compared to other haplorhines. Even when using a very low figure for age at first reproduction [15 years old, from Neel and Weiss (1975)], there is clear evidence that humans have a lower r_{max} that one would predict for a haplorhine of their size. This value would be considerably lower if a later age at first reproduction were to be used, for example the figure of 19.5 years found for the !Kung bushman [Howell, 1976] or the figure of about 17 years from the Mbuti pygmies [Turnbull, 1972]. As compared to the great apes, humans have a similar relative r_{max} to orangutans and chimpanzees, and a lower relative r_{max} than gorillas.

It is perhaps worth looking at this result in the light of a paper by Lovejoy [1981], which suggests, amongst other things, that humans are "r-selected" in comparison to other ape species. Lovejoy's work has been extensively criticized [see references given in discussion, below], but is still widely quoted as providing a useful model for human evolution [e.g. Ciochon and Fleagle, 1987; p.256]. For this reason it was felt that his assumptions deserve examination here. In brief, Lovejoy's model of human evolution can be outlined as follows: Apes and hominids diverged when hominids became adapted to non-forest environments such as woodland and savannah. The hominid line thus became more opportunistic in its choice of habitat and, as a result of this, suffered from a higher degree of density-independent mortality. This, in turn, acted to make hominids more "r-selected". Because of this r-selection, hominids that could decrease their interbirth interval by increasing investment in their young, and hence allowing the young to be weaned at an early age, would be at a selective advantage. It is suggested that this decrease in interbirth interval could be achieved by the father also participating in raising the infants, in particular by acting as a provisioner to the female. This would lead to a monogamous social system, with females occupying a small range and males ranging farther to seek for food, with the need to carry food selecting for a bipedal stance.

Criticisms of this theory can be based on the underlying culturally-biased assumptions made by Lovejoy [e.g. that men are naturally predisposed to be "bread-winners", whereas women are bound to the "home" by their infants] or his assumptions about links between monogamy and other aspects of human biology [e.g. that concealed ovulation in primates is associated with monogamous social systems]. Indeed such criticisms have been raised, e.g. various comments, and Lovejoy's reply, can be found in Science **217** pp. 294-306 and a discussion of concealed ovulation and its correlates in Andelman, 1987. Here, however, I will question only his work on demographic variables and reproductive strategies.

Lovejoy's theory rests on the assumption that hominids evolved several of their unique characteristics as a result of selection for a higher rate of population increase. If this were the case, one might expect that modern humans would show an increased rate of population increase, as compared to modern apes. Table 8.2 compares the reproductive characteristics of the great ape species to those of humans. It can be seen from this data that, if body size is ignored, humans clearly do not have a higher r_{max} than apes, as table 8.2 shows. Even when the very short interbirth interval of 2.5 years taken by Lovejoy [1981] is used, the maximum human r_{max} is below the maximum r_{max} of gorillas and orangutans and is approximately equal to the maximum r_{max} of chimpanzees.

Gorilla females weight about 80-90kg and are therefore considerably larger than women [weighing about 40-55kg] and female chimpanzees and orangutans [both weighing about 40kg]. One might therefore expect gorillas to have the lowest r_{max} of the four species whereas in fact they have the highest. Gorillas can therefore be considered as "r-selected" as compared to other great apes and humans. As women are generally larger than orangutan and chimpanzee females, one might expect that women would have a lower r_{max} than the latter species. However, the data in table 8.2 suggest that the range of r_{max} values of all three species are similar. It therefore appears that humans have relatively higher r_{max} values than orangutans and chimpanzees, but a relatively lower r_{max} than gorillas.

Lovejoy's argument that paternal care is necessary for increased population increase might therefore seem to be true if humans are compared only with chimpanzees and orangutans. However, when the gorilla is included it becomes clear that an increased reproductive output is possible without a high degree of paternal care, with gorillas maintaining a high r_{max} despite their very large size. Although the birth rate of gorillas is not considerably above that of other apes and humans, the gorillas can achieve a high r_{max} by breeding at an earlier age than the

Table 8.2

Reproductive parameters for great apes and humans

Species	IBI[1]	AR[2]	AL[3]	r_{max}
Gorilla [wild]	3.83	10.04	40	0.061
Gorilla [captive]	3.00	8.99	40	0.079
Chimpanzee [wild]	5.50	13.00	40	0.038
Chimpanzee [captive]	3.13	11.17	40	0.068
Orangutan [wild]	5.00	15.00	40	0.037
Orangutan [captive]	4.08	10.67	40	0.057
Orangutan [maximum]	4.08	7.00	40	0.071
Humans [!Kung bushman]	4.00	19.50	40	0.035
Humans [Mbuti pygmies]	3.00	17.00	40	0.051
Humans [Yanomama Indians]	3.50	15.00	45	0.054
Humans [maximum]*	2.50	15.00	50	0.068

(1)Interbirth interval [years] (2)Age at first reproduction [years] (3) Age at last reproduction [years], rough estimate only.

Data on IBI and AR from: Gorilla Harcourt et. al. 1981, Beck 1984, Rudder 1979; Chimpanzees Goodall 1986, Rudder, 1979; Orangutan Goldikas 1981, Rudder 1979, Rodman and Mitani 1986; Humans Howell 1976; Turnbull 1972; Neel and Weiss [1975]. *)Hypothetical figures taken from Lovejoy [1981], although Lovejoy's age at last reproduction is revised down from 60 years to 50 years.

other species. If hominids were strongly selected to breed more rapidly one might expect that they would show a decreased age at first reproduction, a characteristic that is certainly not found in modern humans.

Lovejoy's argument therefore rests entirely on the observation that modern humans have an interbirth interval that is slightly shorter than that found in modern chimpanzees and orangutans. From this evidence he assumes that the common ancestor of both apes and humans all had relatively long interbirth intervals and that humans were selected to decrease this interval. There is no evidence to suggest that modern apes can be regarded as "frozen fossils" and it would be just as valid to assume that the higher rate of increase of modern gorillas could represent the ancestral condition. If this were the case, one might postulate that modern chimpanzees, orangutans and humans could all be regarded as being K-selected in relation to their ancestors, with the former species decreasing reproductive output by increasing the interbirth interval and humans achieving the same end by delaying reproduction. I do not wish to suggest that there is any evidence to support this scenario, only to point out that it appears to be just as plausible as that of Lovejoy.

Furthermore, one might expect that if humans have been selected to have a very short interbirth interval they would show a higher relative postnatal growth rate than other apes. Although this is found for early postnatal growth, humans take relatively longer than apes to reach 20% of adult size [Kirkwood, 1985]. As was noted above, the growth pattern of human infants appears be linked to selection for large brain size. The very high relative growth rates of babies is not extended into later life, as might be expected for an r-selected animal.

It therefore appears that humans cannot be regarded as being more r-selected than other apes, a point also made by Woods [1982]. The results of this study suggest that humans have been selected to breed and develop more slowly than would be predicted for primates of their size. This is a characteristic that they share with chimpanzees and orangutans but not with gorillas. One might then be prompted to ask the question posed by Lovejoy [1982]:

> "How could such a K-selected species succeed in demonstrating r-type characters [for example, the ability to radiate and colonize unstable and novel environments], when other hominoids could not?"

This can perhaps be answered by looking at another widespread and successful species that appears to K-selected in comparison with its relatives, but that is found in apparently unstable habitats. We have seen in Chapter 7 that baboons have relatively low rates of population increase that are comparable with those of forest-living guenons. In many ways, the baboons can be seen to be comparable with humans whereas the forest-living guenons can be compared to chimpanzees and orangutans. In both cercopithecine monkeys and apes the forest-living species are restricted in range whereas humans and baboons are found in a very wide range of habitats.

Chapter 8

A comparison of baboons and humans has been made by previous studies, mainly because baboons are thought to share many of the ecological characteristics of early humans. Baboons are large-bodied terrestrial animals that are found in habitats ranging from forest to savannah and semi-desert. They are highly omnivorous, combining differing amounts of fruit, seeds, grasses, roots and animal food in their diet. Hence, in many ways the evolution of the baboon may be thought of as paralleling that of humans. Another common factor in baboon and human ecology has been noted by Foley [1987], this is that the omnivorous and opportunistic feeding of both species enables them to cope unusually well with seasonal environments. Foley therefore suggests that the success of both baboons and humans can be at least partially explained by their abilities to survive on a wide range of diets. Foley's view of human evolution is that hunting played a large part and that the ability to capture animal prey in the dry season would have been an important adaptation allowing early hominids to survive harsh conditions. Baboons use an alternative strategy of turning to underground roots and tubers during the dry season.

Although there is disagreement about the relative importance of hunting, as compared to gathering and scavenging, in early hominid ecology [e.g. Teleki, 1975; Bleier, 1984], this does not detract from the fact that it is generally agreed that early hominids ate a variety of different foods. The essential point for this study is that the omnivorous habits of baboons and hominids lead them to experience apparently unpredictable environments as stable, at least in terms of food. In addition, their large size enables them to cope with fluctuations in climate and resource availability that could be more detrimental to a smaller animal. As hominids evolved to become tool users and manipulators of their environment, they increased their control of their environment. Hence, even harsher environments could be rendered stable and thus exploited without these essentially K-selected species being disadvantaged by an increase in mortality due to the unpredictability of the environment.

