



To Bronwyn, Tarryn, Travis and Samps

*with love,
always*



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**Life-history patterns of
terrestrial mammals in the southern African
subregion.**

by

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ABSTRACT

Life-history features of terrestrial mammals in the southern African subregion were explored in an attempt to identify the factor(s) that may influence the evolution of common mammalian life-history patterns within this subregion. Allometry and phylogeny were found to underly most of the variation observed in life-history features. Residual variation was considered and age at maturity, gestation period and litter size emerged as additional features influencing life-history patterns. Southern African mammals could generally be arranged along a theoretical r - K continuum with small mammals having relatively short developmental periods and relatively large litter sizes represented at one extreme and large mammals having relatively long developmental periods with relatively small litter sizes at the opposite extreme. However, the carnivores did not conform to this expected general gradient suggesting that they may be an exceptional order as far as their life-histories are concerned.



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CHAPTER 1

INTRODUCTION

Among a species' biological attributes, is its life-history: it grows, differentiates, maintains itself and has a characteristic organisation and structure (see Odum 1983). Furthermore, there are a number of components to life-history traits which have evolved to differ among species (Harvey & Keymer 1991) resulting in a great diversity in these features being exhibited across taxa (Cole 1954). These include total fecundity, maximum longevity and statistical age-structured schedules of growth, reproduction, survival and death. The observed diversity in life-histories suggests that there are constraints operating on what is achievable. This implies that there are trade-offs between life-history characters, *i.e.* that optimization of one component occurs at the expense of another; for instance, early development versus late development (Winemillar 1992) or reduced parental survival due to increased reproductive effort (Reznick 1985).

Evolutionary life-history theory is well developed (Charlesworth 1980; Partridge & Harvey 1988) and is based on the assumption that fitness is maximized in the face of trade-offs (Charnov & Berrigan 1991; Smith 1991). Theoretical studies of life-history evolution almost unanimously incorporate some form of trade-off (or constraint) between life-history variables (Reznick 1985). Within the confines of these theories, resources are allocated to the competing ends of growth, reproduction and survival. These constraints lead to optimal combinations of age-specific survival and fecundity which maximize fitness in a particular environment and are essential for making theoretical predictions about the optimal life-history to adopt in any given environment. Consequently, fitness is determined by survival and fecundity rates at different ages which are influenced by a species interaction with its environment, also referred to as biotic interactions. The contributions of fecundity and longevity to fitness are so direct that the importance of trade-offs is obvious. If there were no trade-offs, all organisms would be most fecund or as long-lived as the most long-lived organism, and would develop as rapidly as the most rapid developer (Smith 1991). Trade-offs ensure that organisms do not become what Law (1979) referred to as 'Darwinian Demons' which 'would start producing copious offspring at birth and continue doing so

through to eternity' (Harvey & Keymer 1991; Partridge & Sibly 1991).

It therefore follows that different environments select for different life-histories and that these trade-offs, also referred to as costs of reproduction, are fundamental in predicting the optimal life-history to evolve in any given environment (Reznick 1985). Consequently, life-history patterns are shaped by selection pressures resulting from the impact of the physical environment as well as from biotic interactions.

Corresponding to every suit of characters is a specific set of population parameters which result in the adherence to a specific life-history pattern. This means that life-history features of individual organisms are consequences of specific population parameters such as birth rates, death rates and the age structure of the population. These population parameters may be related in numerous ways to the ability of a species to survive in a changed physical environment or alternatively, in competition with other species. Various combinations of these population parameters are analogous to a multi-dimensional hypervolume where a change imposed on any one variable can result in changes in all other variables. It is therefore axiomatic that natural selection will shape life-history patterns which results in efficient populations, as the logical alternative is extinction. As a result of this interplay of selection pressures, a species evolves an adaptive complex of population traits by which it can be described. In summary therefore, the life-history of a species is the combination of age-specific survival probabilities and fecundities it displays in its natural environment (see Partridge & Sibly 1991; Smith 1991).

Although each species has a unique life-history, there are several basic life-history strategies which can be recognised. When life-history traits display correlated evolutionary changes with one another, or with ecological or behavioural differences, it is possible to identify potential trade-offs responsible for the observed diversity. The combination of these traits are characteristic of organisms living under specified conditions and can be used to make predictive statements. To understand the evolution of mammalian life-histories in the southern African subregion, it is necessary to know the set of achievable combinations of different life-history variables which describe most of the life-history variance observed within this geographic region.



Although many theoretical studies almost unanimously incorporate some form of trade-off between selective life-history variables (Reznick 1985), selection forces responsible for the evolution of mammalian life-history diversity remain poorly understood (Read & Harvey 1989). Despite many attempts to investigate the life-history patterns of mammals using the comparative approach (Leitch, Hytten & Billewicz 1960; Rosenzweig 1967; Harvey & Zammuto 1985; Read & Harvey 1989; Charnov 1991), no comparative studies have been undertaken of, specifically, mammals that occur within any particular geographic region. A significant feature of the variation found in life-history patterns, is the extent to which the different life-history components covary. For example, Read & Harvey (1989) found that several measures of increased fecundity covaried across orders of mammals: short gestation lengths, early ages at weaning and short periods as independent juveniles before maturation, were all highly correlated with each other independently of adult body mass.

The Class Mammalia is large and diverse, exhibiting a broad array of life-history patterns. Within the southern African subregion, 293 terrestrial species of mammals have been identified. It is widely acknowledged that mammalian orders can generally be arranged along a theoretical continuum characterised by small, rapid reproducing, rapid developing, short-lived species such as rodents at the one extreme to large, slow developing, slow reproducing, long-lived species such as elephants at the opposite extreme (Read & Harvey 1989; Promislow & Harvey 1990).

The small-bodied vs large-bodied dichotomy features prominently in the literature and has resulted in much emphasis being placed on body mass, more than any other single descriptive feature, as the primary determinant of ecological opportunities as well as the organism's physiological and morphological requirements (Rosenzweig 1967; Lindstedt & Calder 1981). For this reason, studies in the field of mammalian life-histories have to date been dominated by two major approaches (Read & Harvey 1989; Charnov 1991): (1) the "allometric constraint" approach and (2) the "selectionist" approach.

The "allometric constraint" approach sees variation as simply reflecting allometric or scaling consequences of adult body size. While allometric relationships are not biological laws, they are used to describe patterns as well as identify those organisms which differ in any way

from these patterns (Lindstedt & Calder 1981). However, this approach tends to oversimplify the explanation of life-histories as the outcome of a single selective pressure (Nichols, Conley, Batt & Tipton 1976) and has been widely criticised (Charnov 1990, Read & Harvey 1989; Promislow & Harvey 1990; Partridge & Sibly 1991). This led to the alternative "selectionist" approach which considers natural selection as shaping life-histories fairly independently of body size, rather acting on a broad array of possible permutations. In fact, a major finding supporting the "selectionist" approach is that life-history variables such as birth rates, death rates and age at maturity are highly correlated with each other even when adult body size is held constant (Charnov 1990).

From the plethora of literature reviewed (Pianka 1972; Nichols *et al.* 1976; Luckinbill 1978, 1979; Taylor & Condra 1980; Mueller & Ayala 1981; Boyce 1984; Read & Harvey 1989; Mueller 1991), it is evident that the concepts of r and K selection have held much theoretical appeal in explaining life-history patterns. Generally, life-history characteristics such as high maximum rate of natural increase, early reproduction, large litter size, semelparity, small body size and short life-span, have been considered components of r -strategists which evolved in restrictive seasonal or unpredictable environments. On the other hand, low maximum rate of natural increase, delayed reproduction, small litter size, iteroparity, large body size and long life-span, are considered characteristic of K -strategists which evolved in more stable or milder environments. These characteristics have been considered to be correlates of r and K selection (Nichols *et al.* 1976; Boyce 1984). The dichotomous nature of these two sets of life-history characteristics led to the visualisation of a theoretical r - K continuum with small-sized organisms reproducing quickly at one end of this continuum and large-bodied organisms that delay reproduction at the other end. It is thus tempting to explain life-history theory in terms of r and K selection. This would however, be an oversimplification.

By definition, r and K selection is a model of density-dependent natural selection. Since demographic selection optimises reproductive effort in order to maximise the average intrinsic rate of natural increase (r_i) in a particular demographic environment, there is no reason why this selection should only be dependent upon densities. For instance, demographic selection can alter life-history parameters irrespective of density. There are



obviously other parameters that come into play here, with density-dependence being only one of these multitude of parameters. Granted, r and K selection can have important ramifications for understanding life-history evolution in, for example, resource limited populations. In these populations, K -selection can increase the efficiency of resource utilization or can favour a decrease in total resource use per individual. This could in turn, be associated with a decreased reproductive output. In contrast, r -selection could result in the use of as many resources as possible to enhance fitness. This could lead to an increase in reproductive output which will enhance fecundity with concomitant enhancement of the chances of survival. Therefore, as a model of density-dependence, r and K selection may be adequate for explaining variation affected by those variables which are related to density-dependence, but will be inadequate for explaining the multivariate nature of life-history patterns observed as influenced by those variables which shape these patterns irrespective of density. In fact, according to Boyce (1984), few empirical studies can identify density dependence that is independent of other potential selective forces.

Additionally, selectionist approaches and several comparative analyses suggest the importance of mortality patterns as a key factor giving rise to different life-histories (Harvey & Zammuto 1985; Promislow & Harvey 1990). By inference, fecundity must balance mortality in natural, constant age-structured populations. Any observed patterns should therefore not only take the short-term consequences of demography into account but should integrate demographic approaches to life-history evolution which make predictions about the optimal schedules of reproductive effort that maximises r_i . Consequently, as possible evolutionary explanations, age-related costs and benefits of reproduction as well as continued parental investment should be incorporated into life-history theory.

There are several components to the fecundity of individuals in a population such as gestation period, postnatal growth and age at maturity, to name but a few. Age at maturity is suggested to be a particularly important component of a population's potential rate of increase (Promislow & Harvey 1990). Taxa with relatively delayed ages at maturity have been found to have relatively low adult mortalities (Charnov 1990). Mammals are selected to maximize their life-time reproductive success which depends on fecundity, adult mortality and juvenile mortality. In this respect, age at maturity becomes significant. Increasing the



age at maturity, prolongs the period of immaturity and decreases the probability of a juvenile surviving to reproduce, with a subsequent loss in fecundity. On the other hand increasing the age at maturity increases the age at which an individual first gives birth to young and increases the chances of being better able to care for the young. This could result in a subsequent increase in the chances of juvenile survival. Thus, rather than one particular component, it is suggested that it is a combination of several of these components which result in the evolution of different life-histories.

The trade-off between present and future reproductive success is one of the most fundamental problems of life-history theory and has been the subject of extensive analysis (Williams 1966; Gadgil & Bossert 1970; Schaffer 1974; Charlesworth & Léon 1976; Stearns 1976; Michod 1979; Law 1979; Charlesworth 1980; Sibly & Calow 1983). One of the most significant features of life-history variation rests on the distinction between semelparous species which reproduce only once in a life-time, and iteroparous species which disperse life-time reproductive effort.

Of particular interest is the dichotomy implied by the terms altricial and precocial. The question is raised whether these traits accurately reflect patterns of neonatal development exhibited by mammals and what selection pressures are involved (Derrickson 1992). Moreover, to what degree does variation in neonatal development correlate with other life-history traits. For instance, all else being equal, it has been found that mammals with altricial young usually have shorter gestation periods than precocial mammals (Case 1978). These two broad demographic alternatives can be summed up as follows (Gaillard, Pontier, Allaine, Lebreton, Trouvilliez & Clobert 1989):

1. The dispersal of lifetime reproductive effort (iteroparity): this tactic ensures that few precocial young are produced which cross the juvenile period as quickly as possible. This implies a high parental investment per individual offspring with a long gestation period, a large birth weight and a high growth rate.
2. The concentration of lifetime reproductive effort (semelparity): this tactic is typical of animals having many altricial young which ensures them against environmental



unpredictability. Therefore, parental investment per offspring is limited by their numbers.

A problem arises when including the altricial/precocial dichotomy in an analysis of this nature. First, some mammals such as insectivores and carnivores can usually be classified as altricial whereas others such as artiodactyls and primates can be classified as precocial. However, there are intermediate groups such as the Lagomorphs and Rodentia which produce both altricial and precocial neonates. These groups would therefore not be so amenable to an across taxonomic analysis. Secondly, it is evident from the literature reviewed that the definition of altricial or precocial is very subjective (Read & Harvey 1989; Webb & McClure 1989; Derrickson 1992). There appears to be no consensus on the degree of development with which each term is associated, or how species can be arranged along a continuum with altriciality or precociality representing polar conditions.

Of equal interest is the variability that is evident in the potential longevity of organisms - some animals such as certain turtles survive for more than a century whereas some rodents only a matter of a year or two (Harvey & Keymer 1991). The life-span of mammals alone varies over two orders of magnitude. Maximum recorded life-span is considered to be the best identified predictor of annual fecundity seeing that high fecundity is associated with short lives (Read & Harvey 1989).

Because evolutionary biology is inherently historical in nature (Martins & Garland Jr. 1991), any comparative analysis on life-histories would not be complete without taking into account the possible effects that phylogeny could have on patterns of life-history covariation. To this effect, it must be kept in mind that as phylogenetic trees are constructed based on morphological design using the similarities shared by closely related species, such similarities could confound comparative studies because of the non-independence of data. Consequently, in the same manner that body size affects life-history covariation, so it is affected by phylogeny. Phenotypic similarities could be a consequence of at least three different biological processes: phylogenetic niche conservatism, phylogenetic time lags and similar adaptive responses. However it is important to note that the correct use of phylogeny can assist in identifying independent evolutionary events (Harvey & Pagel 1991).



From the foregoing discussion, it is evident that there are a **number** of variables that are influential in shaping life-history patterns, rather than a **single** variable. In fact, it appears that this is fast becoming one of life-history theory's most venerable hypotheses. The question therefore remains, not whether there are **several** components that **do** affect life-history patterns but more specifically, which are the **most significant** components, to what **extent** do they affect life-histories and **how** are the important variables related to one another. The key to understanding life-history patterns lies in correctly identifying the specific combination/s of traits (suits) which contribute most significantly to the adoption of a specific life-history pattern. Life-history theory will remain rudimentary unless it takes into account predictions which include possible life-history consequences of natural selection as it is affected by multiple selective pressures acting synergistically.

Objective

The principal objectives of the present study are to define and explain some of the demographic parameters that influence the evolution of common life-history patterns in southern African mammals. Four broad categories of variables will be considered and several components pertaining to each category will be reviewed. The effects of demographic factors on the outcome of life-history evolution will be investigated taking into account details of the age-specificity of these parameters. In attempting to define and explain the relevance of some of these demographic parameters, several key questions are raised:

1. Which suit of demographic traits gives rise to similar life-history patterns within the southern African subregion?
2. Which are the key variables that result in the diversity of life-history patterns observed?
3. Which variables can be universally applied to across taxonomic groupings?
4. Which groups of species allocated to specific life-history categories, can be related

to established taxonomic groupings?

5. Is it possible to categorically arrange mammals within a specific geographic region along life-history continuums so that potential selection gradients can be delineated?

The hypotheses formulated from these key questions within the context of the aforementioned components are:

Hypothesis 1: Specific life-history characteristics may be more influential in describing variation in life-histories for mammals from the southern African subregion.

Hypothesis 2: Certain variables will be universally applicable across taxonomic groupings.

Hypothesis 3: Species that are grouped within life-history categories can be related to established taxonomic groupings.

Hypothesis 4: Mammals in the southern African subregion can generally be arranged at different points along life-history continuums which reflect potential selection gradients.

With respect to the hypotheses formulated above, the specific aims of this project are:

1. To investigate species-specific traits and identify combinations of traits (suits) that are correlated with observed life-history patterns of mammals indigenous to the southern African subregion.
2. To determine those variables which describe most of the variance in mammalian life-history patterns.
3. To establish the universality of these variables across taxonomic groupings.



4. To identify and group species within life-history categories and relate these to established taxonomic groupings.
5. To identify important life-history continuums which reflect potential selection gradients.



CHAPTER 2

MATERIAL AND METHODS

Project outline

As the present project is geographically specific, it consists of a comparative analysis of the life-histories of all terrestrial mammalian species of the southern African subregion for which data are available in the literature. Critique of the comparative method is that it is much better at suggesting hypotheses than testing them. However, it can be a strong tool with a broad scope of application because a larger number of traits of numerous species can be analysed using the comparative method as opposed to using other methods, for instance the experimental method. This leads to a high level of generalization and allows a broad perspective on what causes patterns (Stearns 1983). It would therefore be seen as an exploratory technique.

The southern African subregion is defined, for purposes of this project, according to Skinner & Smithers (1990), as the mainland region of the African continent south of the Cunene/Zambezi rivers and its coastal waters. This region includes the Prince Edward Islands (Marion and Prince Edward). However, due to the specific nature of this project, which concentrates on comparing mammals inhabiting **similar** environments, albeit consisting of different habitat types, within this geographic subregion, the surrounding coastal waters and Prince Edward islands is not included in the present analysis. The mainland region referred to by the aforementioned authors includes Namibia and the Caprivi Strip, Botswana, Zimbabwe, the section of Mozambique south of the Zambezi River, Lesotho, Swaziland and the Republic of South Africa.

Statistical parameter estimates were defined within four broad categories, *viz.* body mass, fecundity, mortality and longevity. Within these categories, a number of components were considered. Data were collated at the species level and both correlation and multivariate analyses used to identify patterns and life-history groupings. This entailed an investigation and analysis of the life-history variation across mammalian species to establish the

importance of the respective parameter estimates. Those parameters which show persistent correlations after the effects of any one of the specific parameters have been removed, are generally perceived to have more explanatory power and offer more parsimonious explanations of observed life-history patterns. To this effect, as life-history covariance is eliminated or drastically altered when the effects of the relevant parameters are statistically controlled for, both the effects of adult body weight and phylogeny were systematically removed.

Once the degree of association between the parameter estimates was established, principal component analysis (PCA) was performed to determine those variables which describe most of the variance in life-history patterns by establishing the nature of the principle axes of variance for the multi-dimensional hypervolume. Additionally, PCA effectively reduces dimensionality thus simplifying the interpretation and explanation of underlying patterns. This method of analysis therefore statistically determines which variables account for the greatest, second greatest and successively smaller amounts of variation (Joliffe 1986).

In order to identify and group species within life-history categories, cluster analysis was used to group those species that are highly correlated and similar to each other while excluding those species from clusters that are dissimilar. The parameters and justification for their inclusion in the analysis are as follows:

1. **Adult body weight:** Larger adults take longer to reach their larger sizes and it follows that they therefore have longer immature periods. Even though body weight may be a principle determinant of life-history variation, it is not the only one, and demographic parameters should covary even after the effects of body weight have been accounted for.

2. **Fecundity:** There are several components to fecundity which will be considered:-
 - (i) neonate weight
 - (ii) mean litter size



- (iii) inter-litter interval
- (iv) age at maturity
- (v) gestation period
- (vi) lactation period
- (vii) age at weaning
- (viii) age at first parturition

3. **Mortality:** Different factors of juvenile and adult mortality can be expected to result in the evolution of different life-histories. Some mortality schedules concentrate on juveniles. some adversely affect adults and some both. Thus, mortality components are:-

- (i) juvenile mortality
- (ii) adult mortality

4. **Longevity:** Juvenile survival is expected to be too variable across taxa therefore longevity components are:

- (i) adult lifespan
- (ii) reproductive lifespan

Data sources and taxonomy

Life history data on all 293 species of terrestrial mammals in the southern African subregion were largely derived from Skinner & Smithers (1990) but supplemented from Western (1979), Eisenberg (1981), van Jaarsveld (1993) and Rowe-Rowe (1994). Data were furthermore extracted from various publications of different sources all of which are referred to individually. Due to the incomplete documentation of data for a large number of species within this subregion, this analysis had to contend with the comparison of some species comprising full data sets across all variables as well as with incomplete data sets across certain of the variables. The final result was a list of partial records for 293 species in 151



genera, 41 families and 13 orders. As the complete data set did not consist of all species with complete records for all 13 traits, data sets had to be extracted by a process of elimination. Taxonomy follows Skinner & Smithers (1990). Although this source lacked data for a large number of the variables used in this analysis, it was found to be the most complete documentation.

Variables

The variables used in this analysis, follow those proposed by Stearns (1983), Read & Harvey (1989) and van Jaarsveld (1993). Weight in kilograms and time in days.

Weight

1. Adult body weight: mean adult female weight excepting where no female weight was documented, then adult male weight was used as a measure of body size.

Timing

2. Gestation period: time of conception to birth.
3. Age at weaning: average time from birth to independence from milk.
4. Age at maturity: average time from birth to sexual maturity.
5. Interlitter interval: average time between the births of successive litters.
6. Juvenile mortality: average number of days from birth to death of juveniles.
7. Maximum recorded lifespan: average number of days a species is expected to live to old age (usually recorded in captivity).
8. Maximum reproductive lifespan: maximum recorded lifespan minus age at maturity.

Reproductive output

9. Neonate weight: mean neonate weight.
10. Litter size: mean number of neonates per litter.

Statistical procedures

Statistical analyses were conducted using statistical procedures described in Sokal & Rohlf (1981), Stearns (1983), Joliffe (1986) and Ludwig & Reynolds (1988). These statistical procedures are described and elaborated on in more detail in each chapter. Note that three different data sets were generated from the observed data set. These comprise a data set for which the effects of adult body weight have been removed (calculation of dimensionless numbers using regression analysis (van Jaarsveld 1993) - see below), a data set for which the effects of phylogeny have been removed (Stearns' method - see below) and a data set for which both the effects of adult body weight and phylogeny have been removed. A drastic reduction in the number of genera used in the present analysis was observed when removing the effects of phylogeny (see chapter 5 for detail).

Data analysis

Correlation and covariance analyses

Data were collated at the species level and entered into a matrix. Correlation and covariance analyses (Sokal & Rohlf 1981) of the data matrix were performed. The correlation and covariance analyses were approached in two ways: on observed data and on residuals established from the relationships of variables with adult body weight (see chapter 3). These relationships were obtained using \log_e transformed data through least squares regression analysis, a procedure which consistently provided the best fit (see Table 3.2). Residuals were calculated and subsequently simplified by back-transforming them to standard SI units (see Table 3.3). Such residual estimates are termed "relative" variables throughout this thesis. Stearns' phylogenetic-subtraction method (see chapter 5) was used to remove the effects of phylogeny from the data (Stearns 1983; Harvey & Pagel 1991). To avoid repetition, this is explained in more detail in chapter 5.

Multivariate analyses

Due to incomplete data for all 293 species across 13 variables, the data sets used for the



multivariate analyses comprised only those species for which data were available. This reduced the number of variables for this section of the analysis in each case to five variables (adult body weight, neonate weight, litter size, age at maturity, gestation period). Principal component (PCA) and cluster analyses (Joliffe 1986) were performed on these complete data sets. Similar reduction in data sets and analyses were performed on residual values following the removal of adult body weight from four variables (neonate weight, litter size, age at maturity, gestation period). Multiple discriminant analyses (MDA) were performed on all data sets to illustrate significant differences between observed groupings (Ludwig & Reynolds 1988).



CHAPTER 3

THE IMPLICATIONS OF BODY WEIGHT ON PATTERNS OF COVARIANCE AMONG LIFE-HISTORY TRAITS AT THE SPECIES LEVEL

Introduction

Eutherian life-history theory has as its central tenet, the implication that body size either directly or indirectly imposes constraints on which strategy to adopt, thus contributing to the diversity of life-history patterns observed (see Peters 1983). Even papers suggesting alternative explanations other than body size, for instance mortality patterns (Read & Harvey 1989) have to take cognisance of the overwhelming impact of body size.

"Animals at the fast end of the fast-slow continuum have high mortality rates for their body weights."

(in Read & Harvey 1989)

The literature is rife with body size implications of life-history variation (Rosenzweig 1967; Sacher 1978; Western 1979; McNab 1980; Lindstedt & Calder 1981; Western & Ssemakula 1982; Millar & Zammuto 1983; Peters 1983; Stearns 1983) with comparative studies showing correlated evolution between body size and other life-history traits (Stearns 1983; Read & Harvey 1989; Harvey & Keymer 1991). Considering the important role played by body size, no comparative study of life-histories would be complete without a thorough examination of the impact of body size on life-history parameters. Consequently, the relationship between body weight and life-history variables of mammals in the southern African subregion will be quantified.

Many comparative studies have shown correlated evolutionary patterns between life-history traits (Stearns 1983; Read & Harvey 1989; Harvey & Keymer 1991). In light of the two prevailing schools of thought, *viz.* the allometric and selectionist approaches, this chapter

focuses on the effect that body weight *per se* has on shaping life-histories by comparing results obtained by the inclusion as well as the removal of the effects of body weight. It is expected that if the effects of body weight are eliminated, patterns of life-history covariation will alter significantly (Read & Harvey 1989). However, if these general patterns should persist, then it becomes clear that although body size influences these life-history variables, it is not the only contributing factor which influences patterns of life-history covariance.

Most body size relations are of the form $Y=aW^b$ where Y is the size-related variable of interest, W represents body weight and a and b are empirically derived constants (Peters 1983). Notably, this equation does not describe a straight line when Y is plotted against W except in special instances when $b=0$ (and $Y=a$) or when $b=1$ (and $Y/W=a$). In effect, depending on the value of b , the relation of Y and W can have very different shapes. Body weight and whichever variable Y represents are therefore two phenomena which increase at different rates. As a result, body size relations are referred to as allometric relationships and the power formula $Y=aW^b$ is considered to be an allometric equation. Consequently, the change of Y with W is referred to as the scaling of a characteristic (Y) to body size (W). To illustrate this principle, if any two organisms were built to the same design (but on a different scale), the different characteristics of the original organism would necessarily be scaled either up or down to produce a working model (Peters 1983). This scaling is achieved by applying the principles of allometric relationships. Thus, variations in the arithmetic rate of change of Y at different values of W make arithmetic plots of body size relationships difficult to draw and interpret. A log transformation of data results in a linear relationship $\log Y = \log a + b \log W$.

Allometric relationships are not biological laws but they do describe patterns as well as identify those organisms that potentially differ from these patterns (Lindstedt & Calder 1981). Criticism against using body size relationships is that they sacrifice precision to achieve generality (Peters 1983). It is however, generality that is needed in an analysis of this nature which is aimed at giving a broad perspective of the possible causes of or associations between underlying patterns, considering the variety of species occurring in the southern African subregion and the number of variables included in this analysis.



Once these variables are linearly regressed with adult body weight as well as with one another, adult body weight will be removed in order to see whether the relative variables (corrected for adult body weight) are still correlated to each other irrespective of adult body weight. This will give an indication of the extent that adult body weight constrains correlations between any of the other variables used in the present study.

Material and Methods

Correlation and covariance analyses were performed on all 293 species within the subregion which were entered into a matrix and used both in the observed form and to calculate residuals (after removal of adult body weight effects). Scatterplots were obtained using both observed and \log_e transformed data in order to evaluate the goodness of fit and to achieve the best possible relationship between each variable and adult body weight. Interactive outlier rejection regression analysis was performed on the observed data to identify possible outliers when regressing variables with adult body weight. For the principal component (PCA) and cluster analyses, which requires full data sets across all species and variables, incomplete data fields were eliminated. This resulted in 38 mammalian species and five variables being used in the final analysis for the observed data and four variables using the residuals (after removal of adult body weight effects). Note that the groupings in the cluster analysis were obtained through the nearest method using Euclidian distances. Clusters were determined after seven levels of convergence as illustrated by a vertical line on the dendograms, unless otherwise specified.

Multiple discriminant analyses (MDA) were used to investigate differences between groups identified within the component space of PCA. However, cluster analyses suggested phylogenetic groupings irrespective of allometric constraints. To see whether phylogenetic groupings remained following the removal of the effects of body weight, MDA were conducted using orders as a classification grouping. Significance was taken at the 95% level.

Results

Correlation and covariance analyses

Although all 293 mammalian species in the southern African subregion were entered into the matrix, the results of the correlations and covariances between variables are for 224 species as incomplete fields are automatically eliminated. The results on the observed data is presented in Table 3.1. Significant correlations and covariations exist between all variables with body weight with the exception of litter size, juvenile mortality and reproductive lifespan. Additionally, significant correlations and covariations are evident between most life-history variables as is generally perceived (Stearns 1983). The relationships of life-history variables with adult body weight calculated using least squares regression, is shown in Table 3.2. Relationships obtained using log transformed data are also shown if it improved the r^2 value. The corrected relationships (back-transformed to standard S.I. units) of life-history variables with adult body weight used to calculate residuals are given in Table 3.3.