This view of human evolution therefore reconciles the fact that humans appear to be selected for slow breeding and slow development with the view of early hominids being non-forest animals. Another explanation for the apparent anomaly would be if hominids evolved in a stable forest environment rather than in the savannah. It has been suggested that some characteristics of *Australopithecus afarensis*, an early hominid, suggest that it was an arboreal species and hence living in forest [Stern and Sussman, 1983]. However, the idea of early hominids being primarily forest animals does not explain the association of their remains with savannah flora and fauna. It has been suggested that the predominance of these associations is mainly due to drier environments being more favourable for fossilization than humid forests [Mann, 1981]. However, the existence of fossils in sites characterized by species associated with savannah does suggest that early hominids spent at least some time in such environments and were not completely restricted to stable forest habitats.

It is worth noting that many of Lovejoy's arguments about the relationship between paternal care and social systems could apply if early hominids were K-selected. A pattern of high investment in a few offspring is a characteristic of K-selected animals, and paternal care would help to increase the investment in each baby. As already noted, the need for postnatal brain growth in humans requires a high rate of growth in babies, and this would be very stressful in nutritional terms for the mother. Paternal care could help maintain infants during this stressful period. Whether the evolution of such a system of paternal care would require these animals to have been monogamous is debatable, particularly in the light of the polyandry that may be seen in marmosets and tamarins, and the strong possibility that males in early hominid groups might have been related and might therefore gain by caring for each others young. Further speculation on this topic is beyond the scope of this thesis, but it will no doubt be examined by future studies.

Further research

Methodology

Some of the methods used in this study were found to be unnecessarily time-consuming or gave confusing results, these will be discussed here in the hope that others can benefit from my experience.

The most time-consuming part of the analyses was the preparation of the data to be analysed. Some of this preparation was unavoidable, the initial collection of the data, checking of primary sources and sifting of data, so as to obtain the best possible data set, are all important tasks that need to be carried out for comparative studies. However, other time-consuming activities were the averaging of data to give mean genus and subfamily values for each parameter. This took a particularly long time as body weight means had to be calculated separately for each bivariate plot, because each parameter was represented by a slightly different set of species. This was done because of suggestions that bias in favour of species-rich groups can significantly alter the scaling parameters and hence their interpretation [Harvey and Mace, 1982]. In order to minimize this possible bias, and to allow comparison of this study with others using a variety of taxonomic levels in their analyses, many analyses in this study were carried out at three levels; species, genus and subfamily. In virtually every case the general results using data at one taxonomic level were also found at the other two taxonomic levels. It can be seen in the tables in chapters 4-6 that the major-axis statistics were also very similar at all taxonomic levels.

While recognizing the possibility of taxonomic bias, this work suggests that, for most practical purposes data for individual species provided a good view of the general relationships found. Very little extra information was gathered by the use of mean genus and subfamily data. It is suggested that the use of such mean values may be more important for the interpretation of data involving species from a wide variety of taxa [e.g. see Elgar and Harvey, 1987] than it is in analysing smaller groups of closely related species, such as a single order.

A second methodological problem, that was only partially solved, was the use of data from a large number of sources. It is hoped that as more data become available it will be possible to carry out these type of analyses using data from either captive or wild animals, rather than relying on a mixture of the two types.

Suggestions for further research topics

This thesis may well raise far more questions than it answers. Many of the questions could be answered if more primate species were the subject of long-term field research. The following are some suggestions for further research that would help to answer some questions raised by this thesis:

1) **Metabolic rates during reproduction.** The research in this thesis suggests that strepsirhine primates will be expected to raise their, normally low, relative metabolic rates during lactation, with a few species also being expected to raise metabolic rates during gestation [the ruffed lemur and the dwarf and mouse lemurs]. In contrast most haplorhine species do not have particularly low relative basal metabolic rates and therefore may not need to raise their metabolic rates in order to support the young during gestation and lactation. Two haplorhine species that are known to have relatively low basal metabolic rates are the owl monkey and a species of black-and-white colobus. The owl monkey will be predicted to raise its metabolic rate during both lactation and gestation, as the young show relatively high growth rates during both these stages of development. No growth rate data are available for the colobus monkey, and it can therefore be predicted that it will either have relatively low growth rates or show an elevated metabolic rate in order to support "normal" rates of growth. Research that tests these predictions might then relate the results to the ecology of the species concerned.

2) **Metabolic rates of the marmosets and tamarins.** The lack of a correlation between the relative basal metabolic rate [BMR] and the relative r_{max} in primates suggests that there is no reproductive disadvantage incurred in having a relatively low BMR. However, having a relatively low BMR may be a disadvantage in species that rely on rapid movements to catch prey or escape from predators. It is notable that the strepsirhine species with relatively low BMRs are either small and cryptic in colouring or live on Madagascar. The comparative lack of large predators on Madagascar may mean that the Malagasy species may not need to rely on rapid escape from predators to the same degree as mainland species. Sluggish movements of small, cryptically coloured species would not put them at a high risk

from predation because their cryptic colouration would be expected to protect them. Another large group of primates that relies on crypsis against predation are the marmosets and tamarins. Some evidence suggests that these species may show night-time metabolic rates that are reduced to a greater degree than is found in other diurnal primates. The body temperature of marmosets is markedly lower at night than during the day [Morrison and Simões, 1962] and they appear to be sluggish in their movements at the start of the day [Ferrari, pers. comm.]. It might therefore be predicted that these species will show a relatively low BMR. Research into this topic could also include an investigation into whether the BMR of pregnant and lactating animals is elevated in order to support their relatively high infant growth rates.

3. **Mortality rates of wild, unprovisioned populations.** Many questions concerning the links between mortality rates and life-histories must await further information on age-specific mortality rates and on how they vary from species to species. The almost total lack of mortality data on forest-living primates is a particular problem that needs to be addressed before a complete picture of primate life-histories can be painted.

4. **Intraspecific variation in life-history strategies.** Although a few primate species have been studied at more than one field site, there is generally a lack of information on how life-histories vary within species. Such information would obviously be complementary to this study and help in our understanding of how life-histories evolve.

5. **Postnatal growth rates of New World monkeys.** There is some evidence that New World monkeys that have paternal care [marmosets and tamarins, owl monkeys] can support higher relative postnatal growth rates than can other haplorhines. Of the cebid monkeys that do not have paternal care, Some hand-reared animals [capuchin monkeys] also showed relatively high postnatal growth rates, although other hand-reared animals [spider monkeys and howler monkeys] did not. Two possible explanations for these results can be suggested. Firstly, species with paternal care can support relatively higher postnatal growth rates, and the faster growing hand-reared species show higher growth rates than could be supported by the mother. Secondly, all New World species are capable of supporting relatively high postnatal growth rates, and the slower growing hand-reared species show slower growth rates than would be supported by the mother. Further studies of the growth rates of mother-reared animals could be used to solve this problem.

6. **The sociobiology of marmosets and tamarins.** It has been suggested in this work that young adult marmosets and tamarins have the capacity either to remain in their natal group

and delay breeding until they are dominant or to leave their natal group and start breeding immediately. One can predict that some factors would encourage the "stay-at-home strategy" whereas others would encourage the "leave-home strategy". To take an extreme example, a marmoset female in a group with a single , relatively old adult female and no other females older than herself would be likely to become the dominant breeding female as soon as the old female died. In this situation the young female would be predicted to remain in the safety of her natal group, and help care for her younger siblings, until she became the breeding female. The stay-at-home strategy would be even more advantageous if the young female were caring for her full siblings, i.e. infants with the same mother and father as herself. At the other extreme, a young female in a large group with several other females dominant to her would probably have to wait a long time before she could breed in this group. Although she could increase her fitness by helping to care for her siblings, the chances of her breeding successfully away from her natal group might be great enough to increase her fitness still further. In this situation, the female would be predicted to be more likely to "choose" the leaving-home strategy.

It might also be predicted that animals would be more likely to "leave home" if the breeding female or the breeding male were not their parent. In this case the younger infants in the group would be only half siblings and the their would be less to gain [in terms of inclusive fitness] by caring for such infants. Similarly, an animal in a group where neither the breeding male nor the breeding female were its parents would be expected to be even more likely to "leave home'.

Research into the validity of these predictions could investigate the age and reproductive state of migrating animals. Genetic studies could investigate the degree of relatedness of individuals within a group, and test the above hypotheses regarding patterns of reproduction and migration in the light of this knowledge. In addition, the degree of care exhibited by animals towards non-relatives could be investigated by a combination of behavioural and genetic studies.