Scatterplots of each variable on adult body weight are shown in Figures 3.1 - 3.12 using both untransformed (observed) as well as log transformed data. As a rule, a scatterplot of log transformed data shows a clear relationship between the respective variable and adult body weight. Insight into the type of relationship between adult body weight and each variable is gained from the scatterplot presentations, particularly the log transformed plots (Figures 3.1-3.12). Considerable scatter is evident in most plots of the log transformed data but the degree of association between adult body weight and all variables excepting litter size, juvenile mortality and reproductive lifespan is significant at the 95% or 99% level (see Table 3.1). Notably, interactive outlier rejection regression analysis identified no outliers in the data set.

With the removal of adult body weight (Table 3.4), the correlation coefficients decreased with many of the variables but they remained significantly correlated. In several instances, negative correlations changed to positive ones and *vice versa*. Noteworthy, the relationship between adult mortality and litter size changed in this respect indicating a trade-off ($r=-0,74$,

Table 3.1 Correlation coefficients (r) (above the diagonal) and covariances (below the diagonal) between life-history variables of mammals in the southern African sub-region. ** denotes significance at the 99% level. * denotes significance at the 95% level. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
ADWT		0,91** (81)	-0,15 (144)	0,61** (36)	0,84** (48)	0,45** (108)	0,78** (18)	0,64** (37)	0,86** (45)	0,05 (12)	0,73** (12)	0,87** (45)	-0,001 (22)
NEOWT	5776 (81)		-0,28** (78)	0,73** (29)	0,80** (43)	0,79** (73)	0,67** (12)	0,53** (32)	0,87** (37)	0,13 (10)	0,80** (10)	0,82** (37)	0,05 (17)
LITSZ	-71 (144)	-12 (78)		-0,30** (33)	-0,30 (48)	-0,51** (97)	-0,47** (15)	-0,48** (37)	-0,42** (41)	-0,26 (11)	-0,48** (12)	-0,39** (42)	-0,13 (21)
INLTIN	103120 (36)	6524 (29)	-203 (33)		0,96** (22)	0,24 (33)	0,51 (8)	0,65** (13)	0,93** (22)	-0,40 (8)	0,82** (7)	0,74** (21)	0,21 (10)
AGEM	220361 (48)	12934 (43)	-413 (48)	229291 (22)		0,42** (51)	0,78** (10)	0,74** (21)	0,96** (28)	0,14 (7)	0,85** (10)	0,87** (29)	0,19 (13)
GESP	22552 (108)	2010 (73)	-119 (97)	21063 (33)	57484 (51)		0,68** (19)	0,66** (37)	0,45** (47)	0,04 (11)	0,90** (11)	0,29** (47)	0,26 (26)
LACP	100169 (18)	6336 (12)	-96 (15)	57414 (8)	159506 (10)	17982 (19)		0,93** (7)	0,73** (6)	- (2)	0,83** (4)	0,92** (10)	0,63 (4)
AGEW	48892 (37)	2765 (32)	-138 (37)	4421 (13)	106080 (21)	17244 (37)	70494 (7)		0,72** (18)	-0,47 (5)	0,76** (5)	0,70** (18)	0,30 (8)
AGEPRT	251881 (45)	16633 (37)	-612 (41)	239150 (22)	497661 (28)	65638 (47)	272397 (6)	132377 (18)		-0,34 (8)	0,69** (5)	0,87** (33)	0,03 (14)
JMORT	261 (12)	76 (10)	-5 (11)	-1366 (8)	2258 (7)	111 (11)	-137 (2)	-602 (5)	-4016 (8)		1,00** (3)	-0,26 (9)	-0,01 (4)
ADMORT	63185 (12)	992 (10)	-1997 (12)	277191 (7)	618685 (10)	34668 (11)	426638 (4)	307234 (5)	317446 (5)	66208 (3)		0,51 (7)	0,41 (4)
ADLIFE	1548940 (45)	94782 (37)	-3055 (42)	1058740 (21)	3 (29)	260828 (47)	1490340 (10)	681537 (18)	2577240 (33)	-12437 (9)	2024230 (7)		0,46** (19)
RELIFE	-460 (22)	3469 (17)	-935 (21)	47790 (10)	266572 (13)	82579 (26)	157323 (4)	132733 (8)	15102 (14)	-356 (4)	1551760 (4)	2824870 (19)	

Table 3.2 The relationships of life-history variables of mammals in the southern African sub-region with adult body weight. The relationships were obtained using least square regression analysis. Relationships obtained with log transformed data were used if it improved r^2 -values. t_i represents the t -value for the intercept, while t_s represents the t -value for the slope. NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

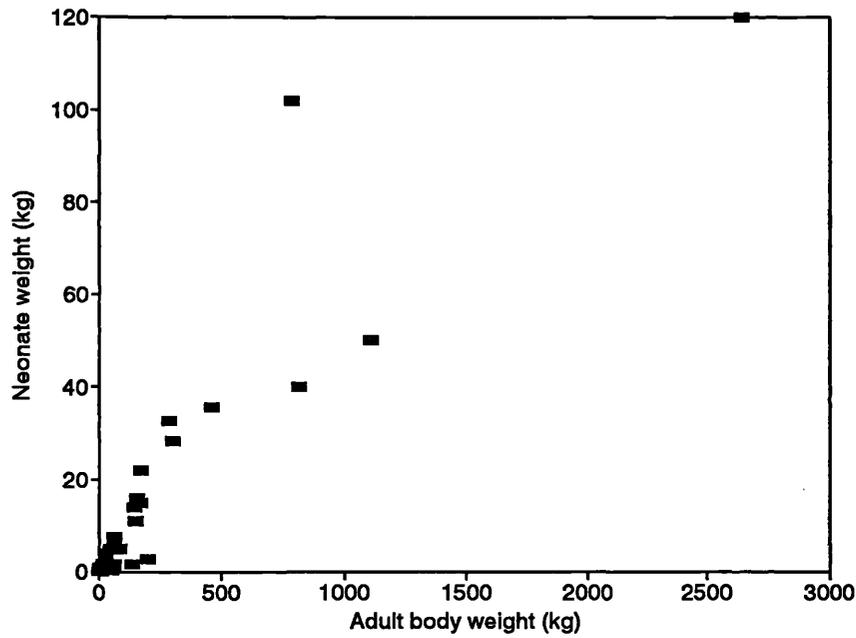
Variable	Relationship	r^2	r	F-ratio	p	t_i	p	t_s	p	df
NEOWT	$\ln y = 0,93 \ln x - 2,79$	0,93	0,97	1121,14	<0,01	-28,16	<0,01	33,48	<0,01	80
LITSZ	$\ln y = 0,70 - 0,05 \ln x$	0,07	-0,26	10,44	<0,01	13,53	<0,01	3,23	<0,01	143
INLTIN	$\ln y = 0,29 \ln x + 4,75$	0,62	0,79	55,55	<0,01	30,18	<0,01	7,45	<0,01	35
AGEM	$y = 1,19x + 425,94$	0,71	0,84	113,00	<0,01	8,40	<0,01	10,84	<0,01	47
GESP	$\ln y = 0,21 \ln x + 4,31$	0,55	0,74	130,05	<0,01	68,66	<0,01	11,40	<0,01	107
LACP	$y = 0,23x + 129,24$	0,61	0,78	25,31	<0,01	4,11	<0,01	5,03	<0,01	17
AGEW	$\ln y = 0,22 \ln x + 4,07$	0,57	0,75	46,06	<0,01	34,76	<0,01	6,79	<0,01	36
AGEPRT	$\ln y = 0,30 \ln x + 5,50$	0,94	0,97	657,11	<0,01	106,84	<0,01	25,63	<0,01	44
JMORT	$\ln y = 0,11 \ln x + 2,94$	0,18	0,42	2,20	0,17	8,94	<0,01	1,48	0,17	11
ADMORT	$\ln y = 0,22 \ln x + 8,01$	0,65	0,81	18,90	<0,01	51,42	<0,01	4,35	<0,01	11
ADLIFE	$y = 7,93x + 4336,71$	0,75	0,86	128,91	<0,01	13,13	<0,01	11,35	<0,01	44
RELIFE	$y = -0,001x + 5920,99$	0,00	-0,0001	0,00001	1,00	6,56	<0,01	-0,002	1,00	21



Table 3.3 Corrected relationships of life-history variables with body weight. Those relationships obtained from log transformed data are presented to represent untransformed data. NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan

Variable	Relationship	r^2
NEOWT	$y=0,06x^{0,93}$	0,75
LITSZ	$y=2,01x^{-0,05}$	0,00
INLTIN	$y=115,58x^{0,29}$	0,40
AGEM	$y=425,94+1,19x$	0,71
GESP	$y=74,44x^{0,21}$	0,20
LACP	$y=129,24+0,23x$	0,57
AGEW	$y=58,57x^{0,22}$	0,42
AGEPRT	$y=244,69x^{0,30}$	0,83
JMORT	$y=18,92x^{0,11}$	0,09
ADMORT	$y=3010,92x^{0,22}$	0,70
ADLIFE	$y=4336,71+7,93x$	0,75
RELIFE	$y=5920,99-0,0001x$	0,00

a)



b)

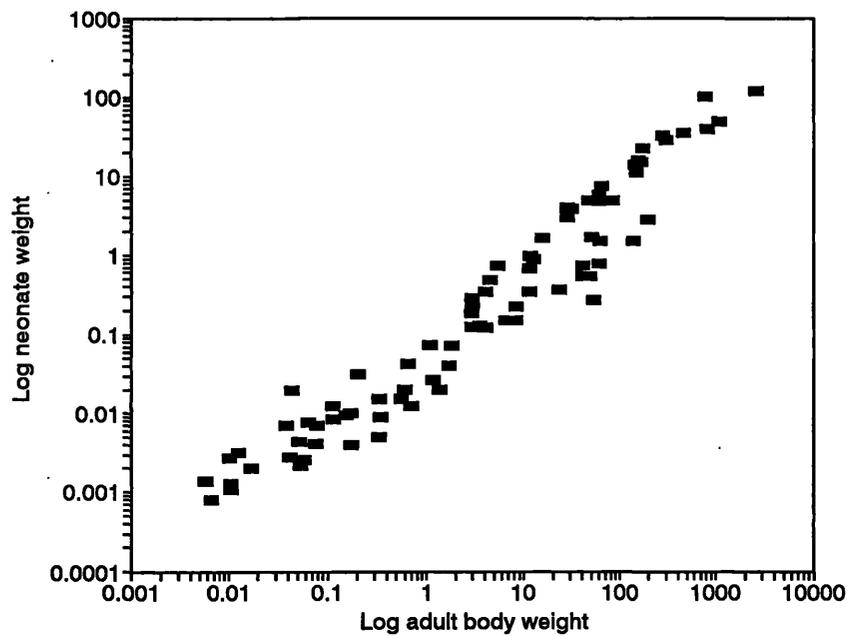
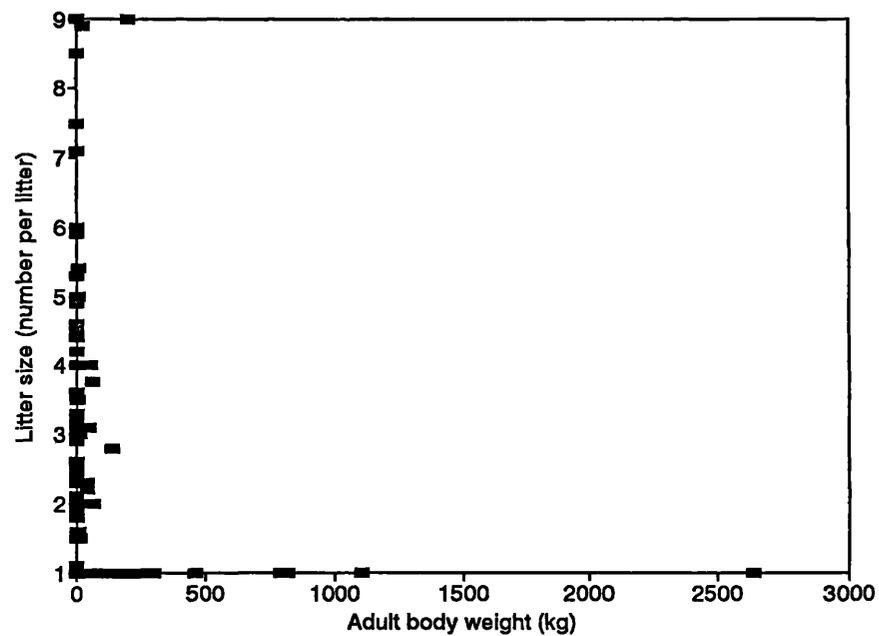


Figure 3.1 Scatterplots of neonate weight on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,93\log x - 1,21$ ($r = 0,97$; $df = 79$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

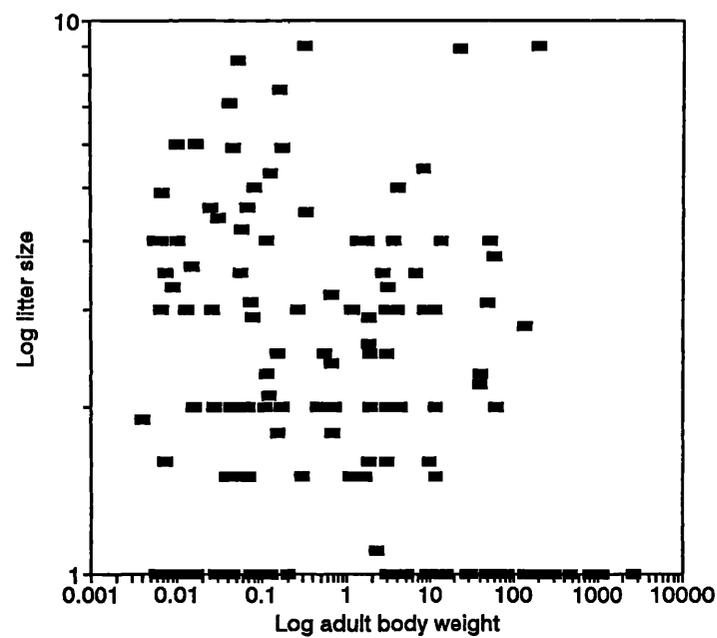
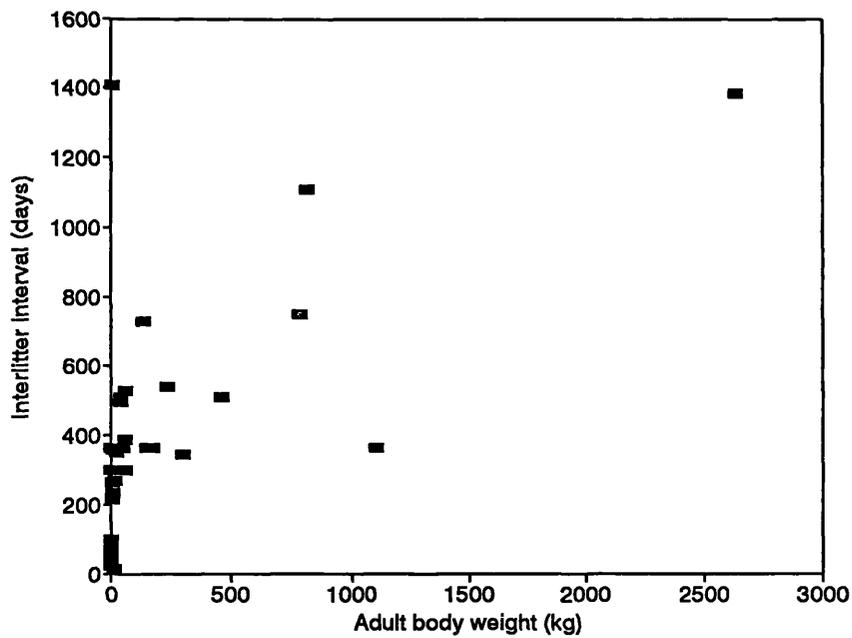


Figure 3.2 Scatterplots of litter size on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = -0,05\log x + 0,30$ ($r = -0,26$; $df = 142$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

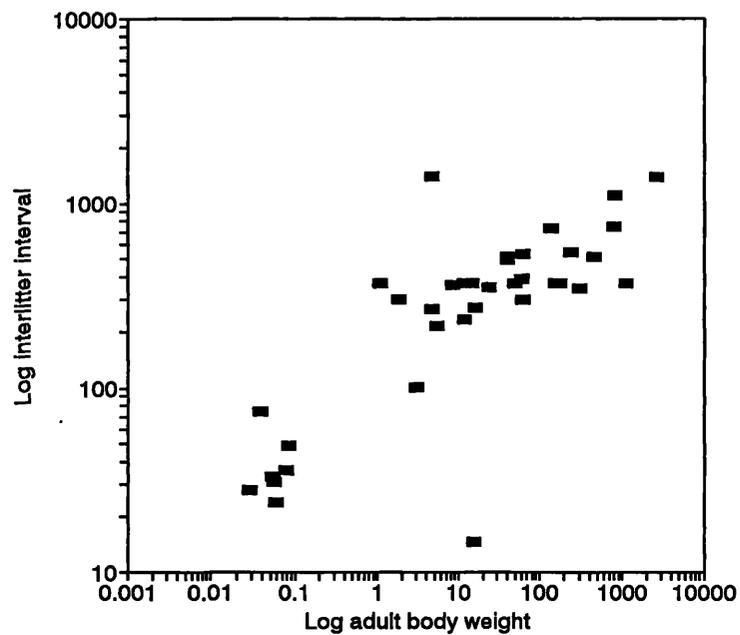
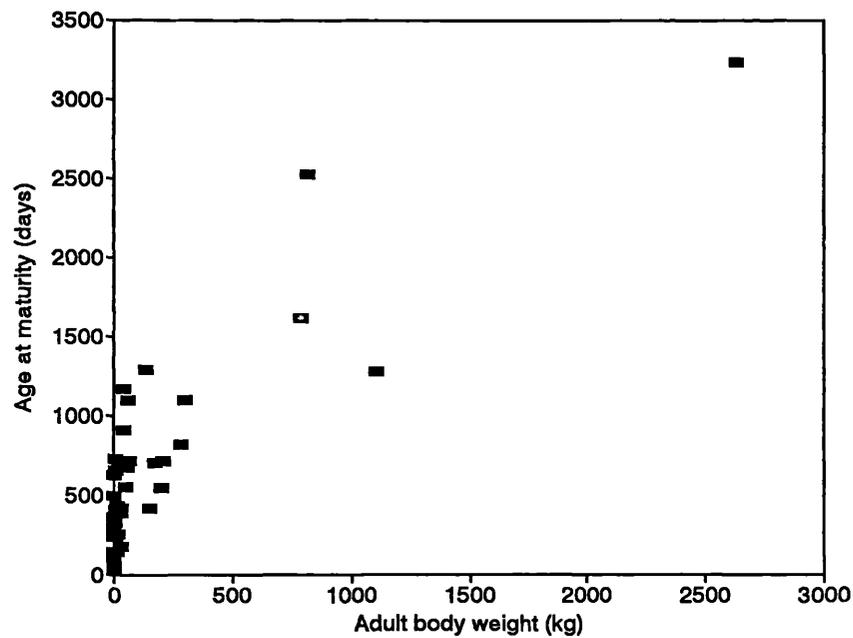


Figure 3.3 Scatterplots of interlitter interval on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,29\log x + 2,06$ ($r = 0,79$; $df = 34$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

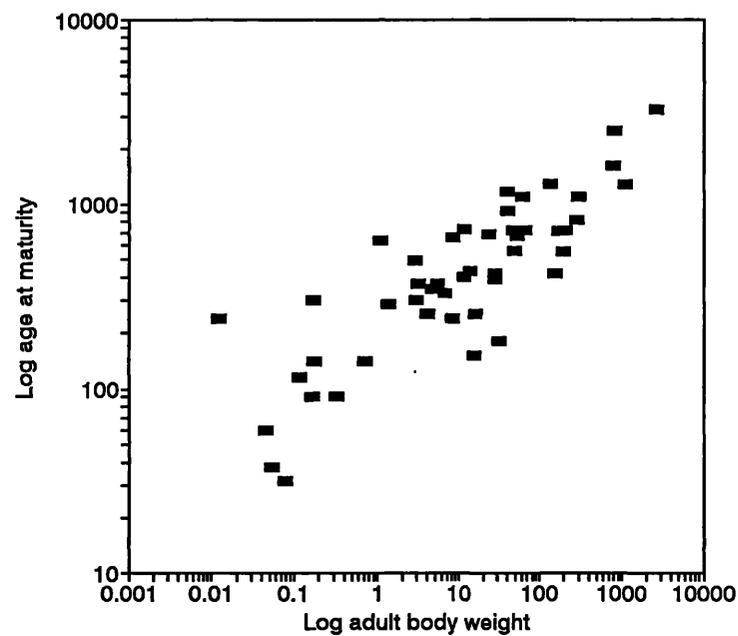
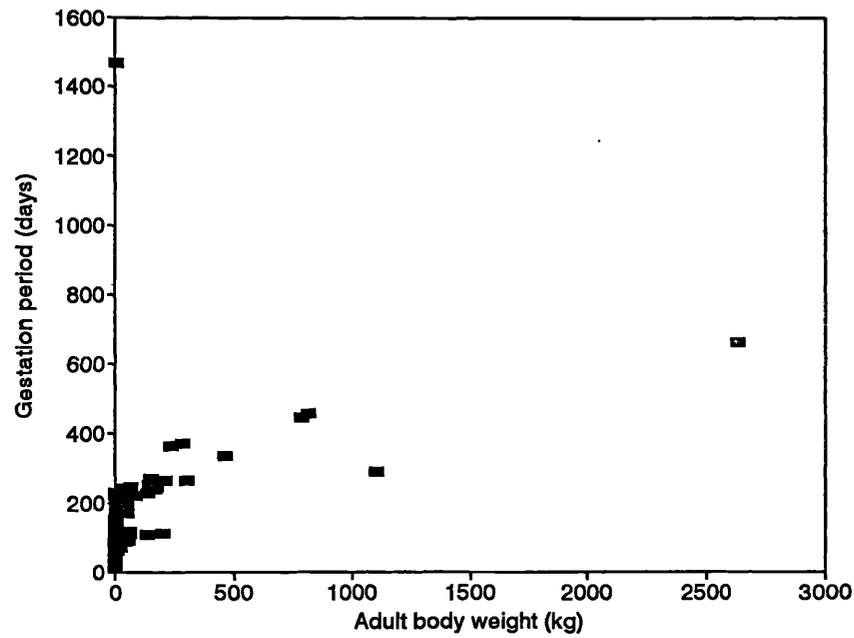


Figure 3.4 Scatterplots of age at maturity on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,28\log x + 2,32$ ($r = 0,84$; $df = 46$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

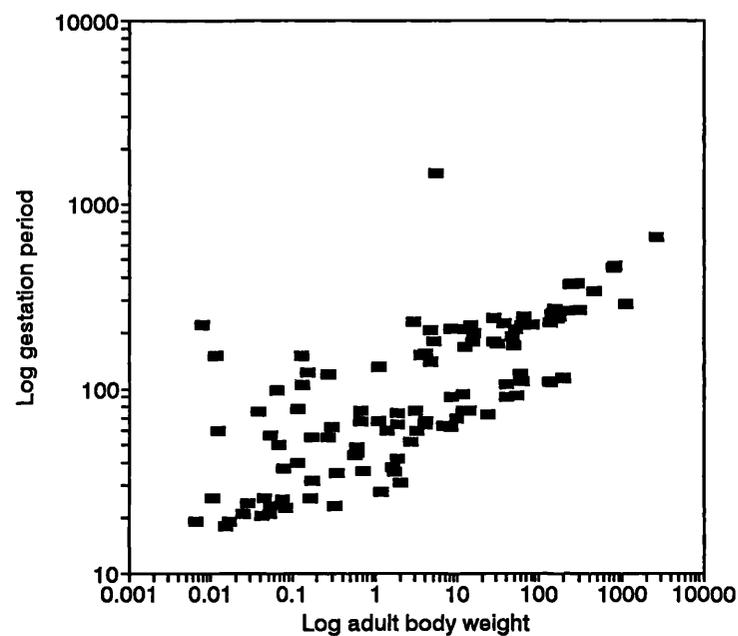
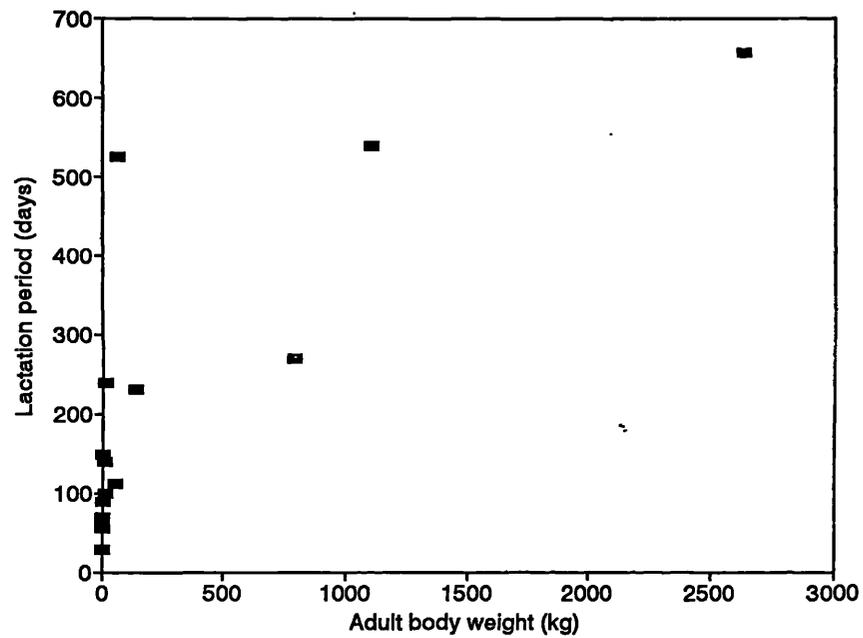


Figure 3.5 Scatterplots of gestation period on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,21\log x + 1,87$ ($r = 0,74$; $df = 106$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

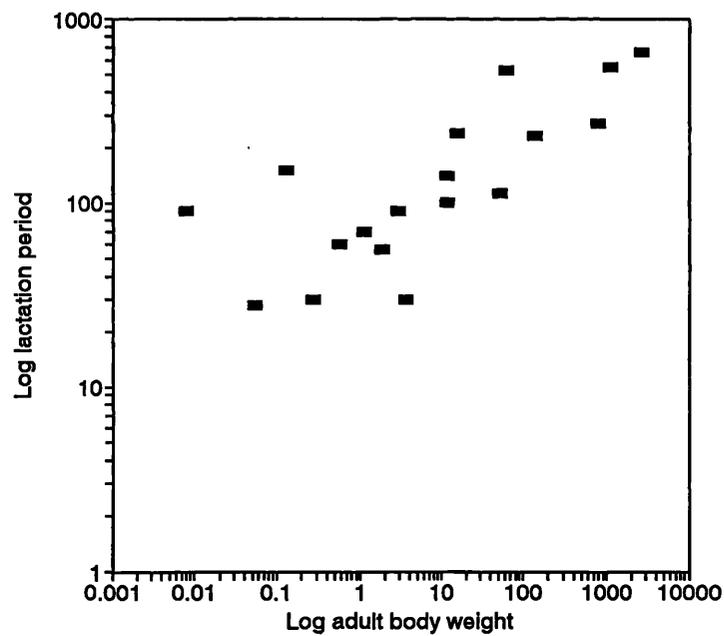
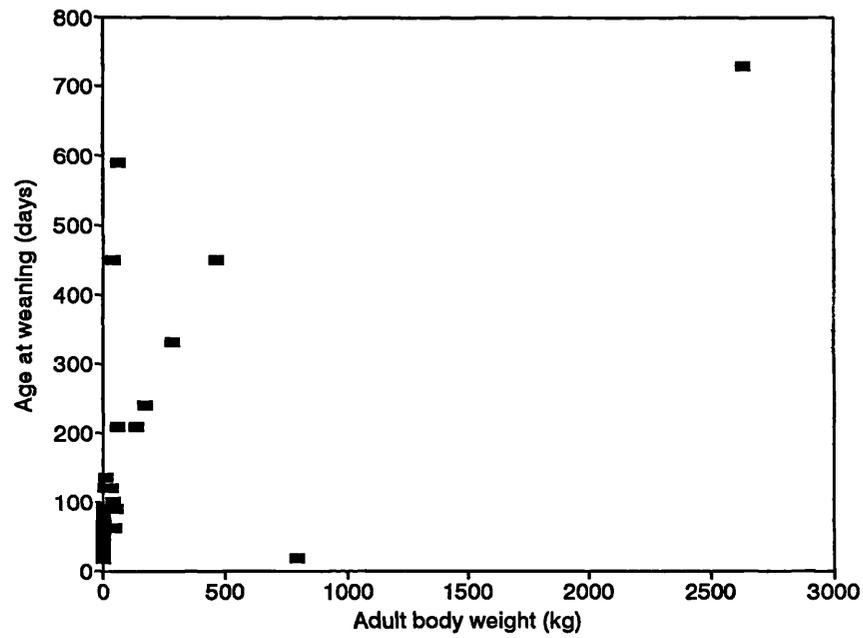