7. **Multivariate analyses.** At the start of this study it was hoped that bivariate analyses would be used in connection with multivariate analyses to help understand patterns of covariation in life-histories. Although some initial inroads were made into this idea, the large amount of information that needed to be interpreted from the bivariate analyses and the logistical problems of changing universities, and hence computers, midway through the study meant that this approach was abandoned. Stearns [1983] has demonstrated the use of one possible multivariate approach in his principal components analysis of mammalian life-histories. It is hoped that similar analyses of primate characters might prove as interesting.

8. **The processes leading to r- and K-selection.** It was suggested above that a study of relative brain size in primates might give some indication about the occurrence of progenesis, neoteny and hypermorphosis in primates, and the links between these processes and life-histories. Relationships between other characters also change during development, and a study of these changes could lead to an understanding of the links between the ontogeny and evolution in primates.

Summary

The findings of this thesis are summarized and discussed in relation to the questions posed at the beginning of this thesis. Variation in primate life-history parameters can be largely explained by body size and phylogeny. Other constraints such as seasonality may also act on the evolution of alternative life-history strategies. Further variation in breeding rate and age at first reproduction is considered to be partly explainable by environmental predictability, but only if one considers the environment in relation to the species concerned. When r_{max} is considered the theory of r- and K-selection appears to fit with the observed patterns, but only when body size effects are accounted for. Bet-hedging theory is probably not supported, although the lack of detailed mortality data from wild populations means that this assertion is only tentative. However, no clear links between reproductive effort and environmental variability could be determined, apart from those that could equally well be explained by a correlation between body weight and environment. This may be due to the incomplete measures of reproductive effort used. Basal metabolic rate appears to act as constraint on pre-natal growth rate but not post-natal growth rate. It is suggested that overall reproductive effort may be increased when both parents care for the young. This is discussed in relation to human evolution and the apparently "K-selected" traits of humans.

Appendix I

Demographic theory

Demography has been defined as Vital statistics, illustrating condition of communities [The Concise Oxford Dictionary, 5th. edition]. The study of the demography of a population will therefore include studies of the numbers and ages of individuals in the population and the way in which these parameters change over time. To carry out such studies, one therefore needs information on birth and death rates and on emigration and immigration. To complete the picture, this information must be found for animals of different ages. Such information can be found from the study of populations over several generations and/or can be estimated from the age distribution of a population at a given time [e.g. see Krebs, 1978; Chapter 10].

The rate of population growth is a particularly interesting parameter, both for academic and practical reasons. In this thesis the intrinsic rate of natural increase, r_{max}, has been used as a measure of the rate of population growth. It has been noted that this measure is derived theoretically and cannot be taken as a measure of the actual rate of population growth in population. The main problem with using r_{max} as a measure of the rate of population growth, is that it does not account for the variation of the birth rate and the death rate with the age of the organism. To account for this variation one must use another parameter, the net reproductive rate first derived by Lotka in 1925.

The net reproductive rate, R_0, can only be calculated if one has a completer survivorship and fertility table for a population, i e. knowledge of the birth and death rates at all ages. R_0 is a measure of the rate of population growth in a single generation, where a generation is defined as the mean period elapsing between the birth of the parents and the birth of the offspring [Krebs 1978 p. 161], and is defined by·

$$R_0 = \frac{\text{females born in generation } (t+1)}{\text{females born in generation } (t)}$$

If l_x is the survival rate and m_x the birth rate, at age x, then R_0 can be calculated as follows:

$$R_0 = \sum_0^\infty l_x m_x$$

In this way a measure of population growth that includes the variation of survival and fertility with age can be calculated. If the initial conditions of a population are known, R_0 can be used to estimate the expected numbers of a population after a given period of time. If initial conditions are not known, the estimation of population numbers is facilitated by the fact that, a population with constant birth and death rates will approach fixed distribution of ages or a stable age distribution [Lotka, 1922]. This means that whatever the initial conditions, a population with constant birth and death rates will eventually reach a predictable state

Once a stable age distribution has been reached the population will increase in numbers in an exponential way [assuming there is no limit on population size]. So that:

$$\frac{dN}{dt} = rN$$ [Where r = the innate capacity for population increase, N =population size and t = time]

The innate capacity for population increase, r, can be estimated from R_0 and the generation time (G) by using the equation below.

$$r = \log_e(R_0)/G$$

As generation time is the mean period elapsing between the birth of the parents and the birth of the offspring, the value of G can only be approximate for any species that reproduce more than once in their lifetimes. Because of this, the value that will be found for r using the above equation is also an approximation, and another calculation must be used for a more accurate value of r This was derived by Lotka (1907, 1913 in Krebs 1978) and can be expressed by the formula:

$$\sum_{x=0}^{\infty} e^{-rx} l_x m_x = 1$$

This equation must be solved by trial and error in order to find r.

It can be seen from this that the use of r as a measure of population increase assumes that a population has a stable age distribution and a fixed schedule of birth and death rates. The parameter used in this work, r_{max}, is based on an even more simplistic model, in that it assumes that there is no variation in birth rate during an organisms breeding life and that there is no mortality before the age at last reproduction [see Chapter 2].

Appendix II
Taxonomy used: when different from Jolly (1972)

Classification in Jolly (1972)	Classification used in this study
Lemur variegatus	*Varecia variegatus.*
Galago senegalensis	Split into:
	i) *Galago braccatus*
	ii) *Galago moholi*
	iii) *Galago moholi*
	iv) *Galago zanzibaricus*
Galago (Euoticus) spp.	*Euoticus* spp.
Galago crassicaudatus	Split into
	i) *Galago crassicaudatus*
	ii) *Galago garnetti*
Cercopithecus (Miopithecus) *talopoin*	*Miopithecus talopoin*
Cercopithecus (Allenopithecus) *nigroviridis*	*Allenopithecus nigroviridis*

Appendix III

Data used

a) Mean adult body weight (M), mean female body weight (M_f),neonatal body weight (M_n), gestation length (G) and mean litter size.

Species	M [g]	M_f [g]	N [g]	G [days]	Litter size
Allenopithecus nigroviridis	5062.0	3225.0	-	-	1.0
Alouatta caraya	6059.0	4882.0	-	187.0	1.0
Alouatta palliatta	6583.5	5824.0	480.0	186.0	1.1
Alouatta seniculus	6573.5	5807.0	-	191.3	1.0
Aotus trivirgatus	733.5	724.0	97.0	133.0	1.0
Arctocebus calabarensis	258.7	253.7	25.2	134.0	1.0
Ateles fusciceps	9026.5	9163.0	-	226.0	1.0
Ateles geoffroyi	7576.0	7669.0	426.0	225.0	1.0
Ateles paniscus	8803.5	8554.0	452.5	-	1.0
Avahi laniger	864.1	875.0	-	-	1.0
Cacajao calvus	3850.0	3600.0	-	180.0	1.0
Callicebus moloch	1074.0	1004.0	-	-	1.0
Callimico goeldii	582.0	582.0	50.6	155.0	1.0
Callithrix argentata	342.0	353.0	35.1	-	2.0
Callithrix jacchus	288.0	287.0	27.0	148.0	2.1
Cebuella pygmaea	71.5	79.0	15.0	137.0	2.1
Cebus albifrons	2490.0	2067.0	234.0	155.0	1.0
Cebus apella	2741.0	2201.0	239.7	155.0	1.0
Cebus capucinus	3005.0	2578.0	230.0	-	1.0
Cercocebus albigena	7362.1	6209.0	425.0	174.9	1.0
Cercocebus atys	8592.5	6225.0	-	168.9	1.0
Cercocebus galeritus	7827.1	5473.0	-	171.0	1.0
Cercocebus torquatus	9109.6	7420.0	-	170.5	1.0

Cercopithecus aethiops	4173.5	3469.0	314.0	163.3	1.0
Cercopithecus ascanius	3608.0	2943.0	-	171.6	1.0
Cercopithecus cephus	3379.5	2805.0	340.0	-	1.0
Cercopithecus diana	5416.5	4533.0	475.0	-	1.0
Cercopithecus lheosti	6600.0	4700.0	-	-	1.0
Cercopithecus mitis	5827.0	4280.0	402.0	-	1.0
Cercopithecus mona	3450.0	2500.0	284.0	-	1.0
Cercopithecus neglectus	5558.0	4081.0	260.0	165.0	1.0
Cercopithecus nictitans	5405.0	4216.0	-	-	1.0
Cercopithecus pogonias	3370.0	3021.0	340.0	-	1.0
Cheirogaleus major	403.0	-	-	70.0	-
Cheirogaleus medius	179.0	173.0	19.0	61.5	2.0
Colobus badius	7989.5	7421.0	-	-	1.0
Colobus guereza	9171.0	8102.0	395.5	-	1.0
Colobus polykomos	9150.0	7662.0	597.0	-	1.0
Cynopithecus niger	5400.0	4600.0	455.0	170.9	1.0
Daubentonia madagascariensis	2800.0	2800.0	-	-	-
Erythrocebus patas	9458.5	6317.0	504.5	167.5	1.0
Euoticus elegantulus	287.0	273.0	-	-	-
Galago alleni	248.0	262.0	24.0	135.0	1.3
Galago crassicaudatus	1204.0	1120.3	44.2	135.6	1.6
Galago demidovii	64.7	62.8	7.5	110.0	1.2
Galago garnetti	779.7	738.5	49.7	131.7	1.0
Galago braccatus	282.5	250.0	18.9	141.6	1.1
Galago moholi	190.5	179.0	11.5	124.2	1.6
Galago senegalensis	212.5	195.0	20.3	-	1.0
Galago zanzibaricus	139.9	132.3	14.0	125.0	1.2
Gorilla gorilla	117549.4	82475.0	2122.9	260.0	1.0
Hapalemur griseus	790.0	-	37.8	140.0	1.5
Homo sapiens	59979.1	55000.0	3375.0	267.0	1.0
Hylobates agilis	5719.5	5530.0	-	-	1.0
Hylobates concolor	5646.5	5749.0	-	202.0	1.0
Hylobates hoolock	6700.0	6500.0	-	-	1.0
Hylobates lar	5555.5	5464.0	400.0	213.0	1.0
Hylobates moloch	5614.0	5292.0	-	195.0	1.0
Indri indri	5550.0	6250.0	300.0	160.0	1.0