Figure 3.6 Scatterplots of lactation period on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,21\log x + 1,91$ ($r = 0,76$; $df = 16$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

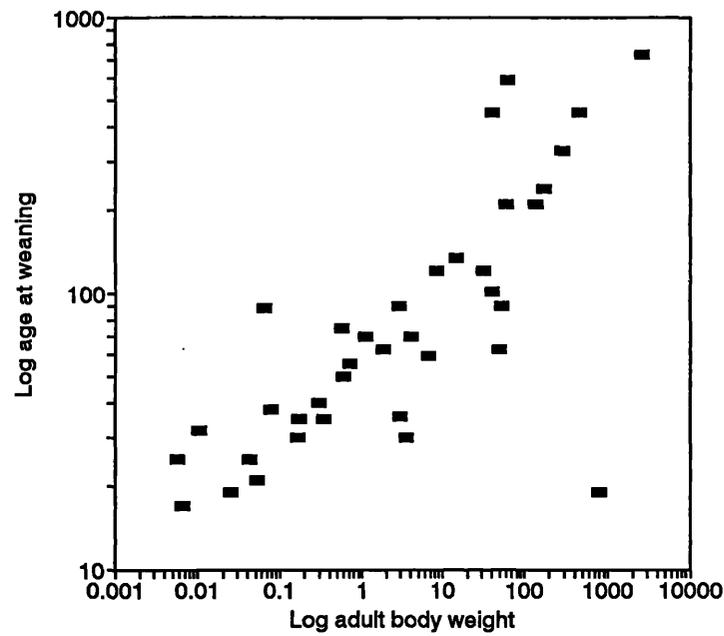
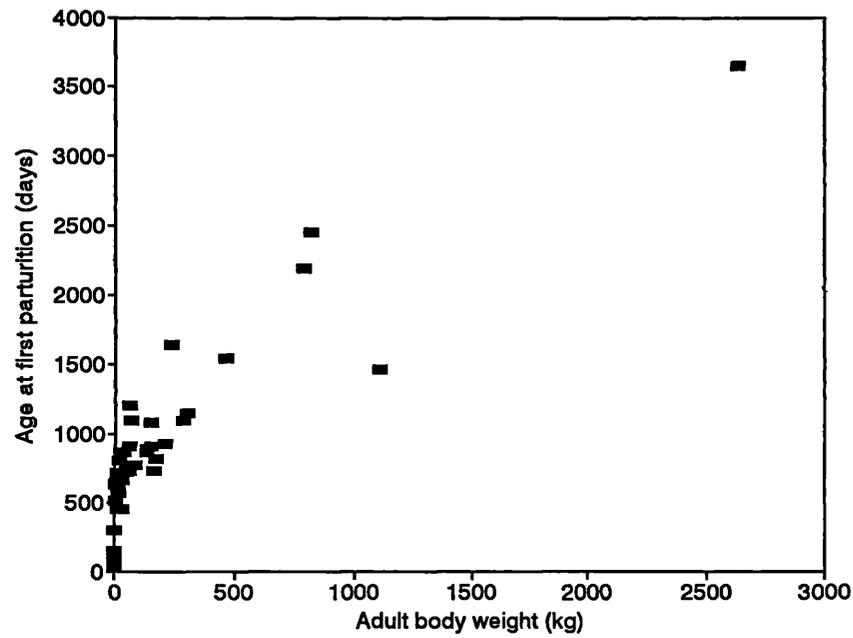


Figure 3.7 Scatterplots of age at weaning on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,22\log x - 1,77$ ($r = 0,75$; $df = 35$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

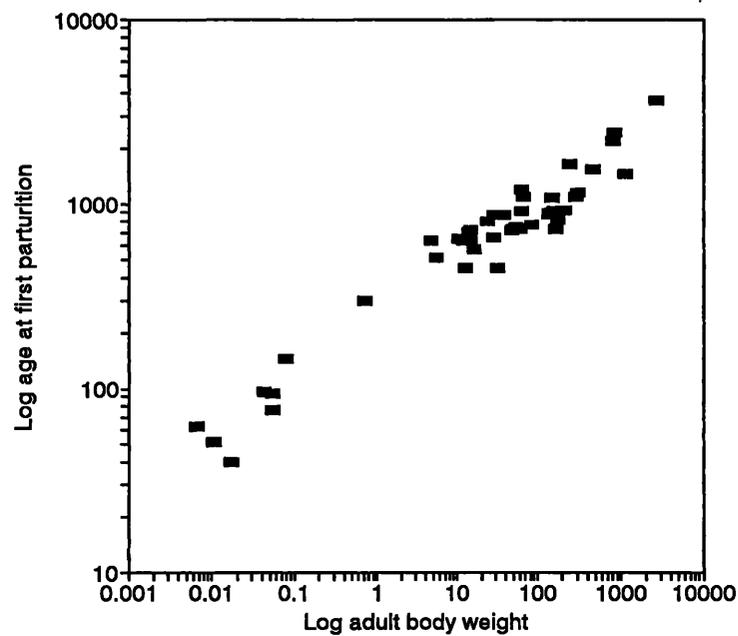
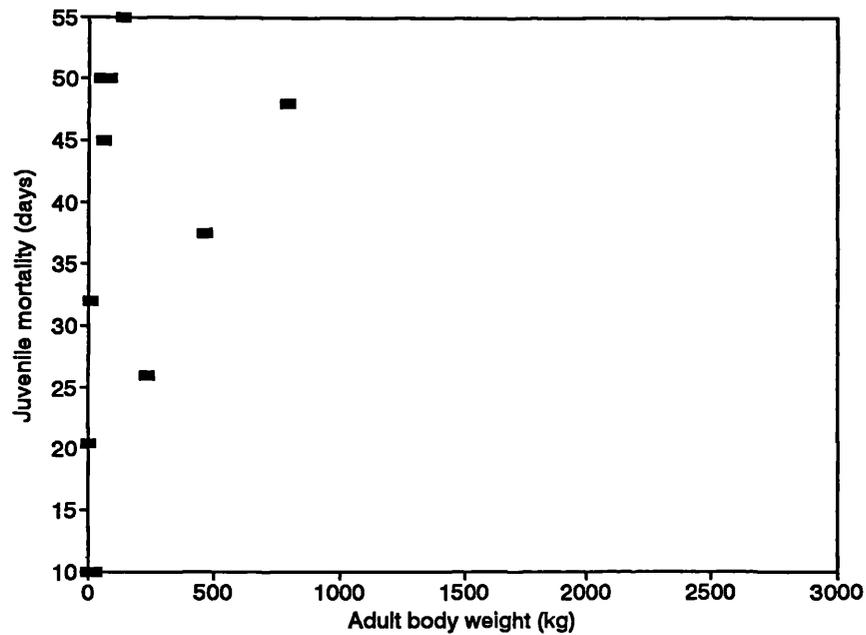


Figure 3.8 Scatterplots of age at first parturition on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,30 \log x + 2,39$ ($r = 0,97$; $df = 43$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

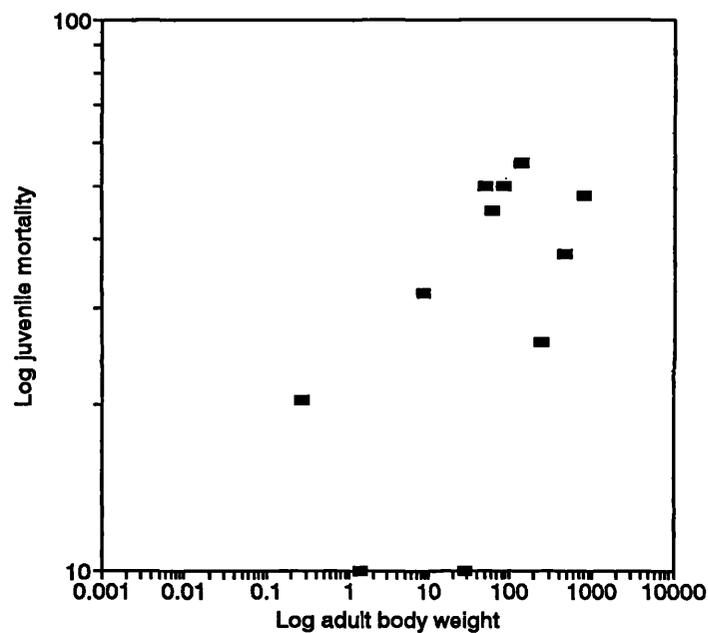
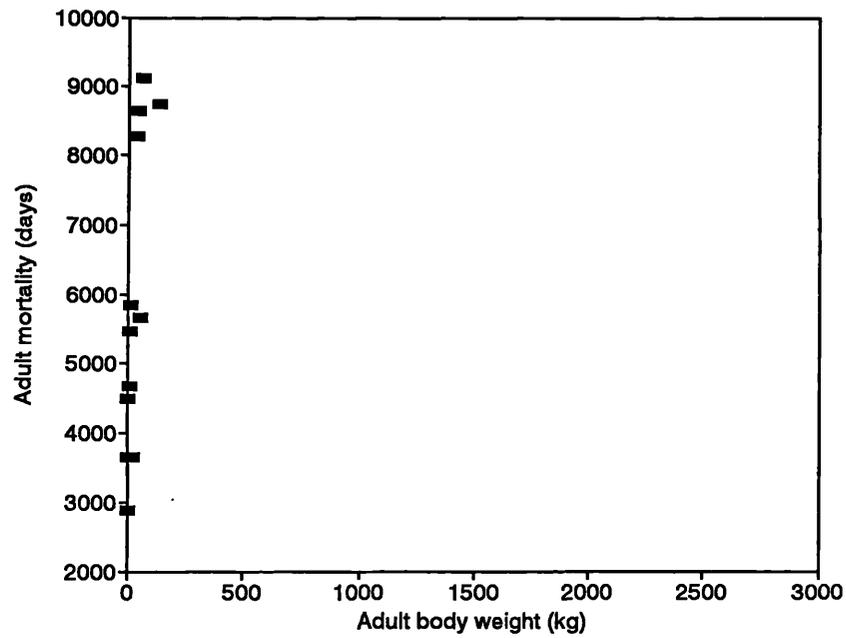


Figure 3.9 Scatterplots of juvenile mortality on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,23 \log x + 1,23$ ($r = 0,59$; $df = 9$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

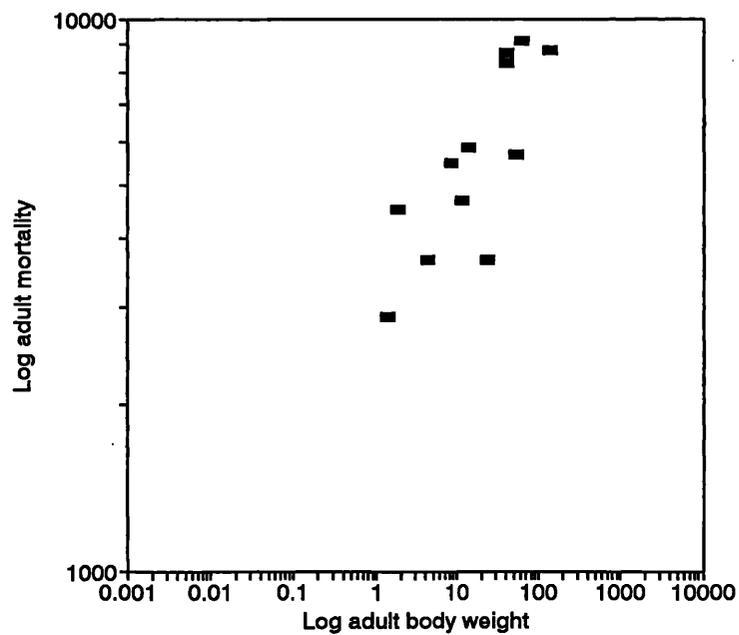
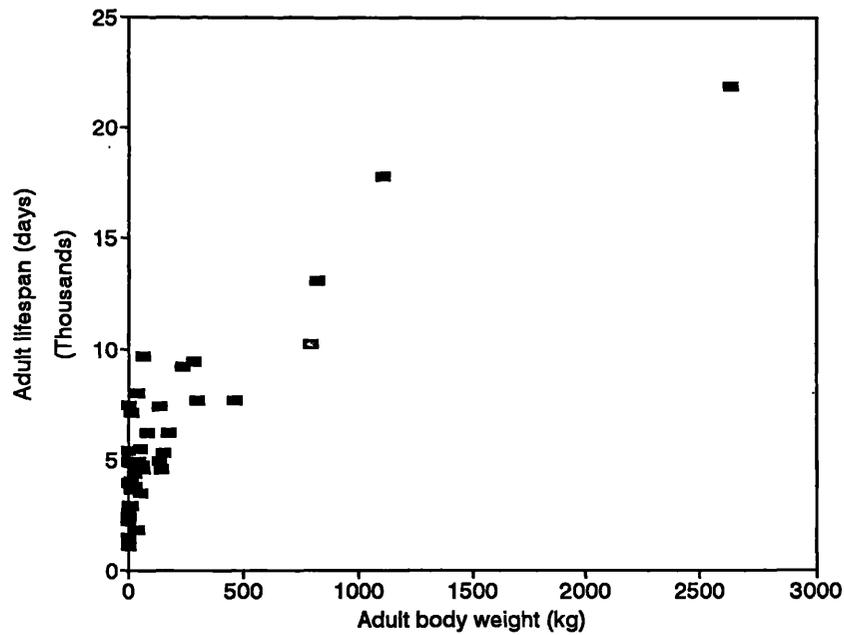


Figure 3.10 Scatterplots of adult mortality on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,22\log x + 3,48$ ($r = 0,81$; $df = 10$) using interactive outlier rejection regression analysis which identified no outliers.

a)



b)

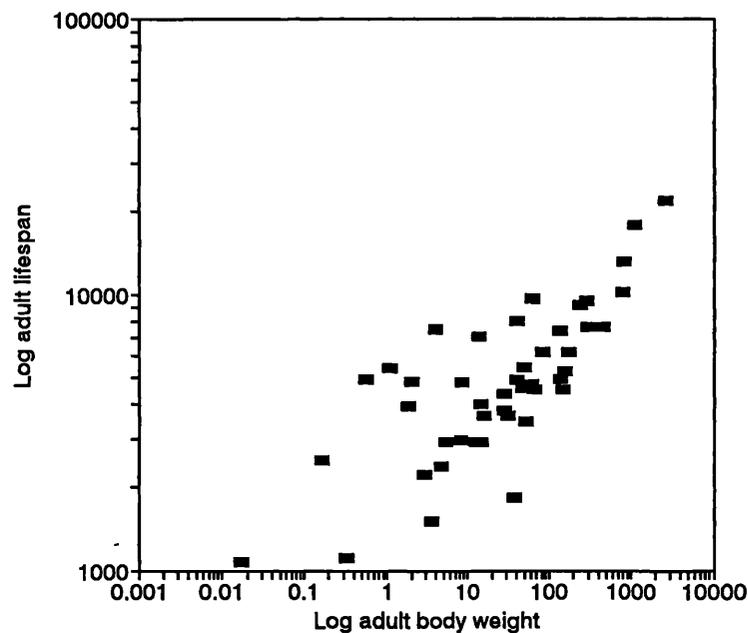


Figure 3.11 Scatterplots of adult lifespan on adult body weight of mammals in the southern African sub-region. (a) A scatterplot using untransformed data. (b) A scatterplot using log transformed data. The relationship was best described by $\log y = 0,20\log x + 3,40$ ($r = 0,76$; $df = 43$) using interactive outlier rejection regression analysis which identified no outliers.

a)

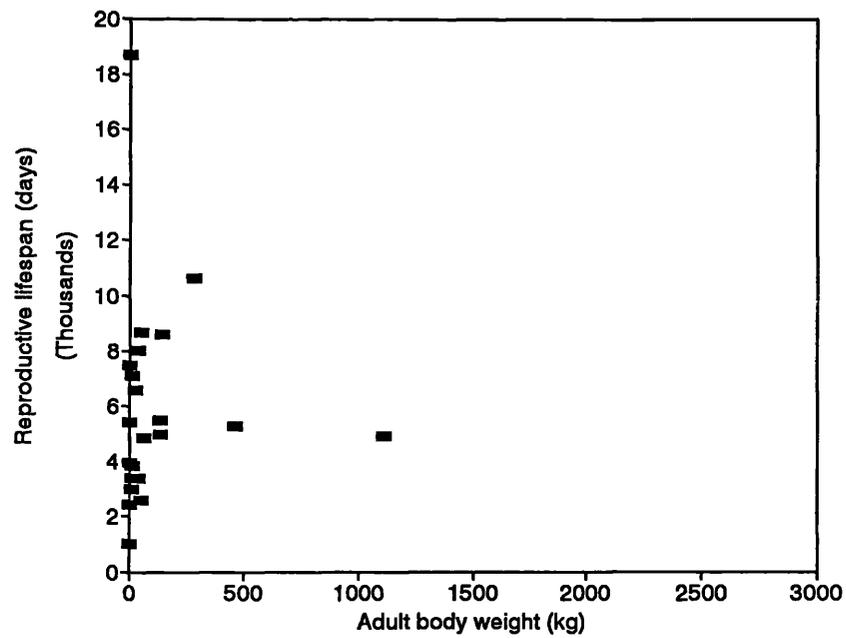


Table 3.4 Correlation coefficients (r) (above the diagonal) and covariances (below the diagonal) of life-history variables of mammals in the southern African sub-region following the removal of the effect of body weight. ** denotes significance at the 99% level. * denotes significance at the 95% level. NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
NEOWT		-0,23** (74)	-0,22** (29)	0,06 (41)	0,17** (77)	-0,18 (12)	-0,11 (30)	0,25** (36)	-0,03 (10)	0,07 (10)	0,03 (36)	0,20 (16)
LITSZ	-4 (74)		-0,01 (32)	-0,11 (45)	-0,50** (91)	-0,08 (15)	-0,23** (33)	-0,02 (38)	0,15 (11)	-0,74** (12)	-0,33** (40)	-0,23** (17)
INLTIN	-539 (29)	-5 (32)		0,57** (21)	-0,01 (32)	-0,26 (8)	0,39** (12)	0,70** (21)	-0,17 (8)	0,44** (7)	-0,26** (21)	0,06 (9)
AGEM	256 (41)	-80 (45)	47007 (21)		-0,04 (47)	0,39** (10)	0,11* (19)	0,23** (26)	-0,11 (7)	0,43** (10)	0,44** (28)	0,36** (10)
GESP	293 (71)	-62 (91)	-399 (32)	-2891 (47)		-0,43** (18)	0,16** (34)	0,23** (44)	-0,61** (11)	0,20 (11)	-0,26** (45)	0,16 (21)
LACP	-518 (12)	-8 (15)	-10833 (8)	23293 (10)	-4987 (18)		0,60** (7)	-0,25 (6)	- (2)	0,56** (4)	0,88** (10)	0,70** (4)
AGEW	-218 (30)	-46 (33)	10680 (12)	10263 (19)	1509 (34)	25030 (7)		0,47** (16)	-0,44** (5)	0,63** (5)	0,18 (17)	0,05 (7)
AGEPRT	928 (36)	-10 (38)	44440 (21)	27718 (26)	13167 (44)	-25324 (6)	26092 (16)		-0,81** (8)	0,38 (5)	-0,21** (31)	-0,22 (12)
JMORT	-10 (10)	2 (11)	-419 (8)	-940 (7)	-775 (11)	769 (2)	-591 (5)	-4297 (8)		0,26 (3)	0,41** (9)	0,14 (4)
ADMORT	135 (10)	-1796 (12)	35428 (7)	170125 (10)	6975 (11)	111478 (4)	196452 (5)	133461 (5)	2167 (3)		0,44** (7)	0,36 (4)
ADLIFE	677 (36)	-1202 (40)	-109312 (21)	345426 (28)	-84355 (45)	359750 (10)	72023 (17)	-132522 (31)	-8790 (9)	648009 (7)		0,71** (18)
RELIFE	5664 (16)	-1841 (17)	26481 (9)	353240 (10)	23917 (21)	80473 (4)	15262 (7)	-108208 (12)	4325 (4)	477462 (4)	3646840 (18)	



$n=12$, $p<0,001$). Of particular interest is the increase in correlation coefficients for most of the variables with reproductive lifespan once the effects of adult body weight were removed as well as the increase in correlation coefficients between juvenile mortality/gestation period and reproductive lifespan/adult lifespan.

Multivariate Analyses

Principal component analysis performed on all 38 species and five variables (adult body weight, neonate weight, litter size, age at maturity, gestation period) for observed data is shown in Table 3.5. Most of the variance can be accounted for by the first two principal components (PC's). Correlation coefficients between variables and PC's are also shown in Table 3.5 giving an indication of the direction of the relationship of each variable with the respective component. A plot of the first two PC's (which account for most of the variance) calculated on observed data (adult body weight included) is given in Figure 3.13 and that of PC-2 and PC-3 in Figure 3.14. Principal component 1 (PC-1) represents a positive gradient of adult body weight, gestation period, neonate weight and age at maturity. This component therefore arranges the species along a dimension that varies from small neonates and adults, short gestation periods and early ages at maturity to the opposite extreme for each trait at the other end.

Principal component 2 (PC-2) represents a positive gradient of litter size thereby arranging the species along a dimension varying from small to large litter sizes. Following the removal of the effects of body weight (Table 3.6, Figure 3.13b), the largest amount of variance is still explained by the first two PC's but there is a reduction in the amount of variance explained by these two PC's of $\approx 19\%$. PC-1 now represents a positive gradient of litter size and a negative gradient of gestation period and neonate weight, whereas PC-2 is dominated by age at maturity. Thus, there has been an interchange of litter size and age at maturity between PC-1 and PC-2 following the removal of adult body weight.

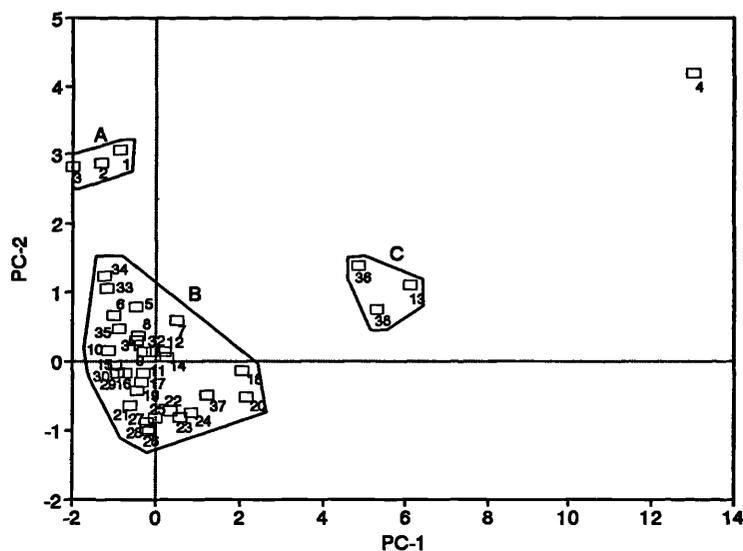
Noteworthy is the relative positions of species along the principal axes as determined by the residual variation of life-history features following removal of adult body weight effects (Figure 3.13b) compared with the observed data (Figure 3.13a). In Figure 3.13a, the



Table 3.5 Eigenvectors and eigenvalues for PCA using five life-history variables. Principle contributions are indicated in brackets. Each components contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components. PC denotes principal component.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult weight	(0,51)	0,33	0,04	-0,19	(0,77)
Litter size	-0,26	(0,76)	(0,56)	0,14	-0,15
Gestation period	(0,38)	-0,48	(0,77)	(-0,58)	-0,04
Neonate weight	(0,52)	0,21	-0,05	0,15	(-0,58)
Age at maturity	(0,50)	0,20	-0,28	(0,76)	-0,22
Eigenvalues	3,67	0,89	0,22	0,15	0,07
Contribution to total variation (%)	63,40	21,89	9,41	3,96	1,37
Cumulative contribution (%)	63,40	85,26	94,67	98,63	100,00
Correlation coefficients					
Adult weight	0,96	0,56	0,21	-0,59	0,91
Litter size	-0,40	0,67	0,78	0,37	-0,28
Gestation period	0,91	0,20	0,15	-0,51	0,63
Neonate weight	0,95	0,43	0,18	-0,72	0,67
Age at maturity	0,90	0,44	0,07	-0,19	0,68

a)



b)

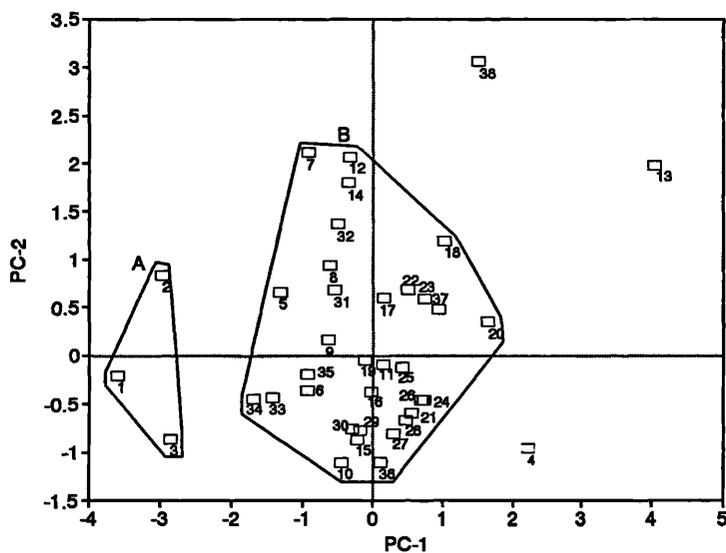
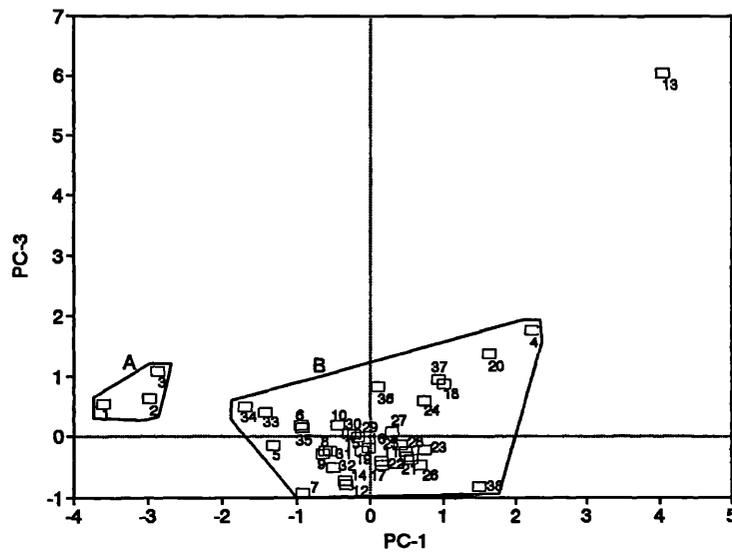


Figure 3.13 a) Principal component plot of the first two components calculated using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for 38 mammal species in the southern African sub-region. b) Principal component plot of the first two components calculated using four life-history variables (neonate weight, litter size, age at maturity and gestation period) of which the effect of body weight has been removed for 38 mammal species in the southern African sub-region. The polygons illustrate groupings within the component space. 1 - *S. scrofa*, 2 - *L. pictus*, 3 - *R. norvegicus*, 4 - *L. africana*, 5 - *A. jubatus*, 6 - *M. mungo*, 7 - *P. leo*, 8 - *C. civetta*, 9 - *P. aethiopicus*, 10 - *M. albicaudatus*, 11 - *P. capensis*, 12 - *P. pardus*, 13 - *G. camelopardalis*, 14 - *C. crocuta*, 15 - *O. irroratus*, 16 - *P. cepapi*, 17 - *F. nigripes*, 18 - *T. oryx*, 19 - *H. africae australis*, 20 - *E. burchelli*, 21 - *T. pumila*, 22 - *A. mēlampus*, 23 - *D. dorcas*, 24 - *T. strepsiceros*, 25 - *T. scriptus*, 26 - *P. monticola*, 27 - *A. marsupialis*, 28 - *S. grimmia*, 29 - *P. albinucha*, 30 - *I. striatus*, 31 - *P. cristatus*, 32 - *H. brunnea*, 33 - *O. megalotis*, 34 - *C. adustus*, 35 - *C. mesomelas*, 36 - *H. amphibius*, 37 - *C. taurinus*, 38 - *D. bicornis*.

a)



b)

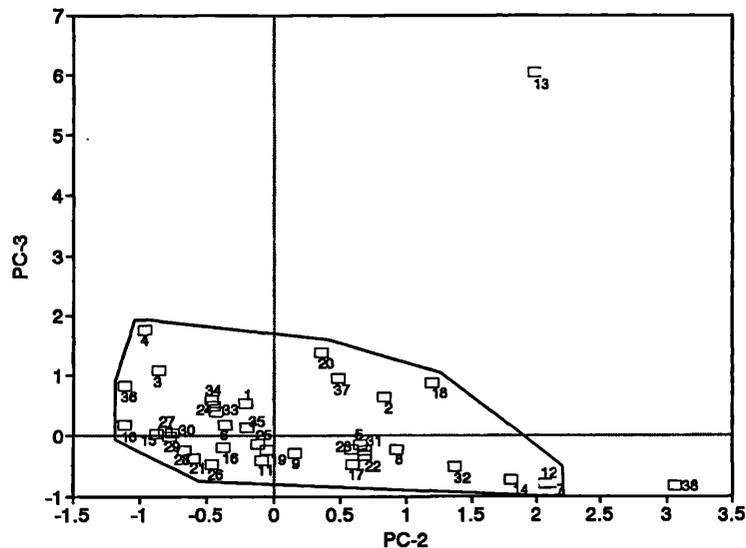


Figure 3.14 a) Principal component plot of components one and three calculated using four life-history variables (neonate weight, litter size, age at maturity and gestation period) of which the effect of body weight has been removed for 38 mammal species in the southern African sub-region. b) Principal component plot of components two and three calculated using four life-history variables (neonate weight, litter size, age at maturity and gestation period) of which the effect of body weight has been removed for 38 mammal species in the southern African sub-region. The polygons illustrate groupings within the component space. 1 - *S. scrofa*, 2 - *L. pictus*, 3 - *R. norvegicus*, 4 - *L. africana*, 5 - *A. jubatus*, 6 - *M. mungo*, 7 - *P. leo*, 8 - *C. civetta*, 9 - *P. aethiopicus*, 10 - *M. albicaudatus*, 11 - *P. capensis*, 12 - *P. pardus*, 13 - *G. camelopardalis*, 14 - *C. crocuta*, 15 - *O. irroratus*, 16 - *P. cepapi*, 17 - *F. nigripes*, 18 - *T. oryx*, 19 - *H. africae australis*, 20 - *E. burchelli*, 21 - *T. pumila*, 22 - *A. melampus*, 23 - *D. dorcas*, 24 - *T. strepsiceros*, 25 - *T. scriptus*, 26 - *P. monticola*, 27 - *A. marsupialis*, 28 - *S. grimmia*, 29 - *P. albinucha*, 30 - *I. striatus*, 31 - *P. cristatus*, 32 - *H. brunnea*, 33 - *O. megalotis*, 34 - *C. adustus*, 35 - *C. mesomelas*, 36 - *H. amphibius*, 37 - *C. taurinus*, 38 - *D. bicornis*.

Table 3.6 Eigenvectors and eigenvalues for PCA using four life-history variables following the removal of the effect of body weight. Principle contributions are indicated in brackets. Each components contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components. PC denotes principal component.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Litter size	(0,66)	0,001	0,25	(0,71)
Gestation period	(-0,62)	-0,29	-0,27	(0,67)
Neonate weight	-0,42	0,20	(0,89)	0,06
Age at maturity	-0,11	(0,93)	-0,28	0,19
Eigenvalues	1,92	1,01	0,73	0,34
Contribution to total variation (%)	40,95	25,64	21,53	11,89
Cumulative contribution (%)	40,95	66,58	88,11	100,00
Correlation coefficients				
Litter size	-0,83	-0,05	0,06	0,84
Gestation period	0,78	-0,04	0,38	-0,02
Neonate weight	0,73	0,23	0,91	0,10
Age at maturity	0,14	0,98	-0,21	0,17

representation of species within the component space as described by the variation in observed data is mainly around the origin (the largest polygon). Following removal of the effects of adult body weight in Figure 3.13b, the data points are spread more regularly in the component space with positional changes in the outliers (4,13,36,38) as well as positional changes within the polygons. Notwithstanding the relative change in positions of these data points, they are still constrained within the same polygons. The exception is *Hippopotamus amphibius* (36) which is included in the largest polygon in Figure 3.13b.

Groupings (polygons A, B and C) differed significantly from each other (MDA; $F_{10,56}=32,72$; $p < 0,0001$). The polygon in Figure 3.13a comprising the feral pig (*Sus scrofa*), the wild dog (*Lycaon pictus*) and the rat (*Rattus norvegicus*) has not changed in composition with the removal of body weight (Figure 3.13b). Once again, only the relative positions changed, with significant differences between groupings (polygons A and B) (MDA: $F_{4,28}=25,55$; $p < 0,0001$).

A dendrogram, drawn from the results of cluster analysis performed on the observed life-history data for 38 mammals and five variables (adult body weight, neonate weight, litter size, age at maturity, gestation period), is shown in Figure 3.15. A dendrogram for data of which the effects of adult body weight have been removed for four variables (neonate weight, litter size, age at maturity, gestation period) is shown in Figure 3.16. Cluster analysis revealed a grouping of the species into 12 clusters prior to removal of adult body weight effects compared with 15 clusters following removal of the effects of this variable. Thus, the removal of adult body weight does not appear to markedly influence the number of clusters that can be identified. However, the composition of species within certain clusters altered.

The cluster analysis reveals some interesting convergences of life-history traits: a rock hyrax (*Procavia capensis* - 11) and warthog (*Phacochoerus aethiopicus* - 9); a feral pig (*S. scrofa* - 1), wild dog (*L. pictus* - 2) and rat (*R. norvegicus* - 3) (Figure 3.15). With the removal of the effects of adult body weight, the latter grouping remains unchanged (Figure 3.16). However, another interesting grouping emerges with the removal of adult body weight in that the vleirat (*Otomys irroratus* - 15), white-tailed mouse (*Mystromys albicaudatus* - 10) and

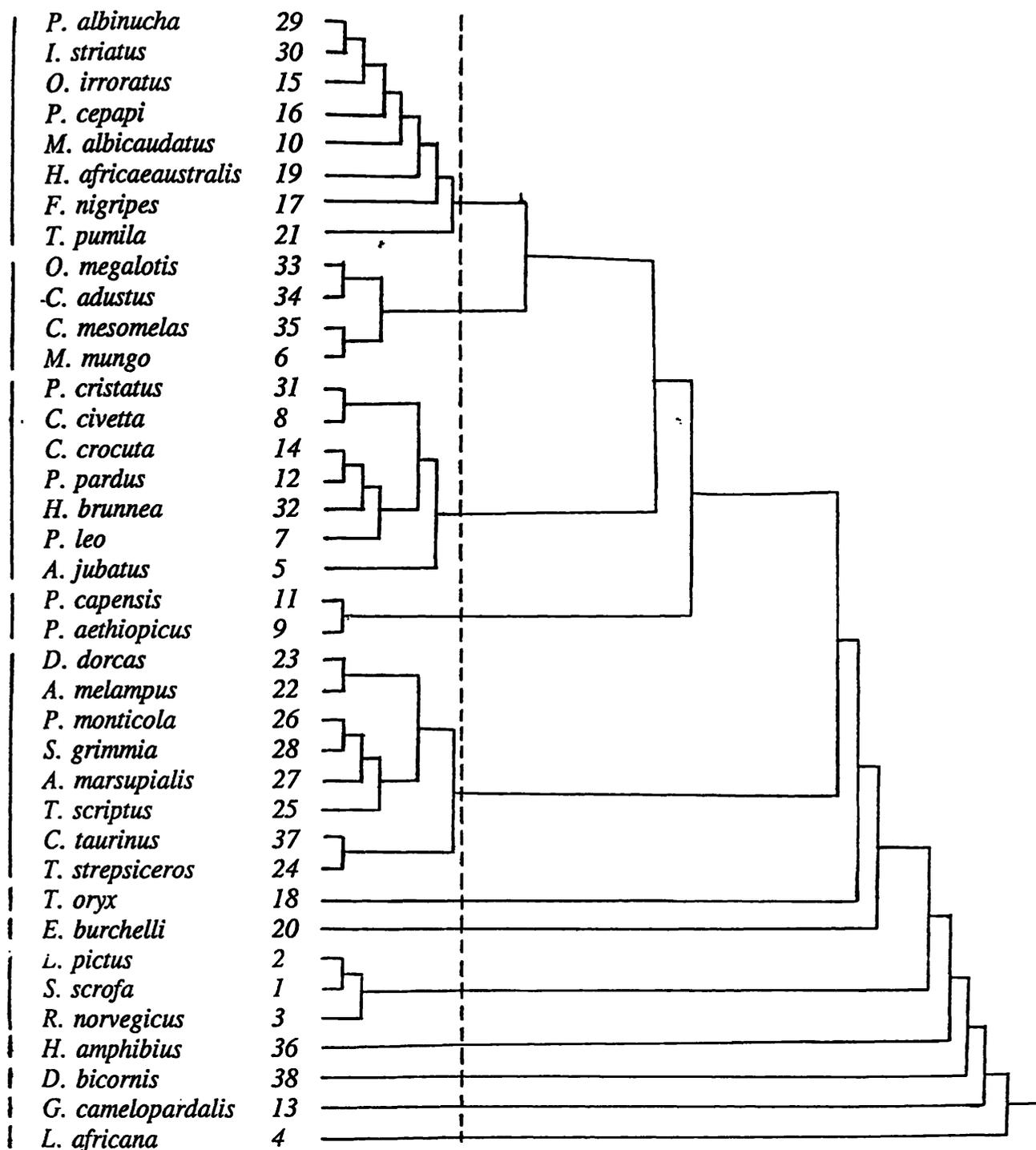


Figure 3.15 Dendrogram illustrating 12 clusters of 38 mammal species in the southern African sub-region using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period). The bars on the left illustrate selected clusters. The vertical broken line illustrates the site of cluster selection after seven convergences.

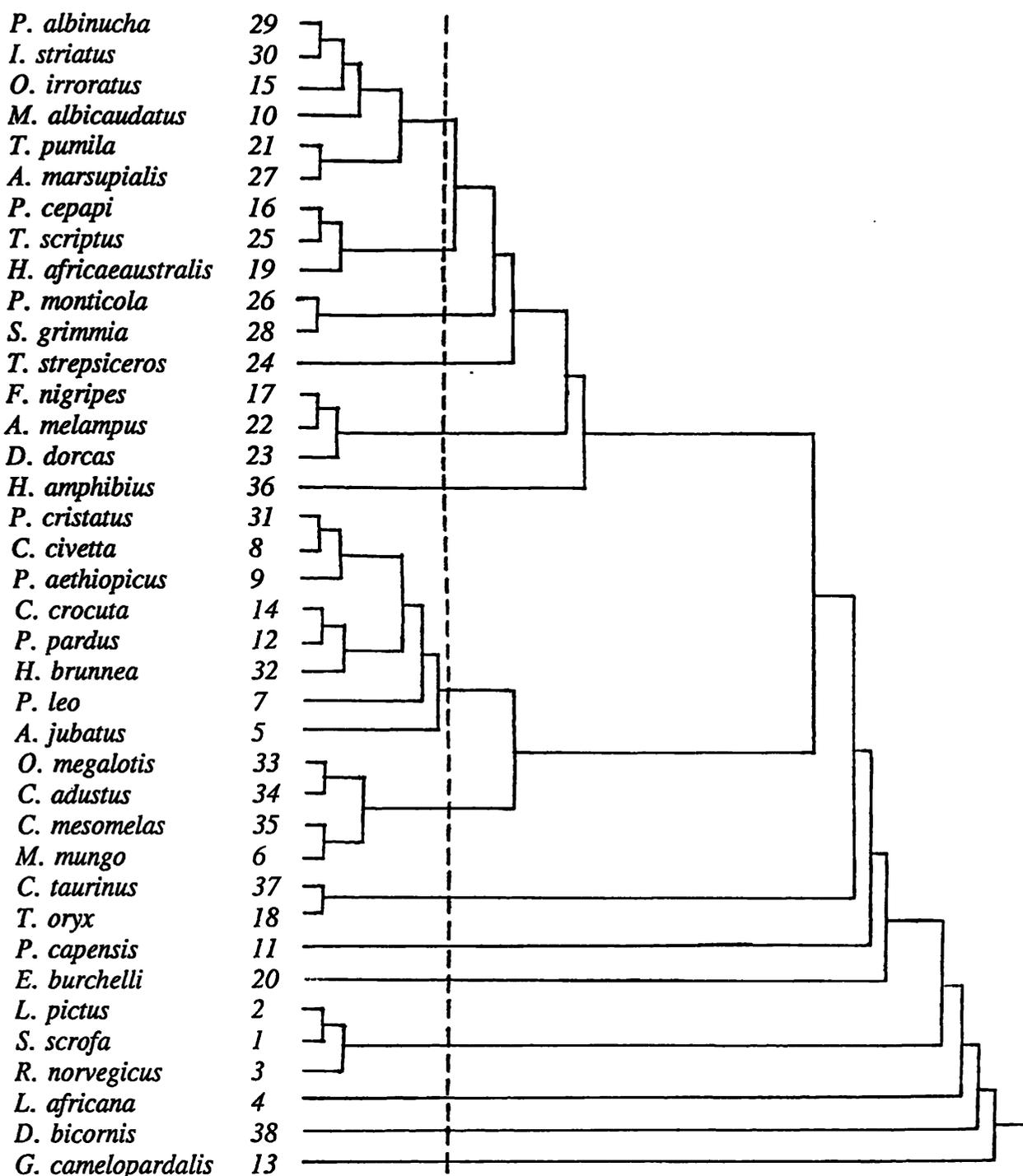


Figure 3.16 Dendrogram illustrating 15 clusters of 38 mammal species in the southern African sub-region using values of four life-history variables of which the effects of body weight have been removed (neonate weight, litter size, age at maturity and gestation period). The bars on the left illustrate selected clusters. The broken vertical line illustrates the site of cluster selection after seven convergences.



little free-tailed bat (*Tadarida pumila* - 21) are clustered together with the springbok (*Antidorcas marsupialis* - 27), African weasel (*Poecilogale albinucha* - 29) and striped polecat (*Ictonyx striatus* - 30), while the small spotted cat (*Felis nigripes* - 17), impala (*Aepyceros melampus* - 22) and bonte/blesbok (*Damaliscus dorcas* - 23) are grouped together. Interesting is the conservation of carnivore groupings following the removal of the effects of body weight. These groupings appear to be as a result of litter size. Thus a convergence of mammalian species appears to have occurred across taxa as far as litter size is concerned, suggesting that although these mammals differ vastly in body size, they have adopted a similar life-history tactic in response to what could have been a similar constraint. However, the overriding effects that adult body weight has is still evident when this variable is removed and certain clusters are broken down into groupings differing in composition even though certain clusters are retained suggesting that constraints other than body size may be influential in describing life-history patterns. A possibility is that phylogeny may constrain life-history features, which is supported by significant differences between orders for the observed data (MDA: $F_{13,74}=10,75$; $p < 0,0001$) as well as for data following the removal of adult body weight (MDA: $F_{12,74}=4,59$; $P < 0,0001$).

Discussion

The significant correlations and covariances evident between most variables with body weight, confirm earlier findings (Fenchel 1974; Western 1979; Harvey & Pagel 1991) that significant associations exist among life-history variables, and persist when the allometric effects of body size are accounted for. Additionally, the scatter plots corroborate the high degree of association found between most life-history variables which also confirms earlier findings (Read & Harvey 1989; van Jaarsveld 1993). The considerable scatter evident in certain plots of the log transformed data may reflect errors of measurement which could be ascribed to the fact that the data used in these analyses were drawn from various sources (see Material and Methods).

Although no significant correlations were detected between litter size, juvenile mortality, reproductive lifespan and most variables (confirmed in scatterplots), once the effects of body weight were removed, these correlations improved considerably. This suggests that adult

body weight may have been masking the real impact these variables have on other life-history variables.

The changes, yet persistence of correlation coefficients with the removal of adult body weight between most variables indicates that although the correlations between observed data are strongly affected by body weight, they cannot only be attributed to body weight. This suggests that simple allometry cannot totally explain the relationships between these variables and that additional selective pressures may be operating (see Read & Harvey 1989).

The change in sign of many of the variables once the effects of body weight is removed, can be interpreted to indicate trade-offs. Although reproductive life-span does not correlate significantly with other variables before body weight is removed, it covaried with several variables thereafter. This could be attributed to one of two reasons. First, the range of data is of such a magnitude that the distribution of the data is dependent on the variability of species used. Thus, although reproductive life-span may covary with certain variables which would influence the overall pattern observed, this relationship does not hold for all species and therefore the correlations would not be significant.

Secondly, an independent unknown factor/factors may be affecting the relationship of reproductive life-span with certain variables so that although reproductive life-span covaries with these variables, the differences between species as far as each factor/factors are concerned may be influencing the correlations. In spite of the improved correlation coefficients between reproductive life-span and certain variables, the fact that these correlations were non-significant suggests that although variables covary, additional selective pressures could be affecting the relationships.

Litter size and juvenile mortality persistently maintained negative correlations across all variables for the untransformed (observed) data and were the variables which did not correlate significantly with adult body weight. The negative relationship between litter size and the other variables suggest that a trade-off may exist between investment in the number of offspring and investment in other developmental phases. The significant negative relationship between adult mortality and litter size suggests another trade-off in that energy

invested in offspring detracts from energy available to invest in maintenance and survival. If adults have a high mortality pattern, it could be advantageous to invest in as many young as possible as soon as possible to increase the chance of at least some of the offspring surviving to reproduce. This could mean that an animal may invest more energy in increasing the number of offspring at the expense of investing energy in other developmental phases. When corrected for body weight, the correlation coefficients with litter size changed dramatically in most cases although as a rule, positive and negative relationships persisted. Thus, irrespective of the effect that other variables may have in shaping certain aspects of a mammal's life-history, the influence that body size has is evident.

With the effects of body weight held constant, juvenile mortality was highly correlated with life-history traits relating to neo- and postnatal growth (gestation period, $r=-0,61$, $n=11$, $p<0,001$ and age at first parturition, $r=-0,81$, $n=8$, $p<0,001$) whereas adult mortality was highly correlated with life-history traits relating to strategies for long-term reproductive output (age at maturity, $r=0,43$, $n=10$, $p<0,001$ and inter litter interval, $r=0,44$, $n=7$, $p<0,001$). This suggests that two possible patterns can be identified here. One is that certain life-history traits could be strongly related to mortality patterns: short gestation period and early age at first parturition with high juvenile mortality as a consequence. The second possibility is that other life-history traits could be a response to mortality patterns: high mortality with long interlitter intervals as a consequence (see Promislow & Harvey 1990). Literature suggests that relatively low parental survival is expected to favour early, but high reproductive output (Charnov & Schaffer 1973; Horn 1978). However, although this expectation is reflected in the relationship between adult mortality and litter size ($r=-0,74$, $n=12$, $p<0,001$), the relationship between adult mortality and age at maturity in this analysis contradicts this ($r=0,43$, $n=10$, $p<0,001$). This suggests that low parental survival favours late but high reproductive output, a pattern which is in contrast with conventional theoretical studies on natural selection and life-history evolution (Charnov & Schaffer 1973; Horn 1978; Promislow & Harvey 1990). One explanation is that although the probability of adults dying may be high, maturity is delayed so that those adults that do survive are more capable of raising larger litters. Alternatively, the inability to reproduce earlier may be seen as a constraint which animals compensate for by producing large litters when this constraint is overcome through age. Seeing that reproductive efficiency increases with age (Adams

1985), older animals that mature later would be able to raise larger litters.

Noteworthy is the relationship between the residuals of gestation period and litter size. With the effect of body weight removed, the correlation coefficient did not change and remained significant at the 99.99% level ($r = -0,50$, $n = 91$, $p < 0,001$). The high correlation coefficient suggests that there is selection independent from body size. However, the impact of body size can be seen in the change of the species positions along PC-1 and PC-2 in figures 3.12 and 3.13. The negative relationship between gestation period and litter size suggests a trade-off between investment in pre-natal developmental phases vs investment in the number of offspring.

With the effect of body weight accounted for, the positive correlation between adult lifespan and lactation period remained significant with $r = 0,88$, $n = 10$, $p < 0,001$. Similarly with reproductive lifespan and lactation period $r = 0,70$, $n = 4$, $p < 0,001$. Thus, extended maternal investment in the form of lactation is associated with an increase in longevity and increased reproductive lifespan. Of particular interest here is the increase in the correlation coefficient between the residuals of reproductive lifespan, age at first parturition and age at maturity in addition to the high correlation coefficients between lactation period, adult lifespan and reproductive lifespan. The significant positive relationships between these variables suggest that an increase in maternal lactational investment is associated with a prolonged juvenile dependence period, a delay in the age at which an animal is first able to reproduce and an extended reproductive lifespan.

Of equal interest is the significant negative correlation between juvenile mortality and age at first parturition ($r = -0,81$, $p < 0,001$). Although the sample size is small ($n = 8$), the correlation coefficient increased significantly following the removal of adult body weight from these two variables. This denotes a significant trade-off suggesting that selection pressures could have resulted in one of two scenarios as a result of juvenile mortality. Low juvenile mortality could result in a delay in the age at which a mammal is first able to reproduce which could be advantageous considering that reproductive efficiency increases with age (until the age of reproductive senescence) (Adams 1985; Promislow & Harvey 1990). Conversely, this delay could increase the chances of an animal dying while waiting

to reproduce (Read & Harvey 1989). If a parent dies before its offspring is independent, the offspring may also die. There is therefore a trade-off between delaying reproduction and increasing the possibility of dying while waiting to do so. The question arises as to why an animal would delay reproduction if this increased the chances of mortality?

By way of explanation, reducing the age at first parturition could be a response to high juvenile mortality given that it is advantageous for juveniles to cross the vulnerable, dependent juvenile period quickly in order to reach the age at which they themselves are able to reproduce as soon as possible. However, these offspring would have received little parental investment and would, as a result, be more susceptible to early mortality. It would therefore be advantageous to adopt a strategy to counteract juvenile mortality. This may suggest that juvenile mortality is higher than adult mortality and that the advantages accruing from delaying reproduction (such as a higher quality of parental care), is more beneficial in counteracting juvenile mortality.

The negative correlation between juvenile mortality and age at first parturition (Table 3.4) suggests an association between low juvenile mortality and late age at first parturition or alternatively, an association between high juvenile mortality and early age at first parturition ($r=-0,81$, $n=8$, $p<0,001$). The notion that juvenile mortality, the age at which an animal is first able to reproduce and degree of maternal care could be influential in describing mammalian life-history patterns within the subregion is supported by the relationship of age at first parturition which is significantly positively correlated with age at weaning ($r=0,47$, $n=16$, $p<0,001$). Thus, mammalian species within the subregion may be characterised by degree of maternal investment which may be a consequence of age at which these species are first able to reproduce. This, in turn, could be a response to juvenile mortality. It follows that these life-history tactics can be self-reinforcing and can help to explain much of the patterns observed among species of the subregion.

The reduction in the amount of variance explained by PC-1 ($\pm 22\%$) once body weight effects had been removed shows the importance of body weight in explaining life-history covariation. This is illustrated in the change of the relative positions of data points within the large polygon when body weight effects were removed in Figure 3.13b. However, the

considerable variation accounted for by PC-2 indicates that life-history traits covary along more than one dimension in southern African mammals, similar to previous findings in mammals in general (Stearns 1983). This is evident from the composition of the data points within the large polygon in Figure 3.13b. Even though body weight effects were removed, the data points were still constrained around the origin suggesting that another factor/factors is having an effect.

The change of the litter size variable from PC-1 to PC-2 shows that adult body weight was masking the effects of this variable. Thus with the removal of adult body weight, the impact of litter size became evident. The impacts of gestation period and neonatal weight were reduced but not eliminated. This suggests that all these variables could have significant independent effects on life-history patterns and together their effects contribute to the ordering of mammals in the southern African subregion onto the theoretical "slow-fast" continuum described for mammals in general (Stearns 1983; Read & Harvey 1989).

Considering the influence of adult body weight on PC-1 before this effect is removed, together with the groupings of species in the dendrogram (3.15), the effects of both size and phylogeny are apparent. Before removal of adult body weight, the groupings of species roughly represent phylogenetic groupings, for instance most of the carnivores and antelope. MDA showed significant differences between these groupings. This suggests that convergent evolutionary forces could have selectively acted on similar sized species and that size-related effects could have been constrained within lineages. An exception is the cluster comprising the feral pig, wild dog and rat which appears to be a litter size grouping (litter size $\approx 9,0$ in each case).

On the other hand, with the effects of adult body weight removed (Figure 3.16), different sized species appear to have adopted similar strategies thus the patterns observed are not a simple consequence of body size. This is evident in the pig (*S. scrofa*), wild dog (*L. pictus*) and rat (*R. norvegicus*) cluster which is still retained indicating the overriding impact of litter size on this grouping. The cluster comprising the spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*) and lion (*Panthera leo*) is also retained. The phylogenetic grouping of the antelope evident before the removal of adult body weight could be a consequence of litter

size equal to one (Figure 3.15). However, the effect of phylogeny is broken down with this group once the effects of adult body weight are removed (Figure 3.16). Thus the patterns observed in Figure 3.15 could be due to a combination of body weight effects, phylogeny as well as litter size. However in Figure 3.16 phylogeny breaks down for the antelope grouping but is retained for the civet (*Civetta civetta*) and cheetah (*Acinonyx jubatus*) as well as the spotted hyaena (*C. crocuta*), leopard (*P. pardus*) and lion (*P. leo*). Thus phylogeny has selective independent effects on different groupings.

The retention of certain clusters irrespective of the effects of adult body weight suggests the importance that another or other life-history traits may have. The affiliation of the rock hyrax (*P. capensis*) with the blue wildebeest (*Chonnochaetes taurinus*), eland (*Taurotragus oryx*) and zebra (*Equus burchelli*) appears to be influenced by the relative late ages at maturity and long gestation periods of the mammals comprising this group. Although the vlei rat (*O. irroratus*) and white-tailed mouse (*M. albicaudatus*) are allied to the springbok (*A. marsupialis*) and free-tailed bat (*T. pumila*), this group is distinct from the latter in that they are characterised by intermediate litter sizes, short gestation periods and early ages at maturity whereas the latter is characterised by a small litter size, later ages at maturity and longer gestation periods. The unusual grouping of feral pig (*S. scrofa*), wild dog (*L. pictus*) and rat (*R. norvegicus*) is a litter size grouping and although this group is allied to the elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*) and giraffe (*Giraffa camelopardalis*), once again this cluster is distinct from the latter in being characterised by earlier ages at maturity and shorter gestation periods in addition to the much larger litters.