Lagothrix lagotricha	6250.0	5585.0	450.0	223.0	1.0
Lemur catta	2196.5	2290.0	85.8	135.0	1.2
Lemur fulvus	2200.5	2428.0	74.7	119.0	1.0
Lemur macaco	2428.0	2428.0	100.0	128.0	1.0
Lemur mongoz	1890.0	1890.0	55.0	128.0	1.0
Leontopithecus rosalia	559.0	559.0	50.0	128.6	2.0
Lepilemur mustelinus	608.0	602.0	34.7	135.0	1.0
Lepilemur ruficaudatus	803.0	602.0	-	-	-
Loris tardigradus	266.0	255.5	11.4	167.2	1.0
Macaca arctoides	9286.5	8523.0	487.0	178.2	1.0
Macaca fascicularis	4532.0	3574.0	345.0	160.3	1.0
Macaca fuscata	10450.0	9100.0	496.0	173.0	1.0
Macaca maurus	7400.0	-	390.0	163.0	1.0
Macaca mulatta	5906.1	5445.0	475.0	165.2	1.0
Macaca nemestrina	7761.0	5571.0	472.0	167.0	1.0
Macaca radiata	6300.0	3700.0	404.0	162.0	1.0
Macaca silenus	5900.0	5000.0	407.0	180.0	1.0
Macaca sinica	4655.0	3590.0	-	-	1.0
Macaca sylvanus	8791.5	8283.0	-	164.7	1.0
Mandrillus leucophaeus	14925.0	8450.0	-	173.0	1.0
Mandrillus sphinx	16440.0	11350.0	613.0	174.6	1.0
Microcebus coquereli	306.5	302.0	15.0	86.5	1.5
Microcebus murinus	66.5	72.0	6.5	60.2	1.9
Miopithecus talapoin	1250.0	1120.0	175.0	162.0	1.0
Nasalis larvatus	15078.5	9593.0	525.0	-	1.0
Nycticebus coucang	677.5	630.0	49.3	193.0	1.0
Pan paniscus	39100.0	33200.0	1162.0	-	1.0
Pan troglodytes	45900.0	40300.0	1742.0	234.5	1.0
Papio cynocephalus	16630.3	11532.0	854.0	172.6	1.0
Papio hamadryas	14347.0	10404.0	-	170.0	1.0
Papio papio	17595.5	16166.0	-	187.0	1.0
Papio ursinus	21700.5	14773.0	-	187.0	1.0
Perodicticus potto	953.5	935.0	46.5	193.5	1.1
Pithecia monachus	2330.0	2170.0	121.0	-	1.0
Pithecia pithecia	1708.4	1604.0	-	163.5	1.0
Pongo pygmaeus	55233.2	37078.0	1735.0	249.5	1.0

Presbytis cristatus	6402.0	5856.0	-	-	1.0
Presbytis entellus	12638.6	10280.0	-	200.1	1.0
Presbytis obscurus	7264.0	6530.0	380.0	-	1.0
Presbytis senex	6069.0	5797.0	360.0	-	1.0
Propithecus verreauxi	3384.0	3183.0	107.0	140.0	1.0
Pygathrix nemaeus	9545.0	8180.0	-	210.0	1.0
Saguinus fuscicollis	345.0	350.0	45.2	-	2.0
Saguinus geoffroyi	478.0	483.0	-	-	2.0
Saguinus labiatus	520.0	520.0	43.5	-	2.0
Saguinus midas	543.5	558.0	40.0	-	2.0
Saguinus nigricollis	350.0	350.0	49.3	-	2.0
Saguinus oedipus	416.5	425.0	44.0	168.0	1.9
Saimiri sciureus	752.0	699.0	95.2	170.5	1.0
Symphalangus syndactylus	10827.0	10568.0	517.0	232.0	1.0
Tarsius bancanus	114.5	109.0	28.0	178.0	1.0
Tarsius spectrum	195.5	220.0	28.5	-	1.0
Tarsius syrichta	125.0	120.0	26.2	-	1.0
Theropithecus gelada	15069.0	11427.0	553.0	170.0	1.0
Varecia variegatus	3100.0	2700.0	97.2	102.1	1.8

b) Interbirth interval (IBI), age at 1st reproduction (AR), age at attainment of adult weight (AW), maximum recorded longevity (l) and r_{max}.

Species	IBI	AR(yrs)	AW (yrs)	l(yrs)	r_{max}
Allenopithecus nigroviridis	-	-	-	28.00	-
Alouatta caraya	-	3.71	6.50	-	-
Alouatta palliatta	1.88	3.58	-	20.00	.18
Alouatta seniculus	1.39	4.58	-	25.00	.18
Aotus trivirgatus	0.75	2.38	1.67	20.00	.35
Arctocebus calabarensis	0.50	1.12	0.71	13.00	.65
Ateles fusciceps	2.25	4.86	-	24.00	.13
Ateles geoffroyi	2.66	5.62	-	27.33	.11
Ateles paniscus	4.00	5.00	-	33.00	.09

Avahi laniger	1.00	-	-	-	-
Cacajao calvus	-	-	-	20.08	-
Callicebus moloch	1.00	3.00	-	12.00	.27
Callimico goeldii	0.47	1.32	0.83	17.92	.63
Callithrix argentata	0.62	1.67	-	-	.70
Callithrix jacchus	0.52	1.50	1.17	11.67	.85
Cebuella pygmaea	0.50	1.88	1.00	11.67	.74
Cebus albifrons	1.50	4.02	-	44.00	.18
Cebus apella	1.79	5.50	-	44.00	.14
Cebus capucinus	1.60	4.00	-	46.92	.17
Cercocebus albigena	2.12	4.08	6.00	32.67	.14
Cercocebus atys	1.08	3.14	-	18.00	.24
Cercocebus galeritus	-	6.50	5.00	19.00	-
Cercocebus torquatus	1.08	4.67	-	27.00	.20
Cercopithecus aethiops	1.33	5.00	-	24.00	.17
Cercopithecus ascanius	4.33	5.00	-	22.50	.09
Cercopithecus cephus	-	5.00	4.74	22.00	-
Cercopithecus diana	1.00	5.42	-	34.80	.19
Cercopithecus lheosti	1.33	-	-	-	-
Cercopithecus mitis	3.92	5.92	-	20.00	.10
Cercopithecus mona	-	-	-	22.00	-
Cercopithecus neglectus	1.62	4.67	3.00	22.00	.16
Cercopithecus nictitans	-	-	5.89	-	-
Cercopithecus pogonias	-	5.00	-	20.00	-
Cheirogaleus major	-	-	-	8.80	-
Cheirogaleus medius	1.00	1.19	0.29	9.00	.64
Colobus badius	2.12	4.08	-	-	.14
Colobus guereza	1.00	4.75	-	22.25	.21
Colobus polykomos	1.04	8.50	-	30.50	.15
Cynopithecus niger	1.48	5.44	-	18.00	.17
Daubentonia madagascariensis	-	-	-	23.25	-
Erythrocebus patas	1.00	3.00	4.50	21.58	.26
Euoticus elegantulus	-	-	0.83	-	-
Galago alleni	-	1.04	0.58	8.00	-
Galago crassicaudatus	1.00	2.21	0.92	15.00	.40
Galago demidovii	1.00	0.97	0.46	13.00	.48