Another interesting grouping is the small spotted cat (*F. nigripes*) with the impala (*A. melampus*) and bontebok/blesbok (*D. dorcas*). These mammals are characterised by relatively late ages at maturity which suggests that given the increased efficiency of reproduction in older animals (Ashmole 1963; Charlesworth 1980), there would be an increased efficiency in reproducing healthier offspring or better care when the mothers are older. This could ensure a concomitant increase in the chances of survival which would be important in animals producing only one or a few young per year or in a life-time.

The reduction in the percentage of variance accounted for by PC-1 after adult body weight



effects were removed suggests the considerable effect that body size has on life-history covariation. However with the loading of litter size onto PC-1 as well as the interesting grouping of rat, feral pig and wild dog which are characterised by large litter sizes, suggests the added effects that litter size has on life-history covariation.

Conclusion

This analysis supports earlier findings that life-history traits covary along more than one influential dimension in mammals. The profound effects of adult body weight on life-history covariation are evidenced by the large reduction in the amount of variance explained by PC-1 once these effects are removed. The concomitant addition of litter size to this component with the removal of adult body weight suggests the importance of litter size on life-history covariation. Thus different sized mammals from different taxa appear to have adopted a similar solution to what could be a similar problem, as illustrated by the litter size convergence in the dendrogram. From the clusters it appears that different effects of body size, phylogeny and litter size are more apparent for certain groupings of mammals than others and that although body size plays a definitive role, these effects are overridden by both phylogeny in certain instances and litter size in others. Within this subregion, the suggestion of phylogenetic effects from the cluster analysis is apparent, but its importance in explaining life-history covariation of mammals within this subregion is still obscure at this point of the analysis and can only be determined by removing the possible effects that this variable has on the other life-history traits (see chapter 5).



CHAPTER 4

THE INFLUENCE OF BODY WEIGHT ON PATTERNS OF LIFE-HISTORY COVARIATION AT THE GENUS, FAMILY AND ORDER LEVEL

Introduction

The influence that body size has on southern African mammalian species life-history variables such as age at maturity and gestation period, was shown in chapter 3. Most variables except for litter size, juvenile mortality and reproductive lifespan, consistently covaried with adult body weight. Consistencies in covariations between adult body weight and other demographic traits at the species and order levels, have been illustrated elsewhere (Eisenberg 1981; Peters 1983; Read & Harvey 1989). However, differences in allometric relations between phylogenetic groups have also been shown (see Gould 1975; Radinsky 1978). The regression of biological variables on size in different mammal groups, have frequently shown differences between the slopes of these regressions (Clutton-Brock & Harvey 1979). For example, numerous variables such as gestation period, litter weight, age at weaning, age at maturity, life span and brain size have been regressed on body weight in different families of primates and rodents and have shown marked differences in slopes between families (Clutton-Brock & Harvey 1979; Mace 1979).

On the other hand, similar demographic traits may be a result of occupying similar environments. Keeping in mind that organisms are generally grouped into taxonomic categories according to morphological features, or more specifically, according to phenotypic traits that they have in common (Mader 1993), those organisms having similar traits will usually be grouped more closely. Consequently, traits in one taxonomic grouping may be more similar in phylogenetically closer groupings. For instance, a relationship between body size and another demographic trait evident at the species level may persist at other taxonomic levels, such as the genus or the family level. This chapter aims to establish whether the

effects of adult body weight that were evident at the species level for mammals from the subregion (see Chapter 3) persist at higher taxonomic levels. This would suggest that body weight is a trait which retains its effects irrespective of lineage (see Stearns 1989).

Material and Methods

Average life-history parameters for all genera, families and orders were calculated (adult body weight, neonate weight, litter size, interlitter interval, age at maturity, gestation period, lactation period, age at weaning, age at first parturition, juvenile mortality, adult mortality, adult life span, reproductive life span) from 293 terrestrial mammal species found within the southern African subregion. As mean values were calculated at each taxonomic level, this resulted in three data sets, one each at the genus, family and order level. Data manipulation thus resulted in a reduction of the data set with each successively higher taxonomic level giving rise to 3 data matrices (genus 13 x 103; family 13 x 34; order 13 x 13). Correlation and covariance analyses were conducted on the three data sets respectively. Wilcoxon matched-pairs signed-ranks tests (Siegel 1956) were done between correlation coefficients obtained for variables at each taxonomic level as well as between observed and residual data for each variable at each taxonomic level. Residual data are values for which the effects of adult body weight have been removed by calculating deviations from allometric relationships to obtain relative values.

Principle component and cluster analyses were performed using only five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) and using only those records having data for the complete set of variables. This resulted in 35 Genera, 19 Families and 9 Orders being included in the analyses. The analyses were also repeated on residual values (see Material and Methods, chapter 2 for how residual values were obtained) following the removal of the effects of adult body weight at all three taxonomic levels which resulted in 3 additional data sets, free of similarity associated with potential body weight groupings. Multiple discriminant analyses (MDA) were used to investigate differences between groups identified within the component space of PCA.

Results

Correlation and covariance analyses

The correlations and covariances of mean genus, family and order life-history variables for mammals from the southern African subregion are presented in Tables 4.1, 4.2 and 4.3 respectively for the observed data. Significant correlations were evident for most variables and at all taxonomic levels. In addition, most variables covaried at all three taxonomic levels. For clarification and comparative purposes, the results of correlations at the species level obtained for the observed data in chapter 3 were included in a summary of analyses (Table 4.4). This summary analysis represents changes in correlations from the species to the genus level, from the species to the family level and from the species to the order level.

For the observed data, 67.5% of the total number of correlations were significant at the species level (95% confidence level), whereas at the genus, family and order levels 83.1%, 80.5% and 80.5% of correlations were significant respectively. Noteworthy, are the additional number of correlation coefficients that increase at the order level (90,8% of the total number of correlations, see Table 4.4). However, paired comparisons between the correlation coefficients obtained at the species level and those obtained at the genus, family and order levels revealed that a significant difference from the species level occurred at all levels with the highest impact at the family level (genus: $z = -3,04$ $p < 0,05$; family: $z = -3,07$ $p < 0,05$; order: $z = -2,22$ $p < 0,05$).

The correlations and covariances of life-history variables, with the effects of adult body weight removed at genus, family and order levels, are presented in Tables 4.5, 4.6 and 4.7 respectively. Similarly, a table of summary analyses was constructed for the residual data (adult body weight removed) (see Table 4.8). The changes in correlation coefficients between life-history variables from the species level to the genus, family and order levels are not as marked as those for the observed data. No significant differences for paired comparisons between correlation coefficients obtained at the species level and correlation coefficients obtained at the genus, family and order levels, could be demonstrated (genus: $z = -1,56$ $p > 0,05$; family: $z = -0,75$ $p > 0,05$; order: $z = 0,29$ $p > 0,05$).



Table 4.1 Correlation coefficients (*r*) (above the diagonal) and covariances (below the diagonal) of life history variables of mammalian genera in the southern African sub-region. ** denotes significance at the 99% level and * at the 95% level. Figures in brackets represent sample sizes. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
ADWT		0,91** (72)	-0,17** (103)	0,62** (24)	0,86** (43)	0,44** (19)	0,78** (18)	0,64** (37)	0,88** (38)	0,07 (11)	0,79** (11)	0,89** (37)	0,01 (18)
NEOWT	6669 (72)		-0,29** (68)	0,59** (31)	0,82** (40)	0,49** (68)	0,67** (12)	0,53** (35)	0,89** (34)	0,16 (10)	0,80** (10)	0,83** (34)	0,07 (16)
LITSZ	-96 (103)	-12 (68)		-0,32** (32)	-0,27** (42)	-0,49** (82)	-0,47** (15)	-0,49** (35)	-0,40** (34)	-0,24 (10)	-0,46** (11)	-0,39** (34)	-0,17 (18)
INLTIN	109777 (34)	5950 (31)	-226 (32)		0,96** (22)	0,25* (32)	0,59** (8)	0,67** (16)	0,95** (23)	-0,49** (8)	0,89** (7)	0,77** (22)	0,43** (11)
AGEM	243665 (43)	12985 (40)	-373 (42)	226726 (22)		0,42** (45)	0,79** (10)	0,73** (21)	0,96** (26)	0,14 (8)	0,86** (9)	0,88** (25)	0,30 (12)
GESP	25947 (90)	2136 (68)	-117 (82)	22863 (32)	62975 (45)		0,69** (18)	0,67** (38)	0,43** (39)	0,07 (11)	0,86** (10)	0,29** (38)	0,36** (21)
LACP	101842 (18)	6336 (12)	-83 (15)	52930 (8)	159847 (10)	21052 (18)		0,93** (9)	0,73** (6)	-1,00** (2)	0,86** (4)	0,93** (10)	0,42 (4)
AGEW	48711 (37)	2570 (35)	-152 (35)	44875 (16)	106057 (21)	17174 (38)	56135 (9)		0,73** (19)	-0,56** (7)	0,76** (6)	0,76** (22)	0,51** (12)
AGEPRT	293461 (38)	17959 (34)	-644 (34)	229441 (23)	532991 (26)	72452 (39)	212397 (6)	127766 (19)		-0,30 (8)	0,71** (5)	0,88** (28)	0,16 (13)
JMORT	376 (11)	86 (10)	-5 (10)	-1691 (8)	1884 (8)	172 (11)	-137 (2)	-936 (7)	-3443 (8)		1,00** (3)	-0,12 (9)	0,16 (5)
ADMORT	51255 (11)	844 (10)	-1954 (11)	229938 (7)	555326 (9)	31609 (10)	427198 (4)	340692 (6)	317362 (5)	63488 (3)		0,64** (6)	0,72* (3)
ADLIFE	2 (37)	102878 (34)	-2757 (34)	1055690 (22)	3107850 (25)	297470 (38)	1485930 (10)	657093 (22)	2942040 (28)	-6079 (9)	2592700 (6)		0,39** (17)
RELIFE	10151 (18)	4371 (16)	-1272 (18)	104118 (11)	408571 (12)	125575 (21)	149418 (4)	193574 (12)	103861 (13)	7040 (5)	2248590 (3)	3298610 (17)	



Table 4.2 Correlation coefficients (*r*) (above the diagonal) and covariances (below the diagonal) of life history variables of mammalian families in the southern African sub-region. ** denotes significance at the 99% level and * at the 95% level. Figures in brackets represents sample sizes. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
ADWT		0,91** (29)	-0,24 (34)	0,77** (17)	0,93** (19)	0,84** (32)	0,77** (17)	0,80** (19)	0,89** (13)	-0,13 (8)	0,97** (4)	0,92** (17)	0,05 (10)
NEOWT	15011 (29)		-0,37** (27)	0,74** (16)	0,88** (19)	0,88** (28)	0,67** (15)	0,61** (19)	0,89** (13)	0,09 (8)	0,98** (4)	0,84** (17)	0,22 (10)
LITSZ	-165 (34)	-15 (27)		-0,45** (17)	-0,35* (19)	-0,40** (31)	-0,22 (17)	-0,50** (18)	-0,50** (13)	0,39 (8)	-0,66* (4)	-0,54** (17)	-0,16 (10)
INLTIN	193621 (17)	10261 (16)	-276 (17)		0,88** (15)	0,85** (16)	0,65** (9)	0,76** (11)	0,96** (12)	-0,21 (8)	0,89** (4)	0,78** (12)	0,76** (8)
AGEM	486796 (19)	25543 (19)	-397 (19)	271560 (15)		0,90** (20)	0,79** (11)	0,80** (14)	0,96** (13)	-0,13 (8)	1,00** (4)	0,90** (14)	0,33 (10)
GESP	65229 (32)	4311 (28)	-78 (31)	58032 (16)	122822 (20)		0,67** (17)	0,74** (19)	0,94** (13)	-0,20 (8)	0,98** (4)	0,80** (17)	0,49** (11)
LACP	10605 (17)	5569 (15)	-34 (17)	54525 (9)	160082 (11)	21343 (17)		0,91** (9)	0,73** (6)	0,18** (4)	0,83** (3)	0,87** (10)	-0,13 (5)
AGEW	92465 (19)	4016 (19)	-134 (18)	65778 (11)	142100 (14)	25122 (19)	48556 (9)		0,77** (11)	-0,51** (8)	0,75** (4)	0,84** (14)	0,52** (8)
AGEPRT	695364 (13)	37501 (13)	-853 (13)	390417 (12)	912625 (13)	196234 (13)	215107 (6)	181107 (11)		-0,52* (7)	0,56 (3)	0,87** (11)	0,57** (7)
JMORT	-687 (8)	51 (8)	9 (8)	-850 (8)	-1061 (8)	-512 (8)	583 (4)	-1198 (8)	-5180 (7)		0,72* (3)	-0,21 (8)	0,24 (5)
ADMORT	38284 (4)	653 (4)	-1872 (4)	200061 (4)	572602 (4)	33198 (4)	372889 (3)	252935 (4)	297838 (3)	29623 (3)		0,98** (4)	0,98** (3)
ADLIFE	3634970 (17)	181885 (17)	-4668 (17)	1816390 (12)	4591180 (14)	838151 (17)	1371920 (10)	956848 (14)	5544400 (11)	-10124 (8)	3782960 (4)		1,00** (11)
RELIFE	52762 (10)	12435 (10)	-912 (10)	358228 (8)	477161 (10)	244794 (11)	-70297 (5)	183081 (8)	809585 (7)	10982 (5)	3575210 (3)	2948630 (10)	



Table 4.3 Correlation coefficients (*r*) (above the diagonal) and covariances (below the diagonal) of life history variables of mammalian orders in the southern African sub-region. ** denotes significance at the 99% level and * at the 95% level. Figures in brackets represent sample sizes. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADLIFE	RELIFE
ADWT		0,99** (12)	-0,29 (13)	0,84** (7)	0,95** (9)	0,86** (12)	0,85** (9)	0,95** (8)	0,95** (6)	-0,63 (3)	0,96** (8)	0,56 (6)
NEOWT	26132 (12)		-0,37 (12)	0,87** (7)	0,98** (9)	0,91** (12)	0,88** (9)	0,98** (8)	0,98** (6)	-0,57 (3)	0,98** (8)	0,58 (6)
LITSZ	-215 (13)	-13 (12)		-0,61* (7)	-0,41 (9)	-0,54** (12)	-0,30 (9)	-0,63** (8)	-0,61* (6)	0,14 (3)	-0,49 (8)	-0,37 (16)
INLTIN	379967 (7)	17824 (7)	-315 (7)		0,89** (7)	0,90** (7)	0,84** (6)	0,89** (6)	0,99** (6)	-0,92** (3)	0,99** (5)	0,99** (4)
AGEM	847669 (9)	40179 (9)	-422 (9)	476722 (7)		0,96** (9)	0,90** (8)	1,00** (7)	1,00** (6)	-0,78* (3)	0,99** (6)	0,72** (5)
GESP	122900 (12)	6003 (12)	-104 (12)	95350 (7)	199370 (9)		0,88** (9)	0,94** (8)	0,96** (6)	-0,37 (3)	0,88** (8)	0,70** (6)
LACP	153011 (9)	7152 (9)	-63 (9)	98278 (6)	206252 (8)	34108 (9)		0,93** (6)	0,93** (5)	1,00** (2)	0,91** (6)	0,18 (5)
AGEW	205313 (8)	9671 (8)	-172 (8)	103017 (6)	266960 (7)	48294 (8)	54676 (6)		1,00** (5)	-0,75 (3)	1,00** (6)	0,62 (5)
AGEPRT	1329250 (6)	61853 (6)	-969 (6)	669446 (6)	1621490 (6)	320777 (6)	355387 (5)	368770 (5)		-0,77* (3)	1,00** (5)	1,00** (4)
JMORT	-1339 (3)	-104 (3)	1 (3)	-2156 (3)	-4246 (3)	-621 (3)	896 (2)	-713 (3)	-3872 (3)		-0,88** (3)	-0,80* (3)
ADLIFE	5743630 (8)	268645 (8)	-3480 (8)	3824050 (5)	8443280 (6)	1229350 (8)	1595680 (6)	1882970 (6)	10577100 (5)	-24073 (3)		0,53 (6)
RELIFE	358838 (6)	32156 (6)	-1612 (6)	1100670 (4)	1413320 (5)	357255 (6)	83075 (5)	268196 (5)	2460990 (4)	-21204 (3)	6207160 (6)	

Table 4.4 Summary of the change in correlations between observed variables from the species level to the genus, family and order level. * denotes significance at the 95% level.

	Percentage significant correlations	Comparison level	Percentage that remained the same	Percentage that decreased	Percentage that increased	Percentage that changed sign	z-value (Wilcoxon matched pairs signed-ranks tests)
Species	67,5						
Genus	83,1	Species to Genus ¹	22,1	19,5	58,4	2,6	-3,04* <i>p</i> < 0,05
Family	80,5	Species to Family ²	7,8	19,5	72,8	9,1	-3,07* <i>p</i> < 0,05
Order	80,5	Species to Order ³	1,5	26,2	90,8	7,8	-2,22* <i>p</i> < 0,05

¹ Represents a comparison between the correlation coefficient matrix based on observed species data (Chapter 3) and a correlation coefficient matrix based on average values calculated for the genus level.

² Represents a comparison between the correlation coefficient matrix based on observed species data (Chapter 3) and a correlation coefficient matrix based on average values calculated for the family level.

³ Represents a comparison between the correlation coefficient matrix based on observed species data (Chapter 3) and a correlation coefficient matrix based on average values calculated for the order level.



Table 4.5 Correlation coefficients (r) (above the diagonal) and covariances (below the diagonal) of life history variables of mammalian genera in the southern African sub-region for which the effects of body weight have been removed. ** denotes significance at the 99% level and * at the 95% level. Figures in brackets represent sample sizes. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
NEOWT		-0,22** (65)	-0,15 (30)	0,27** (38)	0,18** (66)	-0,44** (12)	-0,06 (33)	0,31** (33)	-0,01 (10)	0,21 (10)	0,03 (33)	-0,07 (15)
LITSZ	-5 (65)		-0,02 (31)	-0,11 (40)	-0,51** (78)	-0,05 (15)	-0,23** (33)	-0,01 (33)	0,18 (10)	-0,60** (11)	-0,27** (33)	-0,03 (15)
INLTIN	-12 (30)	-623 (31)		0,73** (21)	0,01 (31)	-0,01 (8)	0,33** (15)	0,80** (22)	-0,25 (8)	0,45** (7)	-0,28** (21)	0,49** (10)
AGEM	1254 (38)	-77 (40)	58257 (21)		0,11 (42)	0,02 (10)	0,53** (19)	0,81** (25)	-0,13 (8)	0,45** (9)	-0,01 (24)	0,22 (10)
GESP	343 (66)	-68 (78)	925 (31)	8224 (42)		-0,27** (18)	0,16** (36)	0,22** (38)	-0,52** (11)	0,11 (10)	-0,23** (37)	0,10 (17)
LACP	-1133 (12)	-4 (15)	-242 (8)	1093 (10)	-263 (18)		0,84** (9)	0,01 (6)	1,00** (2)	0,86** (4)	0,62** (10)	0,03 (4)
AGEW	-116 (33)	-46 (33)	7642 (15)	31648 (19)	1454 (36)	23320 (9)		0,49** (18)	-0,50** (7)	0,80** (6)	0,26** (21)	-0,11 (11)
AGEPRT	1282 (33)	-3 (33)	45373 (22)	101322 (25)	13590 (38)	969 (6)	22883 (18)		-0,69** (8)	0,72** (5)	-0,28** (27)	0,33 (12)
JMORT	-3 (10)	2 (10)	-598 (8)	-974 (8)	-624 (11)	1224 (2)	-873 (7)	-3092 (8)		0,26 (3)	-0,09 (9)	0,17 (5)
ADMORT	269 (10)	-1572 (11)	25133 (7)	101924 (9)	4081 (10)	122748 (4)	233434 (6)	214399 (5)	5096 (3)		0,17 (6)	0,80** (3)
ADLIFE	892 (33)	-775 (33)	-107107 (21)	-8262 (24)	-102397 (37)	222722 (10)	87110 (21)	-176226 (27)	-2062 (9)	328890 (6)		0,25** (16)
RELIFE	-2592 (15)	-255 (15)	241962 (10)	114945 (10)	12054 (17)	3508 (4)	-19150 (11)	169729 (12)	7317 (5)	921213 (3)	1026530 (16)	



Table 4.6 Correlation coefficients (*r*) (above the diagonal) and covariances (below the diagonal) of life history variables of mammalian families in the southern African sub-region for which the effects of body weight have been removed. ** denotes significance at the 99% level and * at the 95% level. Figures in brackets represent sample sizes. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
NEOWT		-0,19 (27)	-0,20 (16)	0,21 (19)	0,36** (28)	-0,46** (15)	-0,28* (19)	0,10 (13)	0,02 (8)	0,20 (4)	0,03 (17)	0,02 (10)
LITSZ	-4 (27)		-0,01 (17)	-0,04 (19)	-0,36** (31)	0,13 (17)	-0,27* (18)	0,13 (13)	0,48** (8)	-0,80** (4)	-0,40** (17)	0,10 (10)
INLTIN	-1001 (16)	-3 (17)		0,25 (15)	0,06 (16)	0,26 (9)	0,20 (11)	0,91** (12)	-0,34 (8)	-0,13 (4)	0,43** (12)	0,45** (8)
AGEM	1231 (19)	-17 (19)	18741 (15)		0,58** (19)	0,17 (11)	0,31* (14)	0,45** (13)	-0,19 (8)	0,23 (4)	0,28 (14)	0,55** (9)
GESP	542 (28)	-37 (31)	1325 (16)	15862 (19)		-0,33** (17)	0,21 (19)	0,07 (13)	-0,41* (8)	0,41 (4)	0,10 (17)	0,45** (10)
LACP	-1179 (15)	10 (17)	10613 (9)	6221 (11)	-2462 (17)		0,97** (9)	0,26 (6)	-0,22 (4)	0,28 (3)	0,39** (10)	0,29 (5)
AGEW	-646 (19)	-39 (18)	4054 (11)	10951 (14)	2249 (19)	18630 (9)		0,28 (11)	-0,38 (8)	0,42 (4)	0,48** (14)	0,18 (8)
AGEPRT	877 (13)	70 (13)	76993 (12)	56408 (13)	2752 (13)	22513 (6)	10587 (11)		-0,43* (7)	0,39 (3)	-0,49** (11)	0,34 (7)
JMORT	8 (8)	10 (8)	-795 (8)	-662 (8)	-641 (8)	-724 (4)	-948 (8)	-1813 (7)		-0,98** (3)	-0,29 (8)	0,01 (5)
ADMORT	44 (4)	-510 (4)	-2057 (4)	28051 (4)	2352 (4)	18790 (3)	31896 (4)	39907 (3)	-6542 (3)		0,32 (4)	0,49 (3)
ADLIFE	1340 (17)	-1245 (17)	-228855 (12)	186055 (14)	22957 (17)	131028 (10)	124998 (14)	-490220 (11)	-6338 (8)	265399 (4)		-0,16 (10)
RELIFE	-528 (10)	503 (10)	252548 (8)	386669 (9)	141202 (10)	63414 (5)	42542 (8)	333854 (7)	342 (5)	347160 (3)	-1203190 (10)	



Table 4.7 Correlation coefficients (r) (above the diagonal) and covariances (below the diagonal) of life history variables of mammalian orders in the southern African sub-region for which the effects of adult body weight have been removed. ** denotes significance at the 99% level and * at the 95% level. Figures in brackets represent sample sizes. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADLIFE	RELIFE
NEOWT		-0,05 (12)	-0,28 (7)	0,71** (9)	0,65** (12)	0,04 (9)	-0,71** (8)	-0,61** (6)	0,25 (3)	0,60** (8)	0,06 (6)
LITSZ	-0,3 (12)		-0,20 (7)	0,10 (9)	-0,31 (12)	0,13 (9)	-0,05 (8)	0,14 (6)	-0,59 (3)	-0,27 (8)	-0,03 (6)
INLTIN	-502 (7)	-43 (7)		-0,27 (7)	-0,22 (7)	-0,28 (6)	0,16 (6)	0,93** (6)	-1,00** (3)	0,21 (5)	0,30 (4)
AGEM	1627 (9)	32 (9)	-21302 (7)		0,79** (9)	0,50* (8)	-0,15 (7)	-0,09 (6)	-0,30 (3)	0,85** (6)	0,28 (5)
GESP	379 (12)	-27 (12)	-5155 (7)	23965 (9)		-0,11 (9)	-0,38 (8)	-0,51* (6)	0,48 (3)	0,31 (8)	0,35 (6)
LACP	12 (9)	9 (9)	-3530 (6)	4894 (8)	-529 (9)		0,06 (6)	-0,05 (5)	1,00** (2)	0,62** (6)	0,17 (5)
AGEW	-327 (8)	-3 (8)	2632 (6)	-3194 (7)	-2400 (8)	209 (6)		0,85** (5)	-1,00** (3)	-0,07 (6)	0,34 (5)
AGEPRT	-1164 (6)	30 (6)	25245 (6)	-6975 (6)	-12235 (6)	-628 (5)	15484 (5)		-0,96** (3)	0,10 (5)	0,41 (4)
JMORT	15 (3)	-4 (3)	-1429 (3)	-724 (3)	456 (3)	315 (2)	-363 (3)	-2002 (3)		-0,63 (3)	-0,99** (3)
ADLIFE	8412 (8)	-437 (8)	59908 (5)	577547 (6)	60023 (8)	73085 (6)	-9897 (6)	49992 (5)	-7316 (3)		0,03 (6)
RELIFE	1130 (6)	-97 (6)	80868 (4)	290785 (5)	113566 (6)	53546 (5)	37257 (5)	162004 (4)	-4955 (3)	211682 (6)	

Table 4.8 Summary of the change in correlations between residual (adult body weight removed) variables from the species level to the genus, family and order level.

	Percentage significant correlations	Comparison level	Percentage that remained the same	Percentage that decreased	Percentage that increased	Percentage that changed sign	z-value (Wilcoxon matched pairs signed-ranks tests)
Species	56,9						
Genus	53,8	Species to Genus ¹	7,7	43,1	47,7	12,3	-1,56 <i>p</i> > 0,05
Family	36,9	Species to Family ²	3,1	44,6	50,8	23,1	-0,75 <i>p</i> > 0,05
Order	31,5	Species to Order ³	0,0	40,7	59,3	38,9	0,29 <i>p</i> > 0,05

¹ Represents a comparison between the correlation coefficient matrix based on species data for which the effects of body weight have been removed (Chapter 3) and a correlation coefficient matrix based on average values calculated for the genus level and for which the effects of body weight have been removed.

² Represents a comparison between the correlation coefficient matrix based on species data for which the effects of body weight have been removed (Chapter 3) and a correlation coefficient matrix based on average values calculated for the family level and for which the effects of body weight have been removed.

³ Represents a comparison between the correlation coefficient matrix based on species data for which the effects of body weight have been removed (Chapter 3) and a correlation coefficient matrix based on average values calculated for the order level and for which the effects of body weight have been removed.



Following the removal of adult body weight, the number of significant correlations decreased at all taxonomic levels with regard to the number of significant correlations found using the observed data (see Table 4.9). In certain instances, variables were affected similarly at all levels while in others, variables were affected differently at different taxonomic levels (see Tables 4.5, 4.6 & 4.7). The percentage of correlations that persist, decrease or increase their significance from observed to residual data at all taxonomic levels, are consistent at all taxonomic levels and were significant at all taxonomic levels (see z -values, Table 4.9). Again, the changes in correlation coefficients due to the removal of adult body weight effects was most pronounced at the family level (see Table 4.9, family: $z = -5,22$; $p < 0,05$).

At the genus level, correlation coefficients between certain variables increased in magnitude following the removal of the effects of adult body weight (Table 4.5), for instance, litter size with gestation period, litter size with adult mortality, adult mortality with age at weaning and adult mortality with reproductive lifespan. Although the correlation coefficients of age at maturity, gestation period, lactation period, age at weaning and interlitter interval decreased in relation to certain variables, some of these correlations remained significant. Of interest is the increased negative correlation between age at first parturition and juvenile mortality ($r = -0,30$ to $r = -0,69$; $n = 8$; $p < 0,01$) at the genus level, when the effects of adult body weight are removed, which is similar to the pattern shown for these two variables at the species level (see Chapter 3, Tables 3.1 & 3.4). Age at first parturition remained significantly positively correlated with both the age at maturity ($r = 0,81$; $n = 25$; $p < 0,01$) and the interlitter interval ($r = 0,80$; $n = 22$; $p < 0,01$) when the effects of adult body weight were removed.

At the family level, correlation coefficients generally decreased once the effects of adult body weight were removed (Tables 4.2 & 4.6). However, the correlation coefficients between adult mortality and litter size and between adult mortality and juvenile mortality increased following the removal of body weight at this level (in both cases correlation coefficients changed from significance at the 95% level to significance at the 99% level). A similar effect is observed between adult mortality and litter size at the species level (see Chapter 3, Tables 3.1 & 3.4). The correlation coefficients between adult lifespan and all other variables decreased following the removal of adult body weight, which is similar to patterns observed

Table 4.9 Summary of the change in correlations between observed and residual (adult body weight removed) variables at the species, genus, family and order level. * denotes significance at the 95% level.

Comparison level	Percentage that remained the same	Percentage that decreased	Percentage that increased	Percentage that changed sign	z-value (Wilcoxon matched pairs signed-ranks tests)
Species: Observed - Residual	0,0	16,92	83,1	27,7	-4,76* <i>p</i> < 0,05
Genus Observed - Residual	1,5	15,4	81,5	23,1	-4,85* <i>p</i> < 0,05
Family Observed - Residual	0,0	15,4	84,6	20,0	-5,22* <i>p</i> < 0,05
Order Observed - Residual	0,0	11,1	88,9	35,2	-3,78* <i>p</i> < 0,05



at the species level. Of particular interest at the family level are the high correlations between age at first parturition and interlitter interval for observed data ($r=0,96$; $n=12$; $p<0,01$) as well as for residual data ($r=0,91$; $n=12$; $p<0,01$). Again, this is similar to results obtained at the species level (see Chapter 3, Tables 3.1 & 3.4). Highly significant correlation coefficients also exist between age at weaning and lactation period for both observed data ($r=0,91$; $n=9$; $p<0,01$) and residual data ($r=0,97$; $n=9$; $p<0,01$). However, this is hardly surprising considering that these two variables represent the same developmental period. Numerous other variables are significantly correlated, even with the effects of body weight removed, but these correlations are characterised by small sample sizes which could bias their interpretation. Note however, that even though sample sizes may be small, the fact that they are significant suggests that they may be particularly meaningful.

At the order level, a similar decrease in correlation coefficients to that observed at the family level for age at first parturition as well as interlitter interval and most variables was evident. At this taxonomic level, age at first parturition and interlitter interval remain significantly positively correlated when the effects of adult body weight are accounted for ($r=0,93$; $n=6$; $p<0,01$). Age at first parturition and age at weaning in addition to adult life-span and age at maturity also remain significantly correlated when adult body weight effects are removed (see Table 4.6). Once again, sample sizes for these correlations are small.

The principle form of covariation found at the species level (chapter 3) appears to be the principle form of covariation found at each of the other taxonomic levels. The increase in the correlation coefficients for certain variables (litter size and neonate weight, gestation period and adult mortality) once the effects of adult body weight are removed shows that body weight has profound effects in masking the relationships between certain variables. On the other hand, although the correlation coefficients of certain variables (age at maturity and gestation period, lactation period and age at weaning, inter litter interval) decrease when the effects of adult body weight are removed, they still remain significantly correlated, suggesting that although adult body weight has an effect on the covariation of these variables, it is not the only constraining parameter.

Principal components and cluster analyses

The eigenvectors and eigenvalues for PCA using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) from 35 mammalian genera, 19 families and 9 orders for observed data are presented in Tables 4.10, 4.11 and 4.12 respectively. At each taxonomic level, only two PCs are needed to explain most of the variance. At all three taxonomic levels, PC-1 represents a positive gradient of adult body weight, neonate weight, age at maturity and gestation period. PC-2 represents a positive gradient of litter size. This is similar to results found at the species level (see Chapter 3, Table 3.5).

The eigenvectors and eigenvalues for PCA with the effects of adult body weight removed using four life-history variables (neonate weight, litter size, age at maturity and gestation period) are presented in Tables 4.13, 4.14 and 4.15 respectively. At the level of genus and family, two PCs are needed to explain about 73-75% of the variance. More variance is explained by PC-1 at the genus level ($\approx 54\%$) than at the family level ($\approx 49\%$) (Tables 4.13 & 4.14 respectively). In comparison, the amount of variance accounted for at the order level by the first PC is almost 63% but with 89% of the variance explained by both PC-1 and PC-2. At the genus level, PC-1 represents a positive gradient of neonate weight and gestation period and PC-2 a positive gradient of litter size and age at maturity. At both the family and the order level, PC-1 represents a positive gradient of neonate weight, age at maturity and gestation period whereas PC-2 represents a positive gradient of litter size. The eigenvectors and eigenvalues for a PCA with the effects of adult body weight removed at the genus, family and order levels differ from those found at the species level with adult body weight removed (see Chapter 3, Table 3.6).

The principal component plots are presented in Figures 4.1a, 4.2a and 4.3a for observed values at the genus, family and order levels respectively and with the effects of adult body weight removed at the genus, family and order levels in Figures 4.1b, 4.2b and 4.3b respectively. At both the genus and family levels, three distinctive groupings (MDA-genus: $F_{10,54}=33,08$; $p<0,0001$ and MDA-family: $F_{10,22}=28,69$; $p<0,0001$) emerge from the observed data (Figures 4.1a, 4.2a & 4.3a): the first comprises *Sus* (feral pig), *Lycaon* (wild



Table 4.10 Eigenvectors and eigenvalues for PCA using five life-history variables of 35 mammalian genera. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult body weight	(0,49)	0,22	-0,20	(-0,57)	(0,59)
Neonate weight	(0,49)	0,11	(-0,57)	-0,01	(-0,65)
Litter size	-0,23	(0,95)	-0,03	0,21	0,02
Age at maturity	(0,48)	0,18	(0,80)	-0,11	-0,31
Gestation Period	(0,49)	-0,07	-0,02	(0,78)	0,37
Eigenvalues	3,71	0,89	0,19	0,15	0,07
Contribution to total variation (%)	74,13	17,78	3,78	2,94	1,36
Cumulative contribution (%)	74,13	91,91	95,70	98,64	100,00
Correlation coefficients					
Adult body weight	0,94	0,21	-0,09	-0,22	0,15
Neonate weight	0,95	0,11	-0,25	-0,01	0,73
Litter size	-0,44	0,89	-0,02	0,08	0,01
Age at maturity	0,92	0,17	0,35	-0,04	-0,08
Gestation period	0,95	-0,06	-0,01	0,30	0,10



Table 4.11 Eigenvectors and eigenvalues for PCA using five life-history variables of 19 mammalian families. Principal contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult body weight	(0,48)	0,22	(0,63)	0,06	(-0,56)
Neonate weight	(0,48)	0,11	-0,08	(-0,82)	0,27
Litter size	-0,27	(0,94)	-0,18	-0,03	-0,06
Age at maturity	(0,48)	0,22	0,10	(0,52)	(0,66)
Gestation Period	(0,48)	-0,02	(-0,74)	0,22	-0,40
Eigenvalues	3,96	0,75	0,13	0,11	0,05
Contribution to total variation (%)	78,22	15,93	2,72	2,21	0,92
Cumulative contribution (%)	78,22	94,16	96,87	99,08	100,00
Correlation coefficients					
Adult body weight	0,95	0,20	0,23	0,02	-0,13
Neonate weight	0,95	0,10	-0,03	-0,27	0,06
Litter size	-0,54	0,84	-0,07	-0,02	-0,01
Age at maturity	0,95	0,20	0,04	0,18	0,14
Gestation period	0,96	-0,01	-0,27	0,08	-0,09



Table 4.12 Eigenvectors and eigenvalues for PCA using five life-history variables of 9 mammalian orders. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult body weight	(0,47)	0,23	-0,06	-0,31	0,51
Neonate weight	(0,49)	0,17	-0,26	0,02	(-0,81)
Litter size	-0,28	(0,94)	0,17	0,11	-0,02
Age at maturity	(0,48)	0,19	0,27	(0,77)	0,26
Gestation Period	(0,48)	0,05	(0,68)	-0,55	0,04
Eigenvalues	4,10	0,78	0,10	0,02	0,01
Contribution to total variation (%)	81,99	15,57	2,04	0,33	0,06
Cumulative contribution (%)	81,99	97,56	99,61	99,94	100,00
Correlation coefficients					
Adult body weight	0,96	0,20	-0,19	-0,03	0,05
Neonate weight	0,98	0,15	-0,08	0,01	-0,02
Litter size	-0,56	0,83	0,06	-0,02	0,01
Age at maturity	0,98	0,17	0,09	0,11	0,04
Gestation period	0,97	-0,04	0,22	-0,06	0,02



Table 4.13 Eigenvectors and eigenvalues for PCA using four life-history variables of 35 mammalian genera for which the effects of body weight have been removed. Principle contributions to each component are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Neonate weight	(0,52)	0,01	(0,70)	-0,48
Litter size	-0,43	(0,67)	0,52	0,31
Age at maturity	0,40	(0,74)	-0,48	-0,24
Gestation Period	(0,61)	-0,03	0,08	(0,78)
Eigenvalues	2,16	0,86	0,69	0,29
Contribution to total variation (%)	53,88	21,58	17,19	7,35
Cumulative contribution (%)	53,88	75,46	92,65	100,00
Correlation coefficients				
Neonate weight	0,77	0,01	0,58	-0,26
Litter size	-0,63	0,62	0,43	0,17
Age at maturity	0,59	0,69	-0,40	-0,13
Gestation period	0,90	-0,02	0,07	0,42



Table 4.14 Eigenvectors and eigenvalues for PCA using four life-history variables of 19 mammalian families for which the effects of adult body weight have been removed. Principal contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Neonate weight	(0,45)	-0,25	(0,85)	-0,10
Litter size	-0,39	(0,72)	0,46	0,35
Age at maturity	(0,50)	0,64	-0,14	-0,57
Gestation Period	(0,63)	0,12	-0,21	(0,74)
Eigenvalues	1,97	0,96	0,74	0,31
Contribution to total variation (%)	48,84	24,46	18,72	7,99
Cumulative contribution (%)	48,84	73,30	92,01	100,00
Correlation coefficients				
Neonate weight	0,63	-0,25	0,74	-0,05
Litter size	-0,55	0,71	0,40	0,20
Age at maturity	0,70	0,63	-0,12	-0,32
Gestation period	0,88	0,12	-0,18	0,42



Table 4.15 Eigenvectors and eigenvalues for PCA using four life-history variables of 9 mammalian orders for which the effects of adult body weight have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principal components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Neonate weight	(0,57)	0,06	(-0,81)	-0,12
Litter size	-0,09	(0,95)	-0,04	0,28
Age at maturity	(0,57)	0,25	0,50	(-0,60)
Gestation Period	(0,59)	-0,15	0,29	(0,74)
Eigenvalues	2,51	2,06	0,29	0,13
Contribution to total variation (%)	62,65	26,61	7,36	3,37
Cumulative contribution (%)	62,65	89,27	96,63	100,00
Correlation coefficients				
Neonate weight	0,89	0,06	-0,44	-0,04
Litter size	-0,14	0,98	-0,02	0,11
Age at maturity	0,90	0,26	0,27	-0,22
Gestation period	0,94	-0,16	0,15	0,27

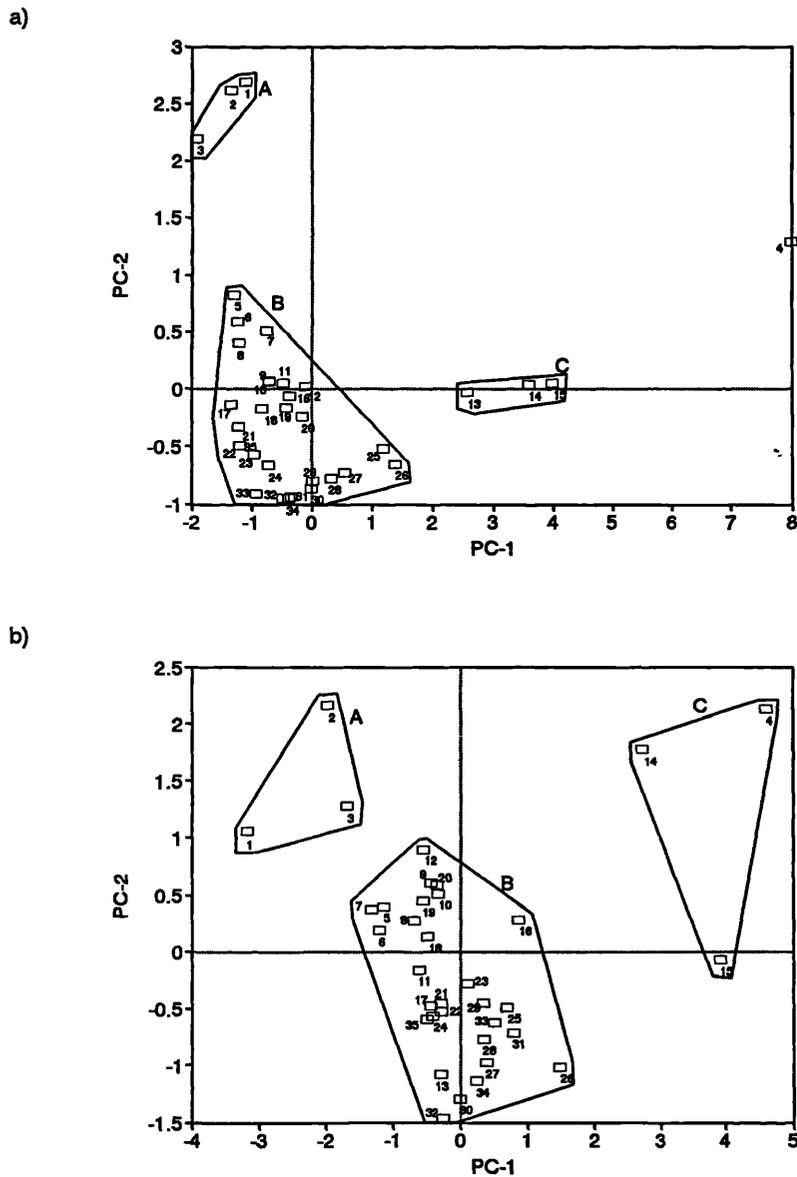


Figure 4.1 a) Plot of the first two principal components of 35 genera in the southern African sub-region using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period). b) Plot of the first two principal components of 35 genera in the southern African sub-region using four life-history variables (neonate weight, litter size, age at maturity and gestation period) for which the effects of adult body weight have been removed. The polygons illustrate groupings within the component space. 1 - *Sus*, 2 - *Lycaon*, 3 - *Rattus*, 4 - *Loxodonta*, 5 - *Otocyon*, 6 - *Canis*, 7 - *Acinonyx*, 8 - *Mungos*, 9 - *Civettictis*, 10 - *Proteles*, 11 - *Phacochoerus*, 12 - *Panthera*, 13 - *Hippopotamus*, 14 - *Diceros*, 15 - *Giraffa*, 16 - *Procavia*, 17 - *Mystromys*, 18 - *Felis*, 19 - *Hyaena*, 20 - *Crocuta*, 21 - *Otomys*, 22 - *Poecilogale*, 23 - *Paraxerus*, 24 - *Hystrix*, 25 - *Taurotragus*, 26 - *Equus*, 27 - *Connochaetus*, 28 - *Damaliscus*, 29 - *Aepyceros*, 30 - *Tragelaphus*, 31 - *Philantomba*, 32 - *Antidorcas*, 33 - *Tadarida*, 34 - *Sylvicapra*, 35 - *Ictonyx*.

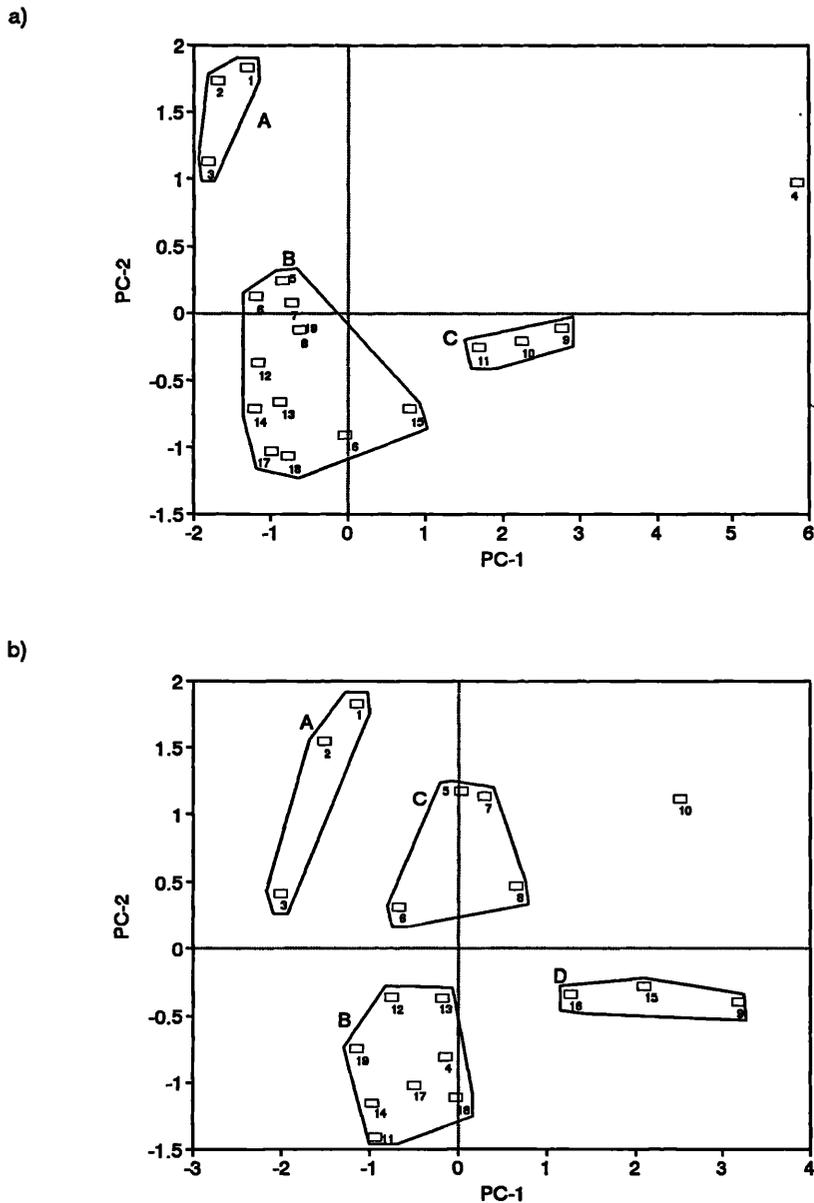


Figure 4.2 a) Plot of the first two principal components of 19 families in the southern African sub-region using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period). b) Plot of the first two principal components of 19 families in the southern African sub-region using four life-history variables (neonate weight, litter size, age at maturity and-gestation period) for which the effects of adult body weight have been removed. The polygons illustrate groupings within the component space. 1 - Suidae, 2 - Canidae, 3 - Muridae, 4 - Elephantidae, 5 - Felidae, 6 - Viveridae, 7 - Hyaenidae, 8 - Procaviidae, 9 - Giraffidae, 10 - Rhinocerotidae, 11 - Hippopotamidae, 12 - Scuridae, 13 - Hystricidae, 14 - Macroscelidae, 15 -Equidae, 16 - Bovidae, 17 - Mollosidae, 18 - Cercopithecidae, 19 - Mustelidae.

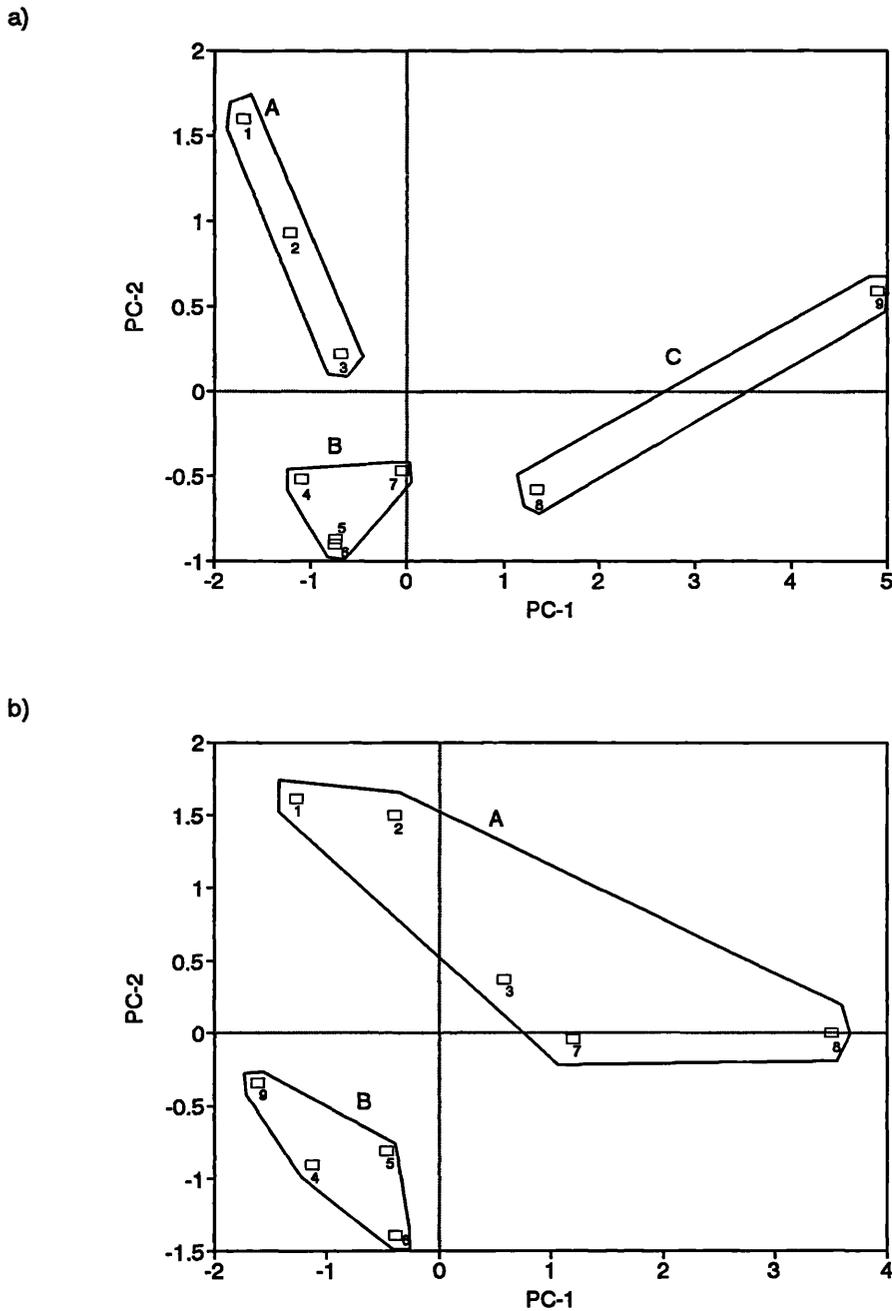


Figure 4.3 a) Plot of the first two principal components of 9 orders in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period). b) Plot of the first two principal components of 9 orders in the southern African sub-region using four variables (neonate weight, litter size, age at maturity and gestation period) for which the effects of body weight have been removed. The polygons illustrate groupings within the component space. 1 - Rodentia, 2 - Carnivora, 3 - Hyracoidea, 4 - Macroscelides, 5 - Primates, 6 - Chiroptera, 7 - Artiodactyla, 8 - Perrisodactyla, 9 - Proboscidea.



dog) and *Rattus* (rat); the second comprises *Loxodonta* (elephant), *Hippopotamus* (hippopotamus), *Diceros* (black rhino) and *Giraffa* (giraffe); the third grouping comprises all the other mammalian genera in this analysis. Note that *Loxodonta* (elephant) is an outlier to these groups. At the genus level, the composition of the groupings (MDA-observed: $F_{10,54}=33,08$; $p<0,0001$ and MDA-residuals: $F_{8,58}=33,19$; $p<0,0001$) are consistent irrespective of whether observed values (Figure 4.1a) or residuals are used (Figure 4.1b) with the exception of the grouping containing the hippopotamus (13) and the outlier (elephant-4). With the removal of adult body weight, the relative position of the hippopotamus changes drastically and it, together with the elephant (4), is included in the largest grouping comprising most other mammals in this analysis (Figure 4.1b). Note that the positions of all mammals relative to one another also change within these groupings. Thus, although the composition of groupings remains consistent at the genus level, there are relative positional changes within these groupings.

A similar pattern was observed at the family level (Figure 4.2a and Figure 4.2b). The relative positions of the Elephantidae, Rhinocerotidae and Hippopotamidae changed following the removal of adult body weight as did the composition of the grouping comprising these families. However, at the family level, the three major groupings evident before removal of adult body weight (MDA: $F_{10,22}=28,69$; $p<0,0001$), were split up to form four groupings once adult body weight was removed (MDA: $F_{12,29}=15,51$; $p<0,0001$). Note that the Rhinocerotidae now appears to be an outlier relative to the major groupings and that the Hippopotamidae is included with the grouping containing the largest number of families. In addition, the largest group in Figure 4.2a is divided into two smaller groups with the removal of the effects of adult body weight (Figure 4.2b), separating certain carnivore families (the Felidae (5), Viveridae (6) and Hyaenidae (7)) with the inclusion of the Procaviidae (8), into a distinct group.

At the order level (Figure 4.3a and Figure 4.3b), the relative positions of the Artiodactyla (7), Perrisodactyla (8) and Proboscidea (9) are most affected by the removal of adult body weight, and to a lesser degree, the Hyracoidea (3). The relative positions of the Carnivora (2) and other orders are not affected much by the removal of adult body weight. The composition of the groupings change only in as far as the Proboscidea and Artiodactyla are

concerned. Prior to the removal of adult body weight (Figure 4.3a), the Artiodactyla (7) were included in the grouping with the Macroscelides (4), Primates (5) and Chiroptera (6) (MDA: $F_{10,4}=27,40$; $p<0,0030$). With the removal of adult body weight (Figure 4.3b), the Artiodactyla are excluded from this grouping and the Proboscidea (9) included (MDA: $F_{4,4}=18,43$; $p<0,0077$). Thus, at all three taxonomic levels, it is apparent that adult body weight effects are having a greater impact on the grouping of the larger mammals as compared with the grouping of the intermediate and smaller sized mammals. No such distinction was apparent at the species level with the smaller, intermediate and larger mammals being similarly affected.

The results of the cluster analyses for the observed data are presented in Figures 4.4, 4.6 and 4.8 whereas the results of the cluster analyses with the effects of adult body weight removed are presented in Figures 4.5, 4.7 and 4.9. At the genus level, both the number and composition of clusters do not alter much once adult body weight is removed with only a few postional changes occurring: *Mungos* (8) and *Phacochoerus* (11) being the most noteworthy (see Figures 4.4 & 4.5). The persistent clustering of *Lycaon* (2) and *Rattus* (3) both with and without adult body weight effects suggests a litter size effect. This is consistent with results obtained at the species level (see Figures 3.15 & 3.16, Chapter 3) and persists at the family and order levels (see Figures. 4.6, 4.7, 4.8 & 4.9).

At the family level, the Hippopotamidae are clustered with the Rhinocerotidae before adult body weight is removed (Figure 4.6). However, once the effects of adult body weight are removed, the Hippopotamidae are included together with the Mustelidae, Macroscelidae, Scuridae, Hystricidae, Viveridae, Cercopithecidae and Mollosidae (Figure 4.8).

The predominant clusters at the order level for the observed data (Figure 4.7) remain the predominant clusters at the order level following the removal of the effects of adult body weight (Figure 4.9). The relative position of the Proboscidea is the most affected by the removal of adult body weight.