Galago garnetti	0.57	1.58	-	17.00	.51
Galago braccatus	0.50	2.00	-	14.00	.50
Galago moholi	0.50	1.00	1.55	16.50	.95
Galago senegalensis	0.51	-	-	-	-
Galago zanzibaricus	0.50	1.00	-	-	.79
Gorilla gorilla	3.83	10.04	9.33	50.00	.07
Hapalemur griseus	-	2.38	-	12.00	-
Homo sapiens	3.50	15.00	16.50	100.00	.06
Hylobates lar	2.69	9.31	-	31.50	.09
Indri indri	2.53	-	8.50	-	-
Lagothrix lagotricha	1.50	5.00	-	25.92	.16
Lemur catta	1.50	2.01	-	27.10	.27
Lemur fulvus	1.50	2.16	-	30.08	.23
Lemur macaco	1.00	2.18	-	27.08	.30
Lemur mongoz	-	2.52	-	25.33	-
Leontopithecus rosalia	0.50	2.38	1.00	14.17	.62
Lepilemur mustelinus	-	1.88	1.50	-	-
Lepilemur ruficaudatus	-	-	-	-	-
Loris tardigradus	0.50	1.5	-	12.00	.56
Macaca arctoides	1.48	3.84	4.00	30.00	.18
Macaca fascicularis	1.07	3.86	-	37.08	.22
Macaca fuscata	1.50	5.54	7.00	33.00	.15
Macaca maurus	-	-	-	28.00	-
Macaca mulatta	1.00	4.50	6.00	29.00	.21
Macaca nemestrina	1.11	3.92	6.00	26.29	.22
Macaca radiata	-	-	-	30.00	-
Macaca silenus	1.38	4.90	-	38.00	.17
Macaca sinica	1.50	5.00	-	30.00	.16
Macaca sylvanus	1.00	4.80	7.00	22.00	.21
Mandrillus leucophaeus	1.23	5.00	-	28.60	.18
Mandrillus sphinx	1.46	4.00	-	46.33	.18
Microcebus coquereli	1.00	1.00	-	15.25	.56
Microcebus murinus	1.00	1.00	0.67	15.42	.67
Miopithecus talapoin	1.00	4.38	4.25	27.67	.22
Nasalis larvatus	-	4.50	-	13.50	-
Nycticebus coucang	1.00	-	0.75	16.00	-

Pan paniscus	4.82	-	14.00	26.83	-
Pan troglodytes	5.50	13.00	14.00	53.00	.05
Papio cynocephalus	1.75	5.50	6.00	40.00	.14
Papio hamadryas	2.00	6.10	7.00	35.60	.13
Papio papio	1.16	-	-	40.00	-
Papio ursinus	-	3.67	-	45.00	-
Perodicticus potto	0.97	2.03	1.50	22.33	.34
Pithecia monachus	-	-	-	14.42	-
Pithecia pithecia	1.58	2.08	-	13.75	.23
Pongo pygmaeus	6.50	9.68	7.00	57.33	.05
Presbytis cristatus	-	-	-	31.08	-
Presbytis entellus	1.68	3.42	-	25.00	.18
Presbytis obscurus	-	-	-	-	-
Presbytis senex	1.67	-	-	-	-
Propithecus verreauxi	1.00	3.50	1.75	18.17	.24
Pygathrix nemaeus	1.36	-	-	10.25	-
Saguinus fuscicollis	1.00	2.33	-	-	.44
Saguinus geoffroyi	0.66	-	-	-	-
Saguinus labiatus	0.82	-	-	-	-
Saguinus midas	0.55	2.00	-	13.25	.66
Saguinus nigricollis	-	-	1.38	13.92	-
Saguinus oedipus	0.58	1.89	1.25	13.50	.65
Saimiri sciureus	1.17	2.50	-	21.00	.26
Symphalangus syndactylus	3.00	9.00	-	35.00	.09
Tarsius bancanus	-	-	-	-	-
Tarsius spectrum	0.42	1.42	-	12.00	.65
Tarsius syrichta	-	-	-	13.50	-
Theropithecus gelada	2.14	4.00	-	19.25	.15
Varecia variegatus	1.00	1.95	0.79	13.00	.46

c) Weaning age, weaning weight and postnatal growth rate

Species	Weaning age (days)	Weaning weight (g)	Growth rate (gd^{-1})	Rearing[1]	Growth period[2]
Alouatta palliatta	630	-	-	-	
Alouatta seniculus	-	-	3.5	2	
Aotus trivirgatus	75	360	3.5	1	
Arctocebus calabarensis	115	160	2.14	1	0-102 days
Ateles fusciceps	-	-	6	2	
Ateles geoffroyi	330	-	2.45	2	1-227 days
Ateles paniscus	-	-	3.41	2	0-214 days
Callimico goeldii	112	220	2.95	1	
Callithrix argentata	-	105	1.7	2	
Callithrix jacchus	90	128.3	1.42	1	
Cebuella pygmaea	90	70	.43	1	
Cebus albifrons	270	-	4.7	2	
Cercocebus albigena	210	1300	5	2	
Cercocebus galeritus	-	-	4.04	2	
Cercopithecus aethiops	365	-	3.51	1	
Cercopithecus cephus	-	-	2.87	2	
Cercopithecus diana	365	-	-	-	
Cercopithecus mitis	-	-	3.5	1	
Cercopithecus neglectus	-	-	3.2	2	
Cercopithecus nictitans	-	-	2.4	2	
Cercopithecus pogonias	-	-	2.57	2	
Cheirogaleus medius	-	-	1.32	1	0-70 days
Colobus guereza	390	-	-	-	
Colobus polykomos	-	2340	6	2	
Cynopithecus niger	-	1090	3.53	2	
Erythrocebus patas	228	2465	6.78	1	
Galago alleni	-	-	1.4	2	
Galago braccatus	98	150	1.62	1	
Galago crassicaudatus	90	500	6.35	1	
Galago demidovii	45	45	.89	2	
Galago moholi	75	95	1.04	1	

Galago zanzibaricus	-	-	1.44	1	0-28 days
Gorilla gorilla	1004	-	15.32	2	3-12 months
Homo sapiens	720	-	16.41	1	
Hylobates lar	730	-	3.12	1	
Indri indri	365	-	-	-	
Lagothrix lagotricha	315	-	-	-	
Lemur catta	105	-	7.62	1	0-4 months
Lemur fulvus	135	-	9.75	1	0-4 months
Leontopithecus rosalia	90	-	1.28	2	
Lepilemur mustelinus	75	-	2.65	2	7-30 days
Loris tardigradus	169	139	.76	1	
Macaca arctoides	-	-	6.43	2	0-12 months
Macaca fascicularis	420	-	3.22	1	0-6 months
Macaca fuscata	365	2730	6.27	1	1-12 months
Macaca mulatta	365	1454	4.39	1	
Macaca nemestrina	365	1417	2.6	1	63-112 days
Macaca radiata	-	2000	4.37	1	0-12 months
Macaca silenus	365	-	-	-	
Macaca sylvanus	-	-	4.28	1	
Mandrillus sphinx	350	3000	6.53	1	
Microcebus murinus	40	-	.71	1	
Miopithecus talapoin	180	450	1.1	1	
Nycticebus coucang	90	-	5.41	1	
Pan paniscus	-	-	10.14	2	0-12 months
Pan troglodytes	1460	-	14.08	1	0-12 months
Papio cynocephalus	365	-	5.1	1	
Perodicticus potto	150	800	5.3	1	0-130 days
Pithecia monachus	-	-	2.66	2	
Pongo pygmaeus	408	-	15	2	0-12 months
Presbytis senex	225	-	-	-	
Propithecus verreauxi	180	-	-	-	
Saguinus fuscicollis	90	-	-	-	
Saguinus midas	70	-	-	-	
Saguinus nigricollis	84	175	1.84	1	
Saguinus oedipus	50	130	1.84	1	
Saimiri sciureus	167	-	1.78	1	

Tarsius bancanus	-	-	.82	2
Tarsius spectrum	68	-	-	-
Theropithecus gelada	450	-	-	-
Varecia variegatus	90	-	16.07	1

1) 1=mother reared species; 2= hand-reared species and those where no information on rearing is given.

2) Period over which postnatal growth rate is measured, for species where no period is given the time is from birth until weaning age.

Appendix IV

Metabolic rate data

Species	Body weight[1]	BMR[2] [mlO_2h^{-1}]	Age[3]	Activity[4]	Temp. [°c]	Post-absorbative?	Data set[5]	Ref.
Alouatta palliata	4670.0	2000.0	A	R	24-26	Yes	G	1
Aotus trivirgatus	820.0	442.0	A	R	TNZ[6]	Yes	G	2
	1030.0	488.0	A	R	27-35	Yes	G	3
Arctocebus calaberensis	206.0	131.0	A	R	28-30	?[7]	G	4
Callithrix jacchus	190.0	152.0	I	A	10-40	?[7]	NU	5
Cebuella pygmeae	116.8	110.6	A	R	31-40	Yes	G	6
Cercocebus torquatus	3750.0	1605.0	I	S	22.7-24	Yes	NU	7
Cercopithecus mitis	8500.0	3391.5	A	S	5-28	Yes	G	8
Cheirogaleus medius	300.0	243.0	A	S	23-28	?[7]	G	9
Colobus guereza	10450.0	2978.0	A	S	5-28	Yes	G	8
Erythrocebus patas	3000.0	1068.0	I	R	18-42	?[7]	NU	10
Euoticus elegantulus	262.0	215.6	A	R	28-30	?[7]	G	4
Galago demidovii	68.0	63.2	A	S	30-35	Yes	G	11
G. garnetti	950.0	412.3	A	S	25-31	Yes	G	12
G. mohili	156.0	120.1	A	S	30-35	Yes	G	11
G. senegalensis	275.0	198.0	A	S	30-35	Yes	G	11
Homo sapiens	60000.0	12457.0	A	R	30-35	Yes	G	13
Hylobates lar	1900.0	1071.0	I	S	23.4-25.7	Yes	NU	7
Lemur fulvus	2330.0	746.0	A	R	30-40	Yes	G	14
Loris tardigradus	283.8	128.0	A	R	32.5-35	?[7]	NU	15
Macaca fascicularis	7100.0	3458.0	A	A	25	?[7]	NU	16
M. fuscata	9000.0	4524.0	A	A	25	?[7]	NU	16
	9600.0	4200.0	A	A	29	?[7]	NU	17
M. mulatta	6225.0	2239.0	A	S	23.25	Yes	G	7
Microcebus murinus	75.0	68.3	A	A	30-37	?[7]	NU	18
Nycticebus coucang	1160.0	272.6	A	R	25-33	Yes	G	19
Pan troglodytes	34150.0	9000.0	A	S	TNZ[6]	Yes	G	20
Papio cynocephalus	14400.0	7929.0	I	A	25	Yes	NU	21

P. papio	6230.0	2611.0	I	S	22.4-24.3	Yes	NU	7
P.ursinus	16900.0	5147.0	I	Ae	22.25	Yes	NU	22
Perodicticus potto	964.2	326.6	A	R	28-32.5	?[7]	G	23
Pongo pygmeaus	16200.0	4941.0	I	S	22.9-24.2	Yes	NU	7
Propithecus verreauxii	3350.0	670.0	A	R	16.5-26.9	Yes	G	24
Saguinus geoffroyi	225.0	234.0	I	R	TNZ[6]	Yes	NU	2
Saimiri scuireus	850.0	690.0	A	R	28-30	Yes	G	3
	800.0	664.0	A	R	23	Yes	G	25
Tarsius spectrum	172.5	149.0	A	R	25-28	Yes	G	26

<u>Notes.</u>

(1) Body weight is for the experimental animals, <u>not</u> the body weights used elsewhere in this thesis; (2) BMR= Basal metabolic rate or the nearest to it that could be obtained; (3) A= adult; I= immature. In some cases the animals are stated to be adult but the body weights given suggest otherwise, such animals are classified as immature; (4) S= sleeping; R= resting; A= active or alert but restrained; Ae= anesthetized; (5) G= good data, used in calculations; NU= not used in calculations; (6) TNZ = temperature not given but stated to be in the thermoneutral zone; (7) Probably post-absorbative, but not clear from data given.

<u>References</u>

1. Milton *et. al.* [1979]; 2. Scholander *et. al.* [1950]; 3. Le Maho *et. al.*[1981]; 4. Hildwein [1972]; 5. Morrison & Simoes [1962]; 6. Morrison and Middleton [1968]; 7. Bruhn [1934]; 8. Müller *et. al.* [1983]; 9. McCormick [1981]; 10. Mahoney [1980]; 11. Dobler [1982]; 12. Müller & Jaksche [1980]; 13. Benedict [1938]; 14. Daniels [1984]; 15. Müller *et. al.* [1985]; 16. Tokura *et. al.* [1975]; 17. Nakayama *et. al.* [1971]; 18. Müller [1983]; 19. Müller [1979]; 20. Bruhn & Benedict [1936]; 21. Funkhauser *et. al.* [1967]; 22.Goldstone *et. al.* [1967]; 23. Hildwein & Goffart [1975]; 24. Richard & Nicholl [1987]; 25. Malinow & Wagner [1966]; 26. Clarke [1943].

Appendix V

Ecological data

a) Habitat, Arboreality and Social structure

Species	Habitat[1]	Arboreality[2]	Social structure[3]
Allenopithecus nigroviridis	2	A	MON
Alouatta caraya	2	A	MM
Alouatta palliatta	2	A	MM
Alouatta seniculus	3	A	MM
Aotus trivirgatus	3	A	MON
Arctocebus calabarensis	3	A	SOL
Ateles fusciceps	1	A	MM
Ateles geoffroyi	1	A	MM
Ateles paniscus	1	A	MM
Avahi laniger	3	-	MON
Cacajao calvus	-	A	-
Callicebus moloch	-	A	MON
Callimico goeldii	3	S-T	SM
Callithrix argentata	2	A	M/P
Callithrix jacchus	3	A	M/P
Cebuella pygmaea	3	A	M/P
Cebus albifrons	2	A	MM
Cebus apella	2	A	MM
Cebus capucinus	3	A	SM
Cercocebus albigena	2	S-T	MM
Cercocebus atys	-	S-T	-
Cercocebus galeritus	2	S-T	MM
Cercocebus torquatus	-	S-T	-
Cercopithecus aethiops	5	S-T	MM
Cercopithecus ascanius	-	-	SM
Cercopithecus cephus	2	A	SM
Cercopithecus diana	1	A	SM
Cercopithecus lheosti	-	-	SM

Cercopithecus mitis	2	A	SM
Cercopithecus mona	3	-	MM
Cercopithecus neglectus	2	S-T	MON
Cercopithecus nictitans	2	A	SM
Cercopithecus pogonias	1	A	SM
Cheirogaleus major	-	A	SOL
Cheirogaleus medius	2	A	SOL
Colobus badius	-	A	MM
Colobus guereza	2	A	SM
Colobus polykomos	2	A	MM
Cynopithecus niger	2	-	-
Daubentonia madagascariensis	-	-	SOL
Erythrocebus patas	6	T	SM
Euoticus elegantulus	-	-	SOL
Galago alleni	2	S-T	SOL
Galago crassicaudatus	3	A	SOL
Galago demidovii	3	A	SOL
Galago garnetti	2	-	SOL
Galago braccatus	-	-	SOL
Galago moholi	5	A	SOL
Galago senegalensis	-	-	SOL
Galago zanzibaricus	-	-	SOL
Gorilla gorilla	3	T	MM
Hapalemur griseus	-	-	MON
Homo sapiens	-	T	-
Hylobates agilis	-	A	MON
Hylobates concolor	-	A	MON
Hylobates hoolock	-	A	MON
Hylobates lar	2	A	MON
Hylobates moloch	-	A	MON
Indri indri	2	A	MON
Lagothrix lagotricha	1	A	MM
Lemur catta	3	S-T	MM
Lemur fulvus	2	A	MM
Lemur macaco	2	A	MM
Lemur mongoz	2	A	MON

Leontopithecus rosalia	2	A	M/P
Lepilemur mustelinus	1	A	SOL
Lepilemur ruficaudatus	-	A	SOL
Loris tardigradus	3	A	SOL
Macaca arctoides	2	-	MM
Macaca fascicularis	4	S-T	MM
Macaca fuscata	3	-	MM
Macaca maurus	-	S-T	MM
Macaca mulatta	3	S-T	MM
Macaca nemestrina	3	S-T	MM
Macaca radiata	3	-	MM
Macaca silenus	1	-	MM
Macaca sinica	-	S-T	MM
Macaca sylvanus	2	-	MM
Mandrillus leucophaeus	-	-	SM
Mandrillus sphinx	3	-	SM
Microcebus coquereli	2	A	SOL
Microcebus murinus	4	A	SOL
Miopithecus talapoin	3	S-T	MM
Nasalis larvatus	2	S-T	-
Nycticebus coucang	2	-	SOL
Pan paniscus	2	-	MM
Pan troglodytes	3	S-T	MM
Papio cynocephalus	5	S-T	MM
Papio hamadryas	6	T	SM
Papio papio	-	-	MM
Papio ursinus	-	S-T	MM
Perodicticus potto	3	A	SOL
Pithecia monachus	1	A	MON
Pithecia pithecia	-	A	MON
Pongo pygmaeus	1	A	SOL
Presbytis cristatus	-	-	SM
Presbytis entellus	-	S-T	MM
Presbytis obscurus	2	A	MM
Presbytis senex	2	A	SM
Propithecus verreauxi	3	A	MM

Saguinus fuscicollis	2	A	M/P
Saguinus geoffroyi	-	A	M/P
Saguinus labiatus	2	-	M/P
Saguinus midas	3	-	M/P
Saguinus nigricollis	3	-	M/P
Saguinus oedipus	4	-	M/P
Saimiri sciureus	3	A	MM
Symphalangus syndactylus	2	A	MON
Tarsius bancanus	2	-	SOL
Tarsius spectrum	2	A	MON
Tarsius syrichta	2	-	-
Theropithecus gelada	6	T	SM
Varecia variegatus	1	-	MON