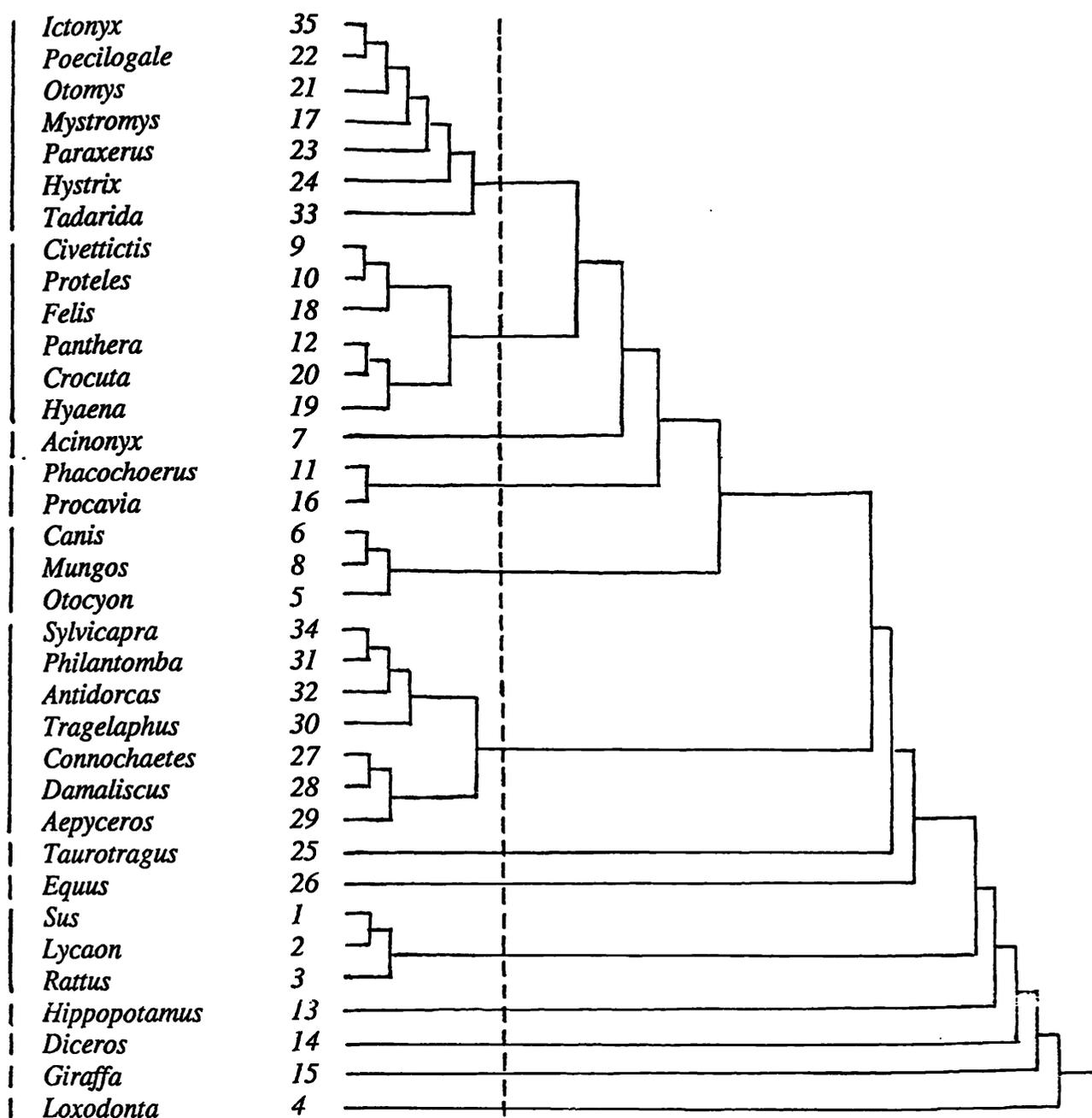


Figure 4.4 Dendrogram illustrating 13 clusters using five life-history (adult body weight, neonate weight, litter size, age at maturity, gestation period) variables of 35 genera in the southern African sub-region. The numbering is similar to the numbering used in the scatterplot of PC-2 on PC-1 (Figure 4.1). The bars illustrate clusters selected using seven convergence levels (indicated by the broken vertical line).

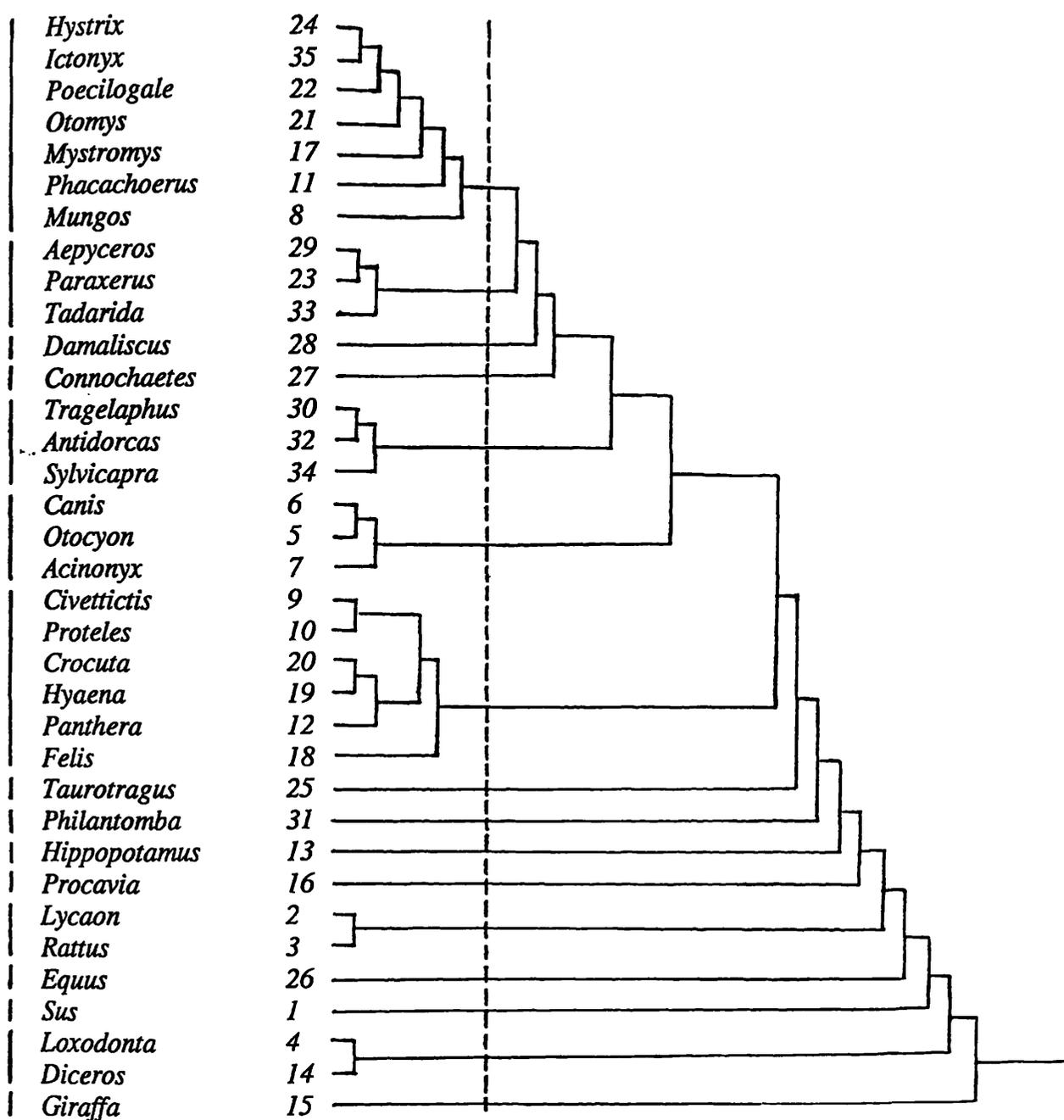


Figure 4.5 Dendrogram illustrating 16 clusters using four life-history variables (neonate weight, litter size, age at maturity, gestation period) of 35 genera in the southern African sub-region for which the effects of adult body weight have been removed. The numbering is similar to the numbering used in the scatterplot of PC-2 on PC-1 (Figure 4.1). The bars illustrate clusters selected using seven convergence levels (indicated by the broken vertical line).

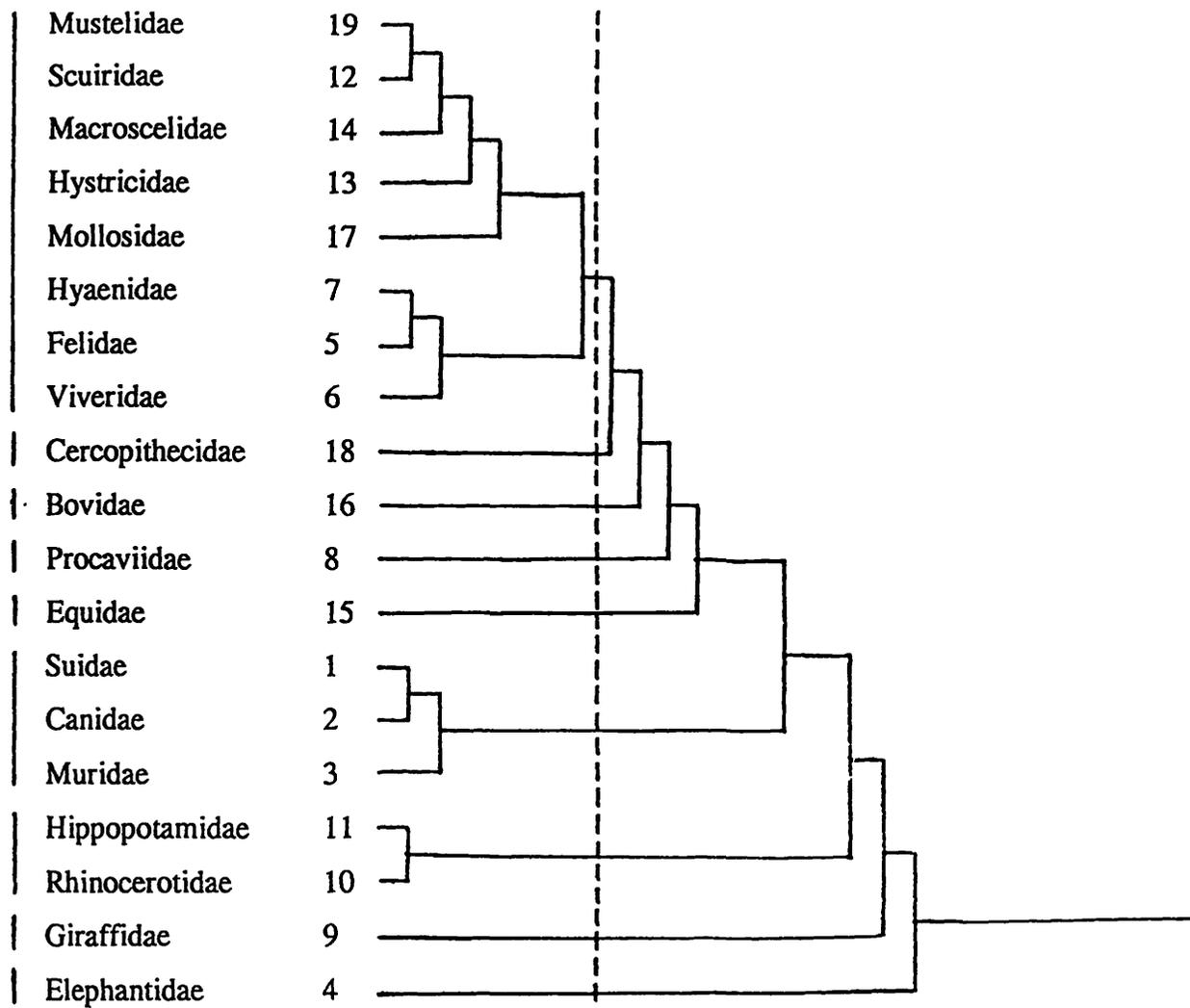


Figure 4.6 Dendrogram illustrating nine clusters using five life-history variables (adult body weight, neonate weight, litter size, age at maturity, gestation period) of 19 families in the southern African sub-region. The numbering is similar to the numbering used in the scatterplot of PC-2 on PC-1 (Figure 4.2). The bars illustrate clusters selected using seven convergence levels (indicated by the broken vertical line).

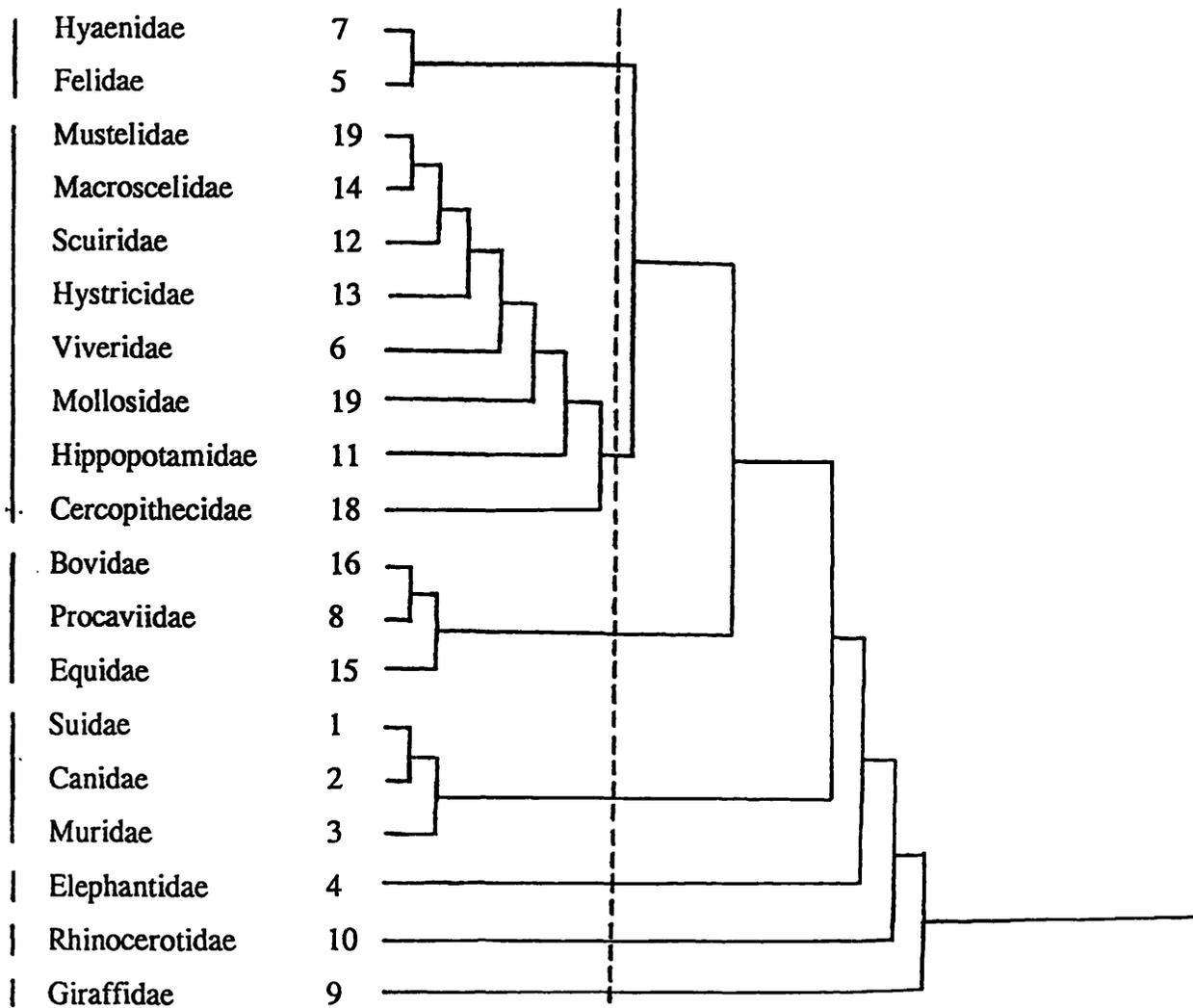


Figure 4.7 Dendrogram illustrating seven clusters using four life-history variables (neonate weight, litter size, age at maturity, gestation period) of 19 families in the southern African sub-region for which the effects of adult body weight have been removed. The numbering is similar to the numbering used in the scatterplot of PC-2 on PC-1 (Figure 4.2). The bars illustrate clusters selected using seven convergence levels (indicated by the broken vertical line).

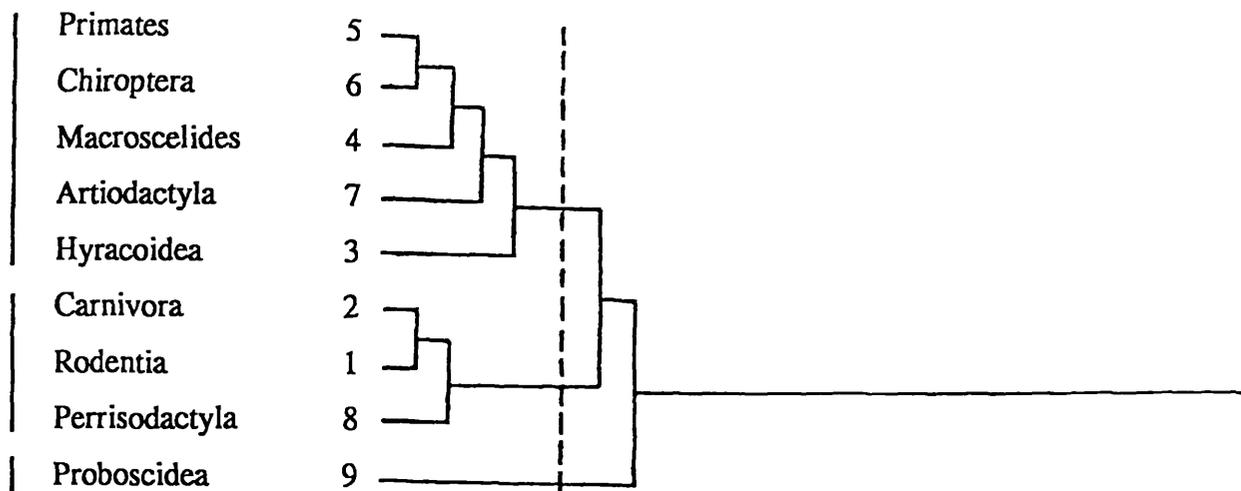


Figure 4.8 Dendrogram illustrating three clusters using five life-history variables (adult body weight, neonate weight, litter size, age at maturity, gestation period) of 9 orders in the southern African sub-region. The numbering is similar to the numbering used in the scatterplot of PC-2 on PC-1 (Figure 4.3). The bars illustrate clusters selected using five convergence levels (indicated by the broken vertical line).

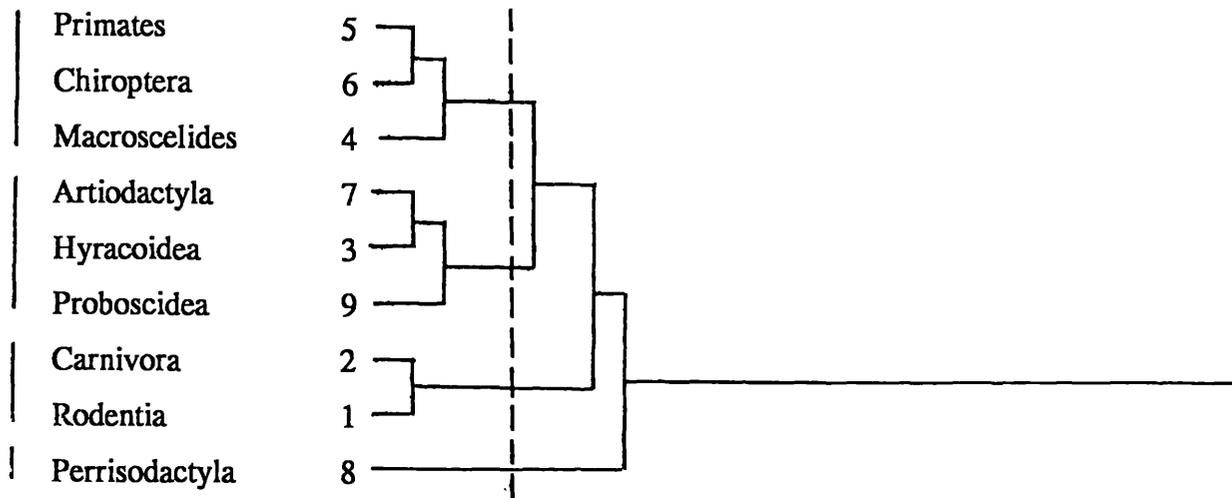


Figure 4.9 Dendrogram illustrating four clusters using four life-history variables (neonate weight, litter size, age at maturity, gestation period) of 9 orders in the southern African sub-region for which the effects of adult body weight have been removed. The numbering is similar to the numbering used in the scatterplot of PC-2 on PC-1 (Figure 4.3). The bars illustrate clusters selected using five convergence levels (indicated by the broken vertical line).



Discussion

The results of the analyses for the observed data at the genus, family and order levels are similar to those obtained at the species level (see Chapter 3). Qualitatively, the results are similar to the fast-slow continuum described for life-histories when the influence of body size is not considered, at all taxonomic levels (see Harvey, Read & Promislow 1989). No major changes in composition of groups are evident following the removal of adult body weight from all taxonomic levels. However, positional changes for certain elements within the various groupings are evident at each taxonomic level. This suggests that body weight effects are influencing the groupings of certain genera, families and orders: specifically, those groups comprising the larger mammals. At the family level, the addition of the Hippopotamidae (hippo) to a group containing the Cercopithecidae (monkeys), Mollosidae (bats) and Hystricidae (porcupines) following the removal of body weight effects, suggests that the hippo has a comparable gestation period, age at maturity and size of neonate (the variables which describe most of the variance at the family level) to these mammals. At the order level, the Proboscidea (elephant) is grouped with the Macroscelidea (elephant-shrews) suggesting relatively similar developmental periods and sizes of neonates (age at maturity, gestation period and neonate weight contribute to most of the variance on PC-1) for these two orders once the effect of body size is eliminated. Thus, size clearly has some effect at all taxonomic levels. However, irrespective of size, those species, genera, families and orders with longer relative gestation periods give birth to relatively small litters and have relatively large neonates which take longer to mature.

Although positional changes are observed at the species level, no clear distinction in the relative positional changes was found between larger, intermediate or smaller mammals. However, the question is raised as to why the larger mammals appear to be more affected by the removal of body weight at higher taxonomic levels? An in-depth consideration of the life-history traits which appear to be most affected by adult body weight effects in this analysis may go some way towards answering this question.

The significant increase in the negative correlation between age at first parturition and juvenile mortality when the effects of adult body weight is removed, suggests that there is



a trade-off between these variables and that adult body weight masks their true relationship. At this point it becomes important to consider the selective processes that could be involved. Selective processes could be interpreted as adaptive in that a delay in the age at which a mammal is first capable of reproducing, could ensure that the older parent is better able to protect and rear young. The assumption is that reproductive efficiency increases with age (see Harvey *et al.* 1989). This would result in more viable offspring with an increased chance of survival, thereby decreasing juvenile mortality. Alternatively, size-related variance could be interpreted to reflect independent nonadaptive evolution in the individual species' comprising this analysis (see Cheverud, Dow & Leutenegger 1985), specifically those most affected by the removal of adult body weight.

For certain species, size may therefore play a more important role than it does in other species, considering that larger mammals delay reproduction, generally have smaller litters and have longer relative life-spans than smaller mammals do. However, irrespective of absolute size, mammals that delay reproduction do produce smaller litters and live longer lives. Considering that altering life-history parameters through an allometric change in body size becomes increasingly less of an option as an animal becomes larger, selection has to act directly on these life-history parameters and would not merely be an allometric response to a changed body size. This would be typical of animals at the upper extreme of their body size which would be limited in their ability to resort to allometric responses to overcome evolutionary constraints. With the obvious effect body size is having on the larger mammals, the emergent pattern suggests that these mammals are nowhere near approaching an upper limit for body size and therefore continue to make use of the allometric co-variance of life-history parameters as an evolutionary strategy.

Body size effects are further illustrated by the relative positional changes of families within the Proboscidea, Perrisodactyla and Artiodactyla (the larger mammals), following the removal of the effects of adult body weight (see Figures 4.2, 4.3 and 4.5, 4.6). However, the fact that certain variables (age at first parturition and age at maturity) are better correlated with variables such as interlitter interval, gestation period and litter size than they are with adult body weight at all taxonomic levels suggests that body size may simply be correlated to other demographic variables which in turn may influence selection of variables such as age

at first parturition or litter size (see Wootton, 1987). Body size-related patterns are observed at all taxonomic levels, although with the removal of adult body weight certain variables and trade-offs become prominent at different levels.

The most prevalent effect of adult body weight is evident at the family level. Although the removal of adult body weight does not change the qualitative loadings along each PC, it does affect the quantitative loadings in that the contribution of variables to PC-1 decreases at the family level. The removal of adult body weight effects at the order and family levels reduces the impact of these variables at these taxonomic levels, but does not eliminate them. However, the possibility that these patterns (e.g., the increased effect of adult body weight at family- and to a certain extent at the order level compared with the species- and genus levels) are statistical artefacts precipitated by a decrease in the number of data points used at each successively higher level, cannot be discounted.

Generally, the observation that variables (gestation period, age at first parturition and age at maturity to name a few) retain their significant correlations at all taxonomic levels suggests that these variables are related, independently of any adult body weight effects. Since each of these variables correlate more highly with each other than with adult body weight, they may hold considerable promise in describing patterns of life-history traits for southern African mammals. Alternatively, the patterns observed could be a result of the effects of phylogeny which may be overriding the effects of adult body weight in most instances. In this event, any size effects observed would be confounded by phylogenetic effects.

It could therefore be expected that groupings based on life-history characteristics would become more similar to phylogenetic groupings based on morphological characteristics when mean values are used. This is because by doing analyses based on means, variability is effectively reduced which emphasises patterns based on similarities and reduces differences. This is evident in the similarities observed at all taxonomic levels before adult body weight effects are removed, suggesting that life-history groupings generally reflect phylogenetic groupings. However, once adult body weight effects are removed, phylogenetic groupings may not be sufficient to explain life-history groupings.



Conclusion

This analysis supports earlier findings that most life-history traits covary along more than one influential dimension in mammals, not only at the species level but at higher taxonomic levels such as the genus, family and order levels. Most life-history variables for mammals from the southern African subregion are influenced by body size at different taxonomic levels. Body size therefore appears to retain its effect irrespective of lineage, yet has a pronounced influence on life-history variables at the family level. In addition, divergent effects of body size, gestation period, age at maturity and litter size are apparent for different groups of mammals at different taxonomic levels, specifically the larger mammal groups. As these mammals may not yet be at the upper extreme of body size, this variable may be constraining other factors such as developmental periods or litter size to a greater degree than they do in the smaller sized mammals from the subregion. However, it should be remembered that body size only represents a single morphological trait and when this variable is controlled for, there is clearly an additional factor(s) influencing life-history groupings, possibly phylogeny (as indicated by the MDA, chapter 3).

Thus, to establish to what extent the patterns observed are a reflection of constraints imposed by body size effects or whether phylogeny affects these groupings, the potential effects that phylogeny could have on life-history groupings should also be eliminated.



CHAPTER 5

THE INFLUENCE OF PHYLOGENY ON PATTERNS OF COVARIANCE AMONG LIFE- HISTORY TRAITS

Introduction

The analyses thus far suggest that phylogeny may feature prominently in describing patterns of life-history traits for mammals in the southern African subregion (see Chapter 4). This is not surprising seeing that phylogeny is considered to be fundamental to comparative biology (Felsenstein 1985, Harvey & Pagel 1991). Generally, a problem with comparative analyses is that phylogeny is often not taken into account (Ridley 1983; Cheverud *et al.* 1985). The importance of *ad hoc* methods for considering phylogeny in comparative analyses have repeatedly been proposed (Clutton-Brock & Harvey 1977, Martin 1979, Ridley 1983, Clutton-Brock & Harvey 1984, Harvey & Clutton-Brock 1985). These proposals include analyzing data at supraspecific taxonomic levels and relying on cladistic reconstructions of character evolution (Cheverud *et al.* 1985).

Classical patterns of variation have been found by evolutionary biologists using morphological traits. Closely related species are phenotypically similar, thus phylogenetic trees are generally based on morphological design (Cheverud *et al.* 1985) and more recently on genetic similarity (Benton 1988; Li, Gouy, Sharp, O'hUigin & Yang 1990). Additionally, the morphological-based design of phylogenetic trees suggests that behavioural patterns should conform to these phylogenetic relationships (see Brown 1975). It is therefore not inconceivable that patterns in life-history variation could also be influenced by phylogenetic relationships between taxa.