1. Data on habitat taken from: Wolfheim [1983], Smuts *et. al.* [1986], Napier and Napier [1985].
2. Data on arboreality from: Pitchford [1985], Smuts *et. al.* [1986].
3. Data on social structure from: Clutton-Brock and Harvey [977a], Smuts *et. al.* [1986]

b) Dietary data

Species	Body	Dietary		% food in diet[3]			
	weight[1]	Category[2]	Fruit	Leaves	Flowers	Gum	Animal
Alouatta palliatta	6583.5	Fol	35	55	9	0	0
Alouatta seniculus	6573.5	Fol	42	53	5	0	0
Aotus trivirgatus	733.5	Fru	46	25	0	0	13
Arctocebus calabarensis	259	Ins	13	0	0	0	87
Ateles belzebuth	6000	Fru	83	7	0	0	0
Ateles geoffroyi	9026.5	Fru	80	20	0	0	0
Ateles paniscus	7575.3	Fru	83	8	-	-	-
Callicebus moloch	1074	Fru	57	31	-	-	10
Callicebus torquatus	970	Fru	71	14	0	0	15
Callithrix jacchus	288	Gum	14	0	0	66	14
Cebus albifrons	2490	Fru	76	4		0	20
Cebus apella	2741	Fru	18	2	-	-	61
Cebus capucinus	3005	Fru	65	15	0	0	20
Cebus nigrivittatus	3450	Fru	55	6	6	-	33
Cercocebus albigena	7362	Fru	58	10	0	0	25
Cercocebus galeritus	7827	Fru	77	14	1	0	3
Cercopithecus aethiops	4173.5	Fru	48	12	23	0	17
Cercopithecus ascanius	3608	Fru	51	13	-	1	25
Cercopithecus cephus	3379.5	Fru	81	6	0	0	13
Cercopithecus diana	5416.5	Fru	41	6	-	-	25
Cercopithecus mitis	5827	Fru	46	18	-	0	19
Cercopithecus neglectus	5558	Fru	77	9	-	0	5
Cercopithecus nictitans	5405	Fru	72	17	-	0	10
Cercopithecus pogonias	3370	Fru	83	1	-	0	16
Chiropotes albinasus	2846.5	Fru	90	10	0	0	0
Chiropotes satanas	2990	Fru	91	3	6	0	0
Colobus badius	7989.5	Fol	8	78	8	0	0
Colobus guereza	9171	Fol	14	82	2	0	0
Colobus satanus	9500	Fru	58	37	0	0	0
Euoticus elegantulus	287	Gum	4	0	0	77	19
Galago alleni	248	Fru	81	0	0	0	19
Galago crassicaudatus	1204	Gum	17	0	0	52	32

Galago demidovii	65	Ins	19	0	0	9	72
Galago garnetti	780	Fru/Gum	50	0	0	0	50
Galago moholi	190.5	Ins	0	0	0	48	52
Galago zanzibaricus	140	Ins	30	0	0	0	70
Gorilla gorilla	117550	Fol	2	86	2	0	0
Hylobates agilis	5720	Fru	58	39	3	0	1
Hylobates hoolock	6700	Fru	67	32	-	-	0
Hylobates lar	5555.5	Fru	59	31	4	-	7
Hylobates moloch	5614	Fru	61	38	1	0	0
Hylobates muelleri	5550	Fru	62	32	4	0	2
Indri indri	5550	Fol	41	57	2	0	0
Lemur catta	2196.5	Fru	48	44	7	0	0
Lemur fulvus	2200.5	Fol	46	49	5	0	0
Lemur mongoz	1890	Fru	18	2	81	0	0
Lepilemur mustelinus	608	Fol	3	91	3	0	0
Loris tardigradus	266	Ins	15	0	0	0	85
Macaca fascicularis	4532	Fru	52	16	5	0	23
Macaca fuscata	10450	Fru	44	41	7	0	6
Macaca mulatta	5906	Fru	63	-	-	0	-
Macaca nemestrina	7761	Fru	72	19	4	0	2
Macaca sinica	4655	Fru	85	0	12	0	2
Macaca sylvanus	8791.5	Fru	33	40	-	-	-
Miopithecus talapoin	1250	Fru	52	2	2	0	43
Nasalis larvatus	15078.5	Fol	5	95	0	0	0
Nycticebus coucang	677.5	Fru	50	0	-	10	30
Pan troglodytes	45900	Fru	61	20	4	0	5
Papio cynocephalus	18500	Fru	63	8	3	0	10
Papio hamadryas	14347	Fru	66	7	22	-	-
Papio ursinus	21700.5	Fru	87	12	0	0	1
Perodicticus potto	953.5	Fru	67	0	0	22	11
Pithecia hirsuta	1870	Fru	71	16	13	0	0
Pithecia pithecia	1708	Fru	94	0	7	0	0
Pongo pygmaeus	55233	Fru	62	22	3	0	1
Presbytis aygula	6695	Fol	35	65	0	0	0
Presbytis entellus	12639	Fol	45	48	7	0	0
Presbytis johnii	8150	Fol	14	78	7	0	0

Presbytis melalopus	6527	Fru	53	37	9	0	0
Presbytis obscurus	7264	Fol	46	48	7	0	0
Presbytis pileatus	1158	Fol	30	70	0	-	0
Presbytis potenziani	6450	Fru	58	42	0	0	0
Presbytis senex	6069	Fol	28	60	12	0	0
Propithecus verreauxi	3384	Fru	40	41	8	0	-
Saguinus fuscicollis	345	Ins	28	3	19	0	50
Saguinus geoffroyi	478	Fru	40	4	0	14	39
Saguinus imperator	490	Ins	23	0	10	1	67
Saguinus midas	543.5	Fru	64	0	5	0	31
Saimiri oerstedii	815	Ins	30	0	0	0	70
Saimiri sciureus	752	Ins	26	0	2	0	72
Symphalangus syndactylus	10827	Fol	44	44	5	-	5
Tarsius bancanus	114.5	Ins	0	0	0	0	100
Tarsius spectrum	195.5	Ins	0	0	0	0	100
Theropithecus gelada	15069	Fol	7	92	1	0	0

1) Body weights to nearest half gram, weights are from MRC file if also included in Appendix III, if not in Appendix III they are from other sources.

2) Fru = frugivore; Fol = folivore; Ins = insectivore; Gum = gum eater

3) Percentages rounded to nearest whole number.

Appendix VI

Weather stations

a) Weather stations used for climate data

Species	Station[†]
Allenopithecus nigroviridis	Boende, Congo/ Kinshasa
Alouatta caraya	Corumba, Brazil
Alouatta palliata	San Salvador, El Salvador
Alouatta seniculus	Maneus, Brazil
Aotus trivirgatus	Maneus, Brazil
Arctocebus calabarensis	Makokou, Gabon
Ateles fusciceps	Cristobel, Panama Canal Zone
Ateles geoffroyi	San Salvador, El Salvador
Ateles paniscus	Uaupes, Brazil
Avahi laniger	Majunga, Madagascar
Cacajao calvus	Sena Madureira, Brazil
Callicebus moloch	Sena Madureira, Brazil
Callimico goeldii	Sena Madureira, Brazil
Callithrix argentata	Maneus, Brazil
Callithrix jacchus	Caetite, Brazil (1)
Cebuella pygmaea	Sena Madureira, Brazil
Cebus albifrons	Uaupes, Brazil
Cebus apella	Maneus, Brazil
Cebus capucinus	Cristobel, Panama Canal Zone
Cercocebus albigena	Impfondo, Congo/ Brazzaville
Cercocebus atys	Sassandra, Ivory Coast
Cercocebus galeritus	Kisangana, Congo/ Kinshasa
Cercocebus torquatus	Coco Beach, Gabon
Cercopithecus aethiops	Yola, Nigeria and Mongu, Zambia
Cercopithecus ascanius	Kindu, Congo/ Kinshasa
Cercopithecus cephus	Lambarene, Gabon
Cercopithecus diana	Gagnoa, Ivory coast
Cercopithecus lhoesti	Goma, Congo/ Kinshasa
Cercopithecus mitis	Lusaka, Zambia

Cercopithecus mona	Gagnoa, Ivory coast
Cercopithecus neglectus	Boende, Congo/ Kinshasa
Cercopithecus nictitans	Coco Beach, Gabon
Cercopithecus pogonias	Makoua, Congo/ Brazzaville
Cheirogaleus major	Tamatave, Madagascar
Cheirogaleus medius	Maintirano, Madagascar
Colobus badius	Kisangani, Congo/ Kinshasa
Colobus guereza	Wau, Sudan
Colobus polykomos	Odienne, Ivory coast
Cynopithecus niger	Menado and Makassar, Celebes (Sulawesi)
Daubentonia madagascariensis	Tamatave, Madagascar
Erythrocebus patas	Jos, Nigeria
Euoticus elegantulus	Mitzic, Gabon
Galago alleni	Mitzic, Gabon
Galago crassicaudatus	Mongu, Zambia
Galago demidovii	Mitzic, Gabon
Galago garnetti	Mombassa, Kenya
Galago senegalensis braccatus	Mombassa, Kenya
Galago s.moholi	Tete, Mozambique
Galago s. senegalensis	Linguere, Senegal
Galago zanzibaricus	Mombassa, Kenya
Gorilla gorilla	Souanke, Congo/ Brazzaville + Goma, Congo/ Kinshasa
Hapalemur griseus	Tamatave, Madagascar
Hylobates agilis	Padang+ Medan, Sumatra
Hylobates concolor	Pattle, Vietnam
Hylobates hoolock	Silchar, India
Hylobates lar	Chomphon, Thailand; + Medan,Sumatra (2)
Hylobates moloch	Pasuran, Java
Hylobates mulleri	Balikpapan, West Borneo
Indri indri	Tamatave, Madagascar
Lagothrix lagotricha	Uaupes, Brazil
Lemur catta	Tuleur, Madagascar
Lemur fulvus	Maintirano and Tamatave, Madagascar
Lemur macaco	Nossi Be, Madagascar
Lemur mongoz	Majunga, Madagascar
Leontopithecus rosalia	Rio de Janeiro, Brazil

Loris tardigradus	Mangalore, India
Macaca arctoides	Wuchow, China (ppt.) + Luang Prabang, Vietnam (temp.)
Macaca fascicularis	Bankok, Thailand; Balikpapan + Pontianak, W. Borneo; + Pasuran, Java
Macaca fuscata	Matsumato, Japan
Macaca maurus	Menado and Makassar, Celebes (Sulawesi)
Macaca mulatta	Silchar, India
Macaca nemestrina	Balikpapan, W. Borneo
Macaca radiata	Bangalore, India
Macaca silenus	Bangalore, India
Macaca sinica	Hambantota, Sri Lanka
Macaca sylvanus	Gibraltar(3)
Mandrillus leucophaeus	Calabar, Nigeria
Mandrillus sphinx	Lambarene, Gabon
Microcebus coquereli	Maintiran, Madagascar
Microcebus murinus	Tuleur, Tamatave, + Maintirano, Madagascar
Miopithecus talapoin	Dolisie, Congo/ Brazzaville
Nasalis larvatus	Balikpapan, W. Borneo
Nycticebus coucang	Bankok, Thailand; Balikpapan+ Pontianak, W. Borneo; + Pasuran, Java
Pan paniscus	Boende, Congo/ Kinshasa
Pan troglodytes	Odienne, Ivory Coast ; + Boende, Congo/ Kinshasa
Papio cynocephalus	Manano, Congo/ Kinshasa
Papio hamadryas	Columbolcha, Ethiopa
Papio papio	Diourbel, Senegal
Papio ursinus	Bulawayo, S. Rhodesia
Perodicticus potto	Coco Beach, Gabon
Pithecia monachus	Sena Madureira, Brazil
Pithecis pithicia	Maneus, Brazil
Pongo pygmaeus	Balikpapan, W. Borneo
Presbytis cristatus	Bankok, Thailand; Balikpapan+ Pontianak, W. Borneo; + Pasuran, Java
Presbytis entellus	Nagpur, India
Presbytis obscurus	Kuala Lumpar, Malaysia
Presbytis senex	Hambantota, Sri Lanka
Propithecus verreauxi	Maintirano, Madagascar

Pygathrix nemaeus	Saigon, Vietnam
Saguinus fuscicollis	Sena Madureira, Brazil
Saguinus geoffroyi	Cristobel, Panama Canal Zone
Saguinus labiatus	Sena Madureira, Brazil
Saguinus midas	Santarem, Brazil
Saguinus nigricollis	Uaupes, Brazil
Saguinus oedipus	Cristobel, Panama Canal Zone
Saimiri scuireus	Maneus, Brazil
Symphalangus syndactylus	Singapore, Singapore + Padang, Sumatra(4)
Tarsius bancanus	Pontianak, W. Borneo
Tarsius spectrum	Menado and Makassar, Celebes (Sulawesi)
Tarsius syrichta	Surigao + Tacloban, Phillipines
Theropithecus gelada	Addis Ababa, Ethiopa
Varecia variegatus	Tamatave, Madagascar

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† The weather data used is all taken from "World Weather Records," most is from the 1951-60 edition, but additional data was also added from the 1949-50 edition. In many cases, particularly in Africa, the names of towns and countries have now changed, but the names given here are those found in the editions of "World Weather Records" used.

Whenever more than one station is mentioned the results were averaged for these stations.

1 *Callithrix jacchus* is said to be found from 0 to 800 metres above sea level but this station is at 878m.

2 *Hylobates lar* is said to be found mostly between 250 and 500 metres above sea level but these station are at 3m. and 26m. respectively.

3 *Macaca sylvanus* occurs naturally in highland areas in Morocco and Algeria. However there were no suitable weather stations to be found near to these areas. As the life-history data used comes from the free-ranging, provisioned population that is found on the rock of Gibralter it was felt that the use of data from Gibralter was preferable to that from an unsuitable weather station in North Africa.

4 *Symphalangus syndactylus* is said to prefer altitudes of between 400 and 500 metres above sea level but these station are both at 3m.

b) Details of weather stations used

Weather Station†	Latitude (rad.)	Longitude (rad.)	Altitude (m)
Africa			
Congo/ Brazzaville			
Souanke	2.07 N	14.03 E	548
Makoua	0.02 S	15.65 W	345
Impfondo	1.36 N	18.10 E	335
Dolisie	4.18 S	12.67 E	330
Tete, Mozambique	16.11 S	33.58 E	130
Congo/ Kinshasa			
Boende	0.22 S	20.85 E	370
Goma	0.68 S	29.23 E	1555
Manano	7.28 S	27.43 E	670
Kindu	2.95 S	25.92 E	475
Kisangana	0.52 N	25.18 E	415
Ethiopa			
Addis Ababa	9.03 N	38.75 E	2408
Columbolcha	11.06 N	39.97 E	1903
Gabon			
Coco Beach	1.00 N	9.60 E	16
Lambarene	1.63 S	13.57 E	426
Mitzic	0.78 N	11.53 E	501
Ivory Coast			
Gagnoa	6.13 N	5.95 W	205
Odienne	9.50 N	7.34 W	433
Sassandra	4.95 N	6.08 W	50
Kenya			
Mombassa	4.03 S	39.62 E	55
Nigeria			
Calabar	4.96 N	8.35 E	63
Jos	9.87 N	8.90 E	1285
Yola	9.23 N	12.47 E	174
Senegal			
Diourbel	14.83 N	16.25 W	9

South Rhodesia					
Bulawayo	20.15	S	23.62	E	1344
Sudan					
Wau	7.70	N	28.02	E	439
Zambia					
Lusaka	15.42	S	29.32	E	1279
Mongu	15.25	S	23.16	E	1053
Europe					
Gibraltar					
Gibraltar	36.15	N	5.35	W	3
Asia and Pacific islands					
Celebes (Sulawesi)					
Makassar	5.07	S	119.55	E	14
Menado	1.50	N	124.85	E	86
China					
Wuchow	23.63	N	111.28	E	11
India					
Mangalore	12.87	N	74.85	E	22
Bangalore	12.97	N	77.58	E	921
Nagpur	21.15	N	79.12	E	310
Silchar	24.82	N	92.80	E	29
Indonesia					
Balikpapan, West Borneo	1.27	S	116.90	E	3
Medan, Sumatra	3.58	N	4.61	E	26
Padang, Sumatra	0.93	S	100.37	E	3
Pasuran, Java	7.63	S	112.92	E	5
Pontianak, W. Borneo	0.02	S	109.33	E	3
Japan					
Matsumato	36.25	N	137.97	E	611
Malaysia					
Kuala Lumpar	3.12	N	101.70	E	34
Phillipines					
Surigao	9.80	N	125.50	E	22
Tacloban	11.25	N	125.00	E	21

Singapore					
Singapore	1.30	N	103.88	E	3
Sri Lanka					
Hambantota	6.11	N	81.13	E	19
Thailand					
Chomphon	10.45	N	99.25	E	3
Bangkok	13.75	N	100.50	E	9
Vietnam					
Pattle	16.55	N	111.62	E	6
Saigon	10.82	N	106.67	E	10

Central and South America

Brazil					
Caetite	14.05	S	42.62	W	878
Corumba	19.00	S	57.65	W	145
Maneus	3.13	S	60.02	W	44
Rio de Janeiro	22.90	S	43.17	W	27
Santarem	2.42	S	54.70	W	20
Sena Madureira	9.13	S	68.67	W	135
Uaupes	0.13	S	67.08	W	85
Panama Canal Zone					
Cristobel	9.35	N	79.91	W	11
El Salvador					
San Salvador	13.72	N	89.20	W	698
Madagascar					
Maintirano	18.05	S	44.03	E	25
Majunga	15.67	S	46.35	E	22
Nossi Be	13.32	S	48.32	E	11
Tamatave	18.12	S	48.40	E	5
Tuleur	23.38	S	43.73	E	9

† see note on names of weather stations in (a) above

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