Frequently, correlates of variation in certain taxa differ from those in other taxa and occasionally, it appears that relationships between variables at one taxonomic level are not the same as those at another (see Harvey & Pagel 1991). Similar patterns may occur within

certain taxonomic groupings but can vary according to the taxonomic level considered. Different taxonomic groupings may even display different degrees of response to similar selective pressures.

Since higher-level taxa represent major differences in morphological design, larger-scale variation in life-history traits could be expected to occur at higher taxonomic levels. Thus, as one descends the taxonomic scale, one would expect much of this variation to be constrained within lineages, with the nature of these constraints differing from lineage to lineage (Stearns 1983). This is consistent with "the idea that organisms are mosaics of relatively recent adaptations contained within a framework defined by relatively old constraints" (Wanntorp 1983, Stearns 1983).

Thus, if phylogeny affected patterns of covariation in life-history traits, it would be expected that accumulative traits would become fixed within each successively smaller taxon and that the representation of these traits would change qualitatively with the removal of the effects of phylogeny. Covariation in life-history traits would therefore be expected to persist within groups but as one descended the taxonomic scale, among fewer and fewer traits (Stearns 1983). In contrast, if the same correlations between life-history traits persist simultaneously in several lineages which evolved independently, then the traits could be considered to have evolved independently albeit in a correlated fashion, suggesting that explanations of phylogenetic history are not likely to apply (Harvey & Pagel 1991).

However, as organisms descend in a hierarchical fashion from common ancestors, data for different species are not independent and normal statistical techniques could be inappropriate, not accounting for the bias that phylogenies may have on life-history variables. This is referred to as phylogenetic "inertia" (see Martins & Garland Jr 1991 and Harvey & Pagel 1991) and may be pertinent to these analyses. If phylogenetic inertia is strong for the traits of interest, then estimates of the correlation between these traits may be biased by those groups containing a greater number of species (from Harvey & Mace 1982). Thus, if data is non-independent because of similarities between closely related species causing a bias, then those groups having larger numbers of species will represent a bias in the estimation of the correlation between these traits. To determine to what degree southern African mammalian

patterns of covariation observed in chapters 3 and 4 are affected by phylogenetic constraints, this chapter aims to establish what the effects of these constraints are at the genus, family and order levels.

Material and Methods

Stearns' (1983) phylogenetic-subtraction method was used. This was the preferred method because it excludes data on time since divergence which is generally needed to construct phylogenetic trees but which is difficult to obtain (see Cheverud *et al.* 1985). It can also be used when analyses lack complete phylogenies. This method is based on differences among orders and among families within orders which assume to represent effects of phylogenetic similarity present in the species data points (Stearns 1983; Harvey & Pagel 1991). In this analysis, differences among orders, families and genera were considered in the same manner. The mean values for order, family and genus were independently subtracted from each species data point thus leaving three sets of species' values (residuals) which are free of similarities associated with phylogenetic groupings at the order, family and genus levels. Correlation and covariance analyses were performed on each of these three data sets. Note that for the principal component analyses as well as the cluster analyses, the number of taxonomic groupings at each level was drastically reduced, especially at the genus level. This was because taxonomic groupings at each level which were characterised by only one record (in other words, one species representing the taxon) were excluded as mean values could not be calculated. Residual values obtained by using only one record would inevitably suggest a 100% effect of phylogeny. Therefore, principal component and cluster analyses were performed on only 6 mammalian species, with more than one species per genus and for which appropriate information regarding five variables was available. Similarly, 29 mammalian species at the family level and 35 mammalian species at the order level using the same number of variables were subjected to analyses. Multiple discriminant analyses (MDA) were used to investigate differences between groups identified within the component space of PCA at each taxonomic level.

Wilcoxon matched-pairs signed-ranks tests (Siegel 1956) were conducted between correlation coefficients obtained at the species level (see Table 3.1, Chapter 3), and each of the three

data sets resulting from the removal of phylogeny and at each taxonomic level (genus, family and order). This was to establish whether the changes observed in correlation coefficients when proceeding up the taxonomic hierarchy were significantly altered by the removal of phylogenetic effects. The comparisons required this non-parametric test due to relatedness of the data sets.

Results

Correlation and covariance analyses

The correlations and covariances of data sets for which phylogenetic effects were removed at the genus, family and order levels are presented in Tables 5.1, 5.2 and 5.3 respectively. Significant correlations and covariances are evident at all taxonomic levels following the removal of the effects of phylogeny, but the correlation coefficients and covariances between variables differed among the taxonomic levels. This is consistent with results obtained in Chapters 3 and 4. Significant correlations and covariances evident between variables following the removal of phylogenetic effects at the genus level, are more often than not influenced by small sample sizes (Table 5.1). Note that even though these sample sizes may be small, the relationship between some of these variables may be particularly meaningful. Following the removal of phylogenetic effects at the family level, interlitter interval and age at maturity are significantly positively correlated with most variables. Noteworthy are the significant negative correlations between litter size and juvenile- and adult mortality (see Table 5.2). Following the removal of phylogenetic effects at the order level, significant relationships also exist between adult mortality and most variables as well as adult body weight and several variables (see Table 5.3). A significant negative relationship exists between litter size and gestation period at the order level (Table 5.3) but there is no such relationship at the family level (Table 5.2). However, a significant negative relationship exists between litter size and adult mortality at the order and family levels (Tables 5.2 & 5.3).

A summary of the changes in correlation coefficients from species (see Chapter 3, Table 3.1) to genus, family and order levels following the removal of the effects of phylogeny is



Table 5.1 Correlations and covariances of life history variables of mammals in the southern African sub-region with the effect of phylogeny removed at the genus level. ** denotes significance at the 99% level and * at the 95% level. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
ADWT		0,77** (20)	0,08 (74)	0,86** (4)	0,23 (10)	0,42* (38)	- (2)	0,99** (3)	-0,01 (14)	- (2)	- (2)	-0,08 (16)	-0,64 (7)
NEOWT	58 (34)		0,01 (18)	0,35 (4)	0,06 (6)	0,65** (16)	-	-	0,57 (8)	- (2)	- (2)	0,28 (7)	- (2)
LITSZ	1 (74)	0 (18)		0,96** (4)	-0,61** (12)	-0,05 (33)	-	-0,08 (4)	-0,03 (13)	- (2)	- (2)	0,04 (13)	0,28 (7)
INLTIN	4567 (24)	156 (4)	22 (4)		0,99** (3)	0,29 (4)	-	-	- (2)	-	- (2)	0,90** (3)	- (2)
AGEM	499 (10)	11 (6)	-2 (12)	6600 (3)		-0,06 (12)	-	-	1,00** (4)	-	- (2)	-0,74** (8)	0,86** (6)
GESP	145 (38)	35 (16)	-11 (33)	661 (4)	-60 (12)		- (2)	1,00** (3)	0,20 (16)	-	- (2)	0,09 (7)	0,31 (9)
LACP	4 (2)	0 (0)	0 (0)	0 (0)	0 (0)	-2100 (2)		-	-	-	-	-	-
AGEW	126 (3)	0 (1)	-1 (4)	0 (0)	0 (0)	328 (3)	0 (0)		-	-	-	-	-
AGEPRT	-56 (14)	149 (8)	-2 (13)	0 (2)	0 (4)	499 (16)	0 (0)	0 (1)		-	-	0,15 (10)	0,00 (3)
JMORT	57 (2)	-2 (2)	0 (2)	0 (0)	0 (0)	0 (1)	0 (0)	0 (1)	0 (1)		-	-	-
ADMORT	23304 (2)	228 (2)	144 (2)	52800 (2)	28800 (2)	780 (2)	0 (0)	0 (0)	0 (0)	0 (0)		- (2)	- (2)
ADLIFE	-2707 (16)	1100 (7)	26 (15)	-159553 (3)	-49874 (8)	1747 (17)	0 (0)	0 (1)	19134 (10)	0 (1)	-731520 (2)		0,99** (7)
RELIFE	-25869 (7)	-1448 (2)	236 (7)	-335280 (2)	-69824 (6)	3321 (9)	0 (0)	0 (0)	0 (4)	0 (0)	-731520 (2)	1859000 (7)	

Table 5.2 Correlations and covariances of life history variables of mammals in the southern African sub-region with the effect of phylogeny removed at the family level. ** denotes significance at the 99% level and * at the 95% level. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPR - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPR	JMORT	ADMORT	ADLIFE	RELIFE
ADWT		0,93** (66)	0,10 (133)	0,24 (24)	0,65** (37)	-0,03 (96)	0,69 (4)	0,65** (26)	0,76** (37)	0,17 (6)	0,63** (11)	0,64** (34)	0,06 (16)
NEOWT	326 (66)		0,02 (66)	0,58** (19)	0,50** (35)	-0,10 (60)	- (2)	0,56** (21)	0,79** (29)	0,15 (5)	0,80** (9)	0,72** (26)	-0,07 (11)
LITSZ	5 (133)	0 (66)		0,03 (21)	0,02 (38)	-0,02 (85)	- (2)	-0,10 (27)	-0,04 (33)	-0,80** (5)	-0,70** (11)	-0,03 (32)	0,09 (15)
INLTIN	5281 (24)	492 (19)	7 (21)		0,69** (14)	-0,10 (22)	- (1)	0,84** (10)	0,71** (14)	- (2)	0,77** (5)	0,43* (14)	-0,04 (7)
AGEM	8430 (37)	651 (35)	8 (38)	16869 (14)		-0,08 (40)	- (1)	0,58** (13)	0,74** (19)	- (2)	0,89** (9)	0,54** (22)	-0,30 (8)
GESP	-211 (96)	-86 (60)	-1 (85)	-6087 (22)	-3711 (40)		-0,43 (4)	0,54** (26)	-0,12 (39)	- (10)	0,66** (10)	-0,11 (36)	0,00 (19)
LACP	137 (4)	26 (2)	4 (2)	0 (0)	0 (1)	-532 (4)		- (2)	- (2)	- (2)	- (2)	- (2)	- (2)
AGEW	4427 (26)	345 (21)	-9 (27)	8607 (10)	11736 (13)	1361 (26)	0 (0)		0,88** (12)	- (2)	0,83** (5)	0,69** (11)	0,45 (6)
AGEPR	14651 (37)	1462 (29)	-9 (33)	17068 (14)	37766 (19)	-5190 (39)	0 (3)	18834 (12)		0,10 (3)	0,95** (3)	0,62** (28)	0,24 (11)
JMORT	381 (6)	33 (5)	-3 (5)	-446 (2)	313 (2)	16 (5)	0 (1)	-900 (2)	859 (3)		- (1)	- (1)	- (2)
ADMORT	28558 (11)	558 (9)	-684 (11)	136577 (5)	387164 (9)	11486 (10)	7560 (2)	239261 (5)	139436 (3)	0 (1)		0,31 (6)	-0,37 (3)
ADLIFE	91278 (34)	9339 (26)	-61 (32)	91764 (14)	209616 (22)	-34551 (36)	0 (0)	184547 (11)	226975 (28)	24181 (3)	1011370 (6)		0,62** (13)
RELIFE	17136 (16)	-1736 (11)	369 (15)	-5508 (7)	-108181 (8)	109 (19)	0 (0)	54059 (6)	62493 (11)	-17738 (2)	-905333 (3)	1303940 (13)	



Table 5.3 Correlations and covariances of life history variables of mammals in the southern African sub-region with the effect of phylogeny removed at the order level. ** denotes significance at the 99% level and * at the 95% level. ADWT - Adult body weight; NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	ADWT	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
ADWT		0,82** (78)	-0,01 (141)	0,34** (34)	0,69** (43)	0,09 (106)	0,11 (14)	0,06 (34)	0,80** (43)	0,16 (12)	0,73** (12)	0,86** (41)	-0,06 (20)
NEOWT	1562 (78)		-0,10 (76)	0,58** (27)	0,58** (40)	0,11 (70)	-0,19 (9)	-0,10 (30)	0,80** (30)	0,16 (10)	0,80** (10)	0,66** (34)	-0,21 (15)
LITSZ	-2 (141)	-2 (76)		-0,15 (31)	-0,15 (43)	-0,30** (95)	-0,33 (11)	-0,23 (35)	-0,06 (39)	-0,24 (11)	-0,48** (12)	-0,20 (39)	0,10 (19)
INLTIN	17116 (34)	1664 (27)	-55 (31)		0,77** (20)	-0,03 (31)	-0,17 (7)	-0,04 (12)	0,77** (21)	0,16 (8)	0,82** (7)	0,41* (20)	0,18 (10)
AGEM	51689 (43)	3738 (40)	-110 (43)	48748 (20)		0,05 (46)	-0,11 (6)	-0,28 (19)	0,90** (26)	0,58** (7)	0,85** (10)	0,64** (27)	-0,01 (12)
GESP	1577 (106)	219 (70)	-23 (95)	-1601 (31)	3768 (46)		0,01 (15)	0,18 (34)	0,06 (45)	0,13 (11)	0,90** (11)	-0,01 (43)	-0,09 (24)
LACP	3994 (14)	-834 (9)	-32 (11)	-9801 (7)	-5129 (6)	43 (15)		1,00 (4)	-0,52 (4)	- (2)	0,83** (4)	0,49 (7)	0,71 (3)
AGEW	987 (34)	-212 (30)	-35 (35)	-977 (12)	16751 (19)	1065 (34)	45755 (4)		0,23 (17)	-0,92** (5)	0,76** (5)	0,19 (16)	-0,33 (7)
AGEPRT	59254 (43)	5467 (36)	-34 (39)	50116 (21)	158383 (26)	3797 (45)	-48391 (4)	14959 (17)		-0,02 (8)	0,69** (5)	0,69** (32)	-0,08 (13)
JMORT	586 (12)	78 (10)	-2 (11)	327 (8)	6100 (7)	153 (11)	1135 (2)	-755 (5)	-228 (8)		1,00** (3)	0,03 (9)	-0,08 (4)
ADMORT	63185 (12)	992 (10)	-1997 (12)	277191 (7)	618685 (10)	34668 (11)	426638 (4)	307234 (5)	317446 (5)	66208 (3)		0,51 (7)	0,41 (4)
ADLIFE	513154 (41)	35203 (34)	-719 (39)	235570 (20)	875748 (27)	-893 (43)	384291 (7)	64916 (16)	809977 (32)	1122 (9)	2024230 (7)		0,24 (17)
RELIFE	-39303 (20)	-7106 (15)	463 (19)	38643 (10)	-14936 (12)	-9823 (24)	58960 (3)	-83893 (7)	-36137 (13)	-3194 (4)	1551760 (4)	1557680 (17)	



presented in Table 5.4. Note the increase in the percentage of significant correlations from order to family level following the removal of phylogenetic effects. If this trend were to continue from family to genus level and then to species level, it would suggest that phylogeny is having less of an effect on successively lower taxonomic levels with covariations between traits reduced such that the least co-variation would be expected at the species level with the most co-variation at the order level. This could mean that as fixation of additional traits occurs within each smaller taxon and at each subsequent level, the co-variation among traits evident at a higher taxonomic level will decline as one descends the taxonomic hierarchy. This general trend may, however, be peculiar to certain taxonomic groups (see Stearns 1983). However, the paucity of data points at the genus level, does not allow for meaningful comparisons between variables at the generic level with variables at the order and family levels.

The highest percentage of significant correlations were observed at the family level following the removal of phylogenetic effects. Also, the percentage of correlations that increased in significance from species to subsequent taxonomic levels were highest at the family level. In contrast, the highest percentage reduction in significant correlations was observed at the order level. Consequently, the removal of the effects of phylogeny had the most dramatic impact at this taxonomic level. Furthermore, there were significantly less correlation coefficients that declined from the order to the genus level following the removal of phylogenetic effects from variables. The changes observed at the family and the order levels in Table 5.4 were significant at the 95% level but were most significant at the order level (family: $z = -2,06$; $p=0,02$ order: $z = -3,78$; $p < 0,01$).

Several significant relationships between variables which were not evident at the order level, became significant at the genus level (age at maturity and litter size, gestation period and neonate weight, age at maturity and reproductive lifespan). In addition, several significant relationships between variables at the order level were not significant at the genus level (age at maturity and neonate weight, adult lifespan and adult body weight, gestation period and litter size). The correlation between age at maturity and interlitter interval remained significant at the 99% level at all taxonomic levels. Age at weaning and gestation period showed an increased significance in correlation coefficient at the family level as did interlitter



Table 5.4 Summary of the change in correlation coefficients from species (see Chapter 3, Table 3.1) to genus, family and order with the removal of the effect of phylogeny. * denotes significance at the 95% level.

	Percentage significant correlations	Comparison level	Percentage that remained the same	Percentage that decreased	Percentage that increased	Percentage that changed sign	Percentage that did not have enough data	z-value (Wilcoxon matched pairs signed-ranks tests)
Species	67,5							
Genus	38,9	Species to Genus removed ¹	0,0	23,4	23,4	11,7	53,2	-0,52 <i>p</i> =0,30
Family	50,8	Species to Family removed ²	1,3	46,8	31,2	23,4	20,1	-2,06* <i>p</i> =0,02
Order	36,4	Species to Order removed ³	15,6	58,4	26,0	22,1	0,0	-3,78* <i>p</i> <0,01

¹ Represents a comparison between the correlation coefficient matrix based on observed species data (Chapter 3) and a correlation coefficient matrix based on data for which phylogenetic effects were removed at the genus level.

² Represents a comparison between the correlation coefficient matrix based on observed species data (Chapter 3) and a correlation coefficient matrix based on data for which phylogenetic effects were removed at the family level.

³ Represents a comparison between the correlation coefficient matrix based on observed species data (Chapter 3) and a correlation coefficient matrix based on data for which phylogenetic effects were removed at the order level.

interval and age at weaning. The correlation coefficient between lactation period and gestation period also increased in significance at the family level. However, the sign changed to negative, a phenomenon observed with a number of other variables (adult body weight and gestation period; neonate body weight and gestation period; interlitter interval and gestation period; age at first parturition and gestation period; adult lifespan and gestation period; reproductive lifespan and age at maturity; reproductive lifespan and interlitter interval).

The percentage of correlations that remained unaffected by the removal of the effects of phylogeny was highest at the order level (see Table 5.4). Therefore, even though phylogeny has a profound effect at this level which is supported by the high number of correlations that are reduced as the effects of phylogeny are removed at this taxonomic level, additional factors may influence this general pattern. Similar corresponding increases and reductions in correlation coefficients at different taxonomic levels were evident between variables in chapters 3 and 4. However, the same variables are not similarly affected at all taxonomic levels.

Principal components (PCA) and cluster analyses

The eigenvectors and eigenvalues for PCA with the effects of phylogeny removed at the genus, family and order levels using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) are presented in Tables 5.5, 5.6 and 5.7 respectively. Also, plots depicting the first two principal components representing variation in life-history variables of the relevant mammalian species at each taxonomic level, are shown in Figures 5.1, 5.2 and 5.3 respectively.

At each taxonomic level, three principal components were needed to account for most of the variation in life-history covariation ($\pm 90\%$). In contrast, following the removal of body size effects at each taxonomic level (chapters 3 and 4), only two PC-s were required to account for most of the variation among life-history traits. Thus, following the removal of the effects of phylogeny at all three taxonomic levels, an extra dimension is needed to explain the same amount of variation ($\pm 90\%$) explained previously by two components. At the genus level,



Table 5.5 Eigenvectors and eigenvalues for PCA using five life-history variables of which the effects of phylogeny at the genus level have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlations coefficients between variables and principal components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult weight	(0,57)	-0,03	(-0,54)	0,02	(0,61)
Litter size	-0,06	(-0,70)	(-0,38)	(0,50)	-0,33
Gestation period	(0,51)	-0,12	(0,69)	(0,48)	-0,37
Neonate weight	(0,63)	-0,10	-0,04	(-0,49)	(-0,60)
Age at maturity	0,14	(0,70)	-0,29	(0,52)	-0,11
Eigenvalues	2,40	1,77	0,64	0,19	0,01
Contribution to total variation (%)	45,07	33,28	13,86	4,98	2,81
Cumulative contribution (%)	45,07	78,55	92,21	97,19	100,00
Correlation coefficients					
Adult weight	0,97	-0,22	-0,83	0,71	0,99
Litter size	0,09	-0,87	-0,46	0,70	0,08
Gestation period	0,92	-0,32	0,37	0,32	0,79
Neonate weight	0,93	-0,32	-0,42	0,31	0,81
Age at maturity	0,34	0,63	-0,62	0,35	0,57



Table 5.6 Eigenvectors and eigenvalues for PCA using five life-history variables of which the effects of phylogeny at the family level have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlations coefficients between variables and principal components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult weight	(0,62)	-0,05	0,09	-0,21	(0,75)
Litter size	(0,59)	-0,07	-0,02	(-0,49)	(-0,64)
Gestation period	0,06	(0,80)	(0,60)	0,02	-0,06
Neonate weight	(0,50)	-0,05	-0,03	(0,85)	-0,18
Age at maturity	-0,08	(-0,59)	(0,80)	0,03	-0,05
Eigenvalues	2,49	1,49	0,79	0,16	0,06
Contribution to total variation (%)	48,40	20,10	19,77	10,95	0,78
Cumulative contribution (%)	48,40	68,50	88,27	99,22	100,00
Correlation coefficients					
Adult weight	0,97	0,01	0,40	-0,35	0,82
Litter size	0,92	-0,17	0,23	-0,50	0,50
Gestation period	0,18	0,96	0,95	0,02	0,22
Neonate weight	0,76	-0,10	0,24	0,44	0,38
Age at maturity	0,43	-0,28	0,22	0,03	0,17



Table 5.7 Eigenvectors and eigenvalues for PCA using five life-history variables of which the effects of phylogeny at the order level have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlations coefficients between variables and principal components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult weight	(0,59)	0,16	0,12	-0,16	(0,76)
Litter size	-0,13	(0,72)	(0,67)	0,17	-0,12
Gestation period	0,13	(-0,69)	(0,70)	0,15	-0,03
Neonate weight	(0,57)	0,08	0,06	(-0,56)	(-0,59)
Age at maturity	(0,53)	0,07	-0,21	(0,78)	-0,24
Eigenvalues	3,03	1,01	0,46	0,41	0,09
Contribution to total variation (%)	48,67	25,35	14,37	8,51	3,09
Cumulative contribution (%)	48,67	74,02	88,40	96,91	100,00
Correlation coefficients					
Adult weight	0,95	0,24	0,31	-0,42	0,84
Litter size	-0,18	0,95	0,90	0,25	-0,09
Gestation period	0,75	-0,27	0,04	-0,25	0,20
Neonate weight	0,90	0,06	-0,27	-0,64	0,38
Age at maturity	0,80	0,01	0,08	0,21	0,43

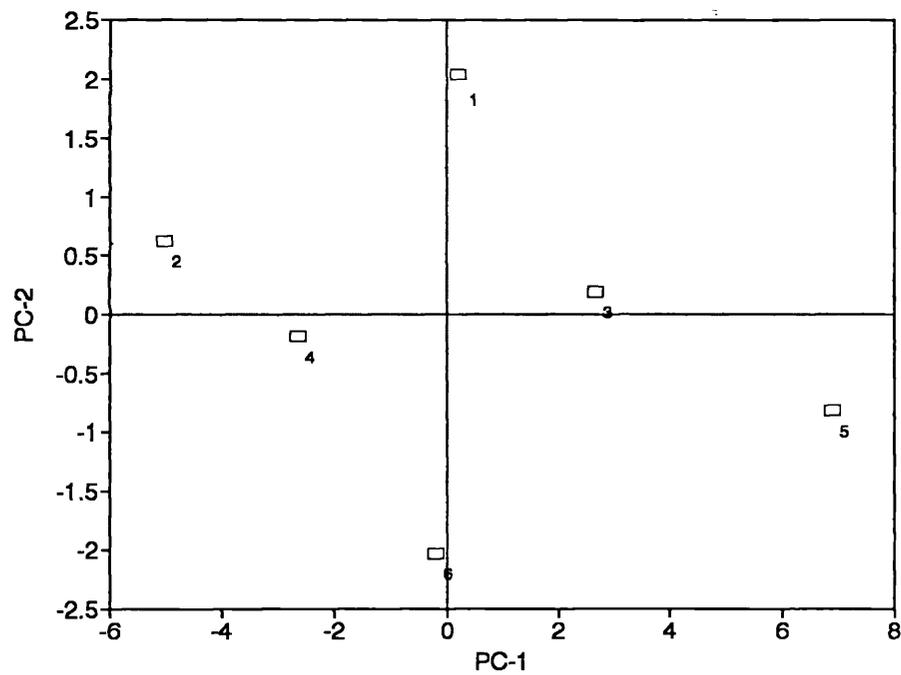


Figure 5.1 Plot of the first two principal components (PCs) of 6 mammal species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the genus level have been removed. 1 - *C. mesomelas*, 2 - *T. scriptus*, 3 - *P. leo*, 4 - *P. pardus*, 5 - *T. strepsiceros*, 6 - *C. adustus*.

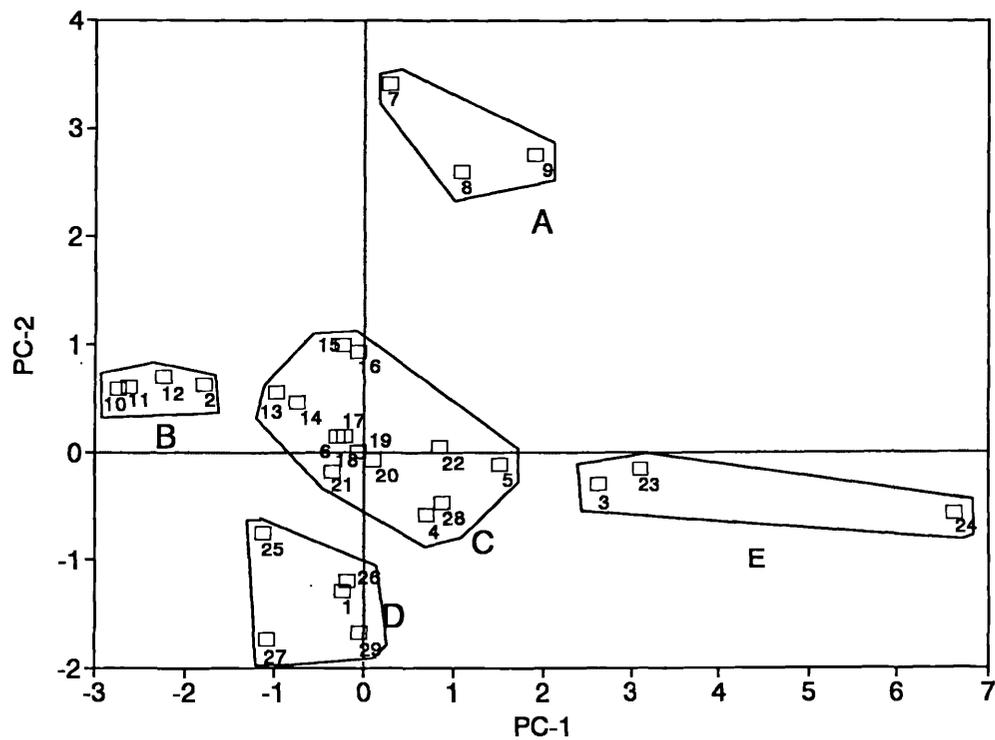


Figure 5.2 Plot of the first two principal components (PCs) of 29 mammal species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the family level have been removed. The polygons (A, B, C, D and E) denote groupings within the component space. 1 - *C. mesomelas*, 2 - *T. scriptus*, 3 - *P. leo*, 4 - *P. pardus*, 5 - *T. strepsiceros*, 6 - *C. adustus*, 7 - *R. norvegicus*, 8 - *L. pictus*, 9 - *S. scrofa*, 10 - *P. monticola*, 11 - *S. grimmia*, 12 - *A. marsupialis*, 13 - *P. cristatus*, 14 - *A. melampus*, 15 - *M. mungo*, 16 - *A. jubatus*, 17 - *D. dorcas*, 18 - *I. striatus*, 19 - *P. albinucha*, 20 - *H. brunnea*, 21 - *O. megalotis*, 22 - *C. civetta*, 23 - *C. taurinus*, 24 - *T. oryx*, 25 - *F. nigripes*, 26 - *M. albicaudatus*, 27 - *P. aethiopicus*, 28 - *C. crocuta*, 29 - *O. irroratus*.

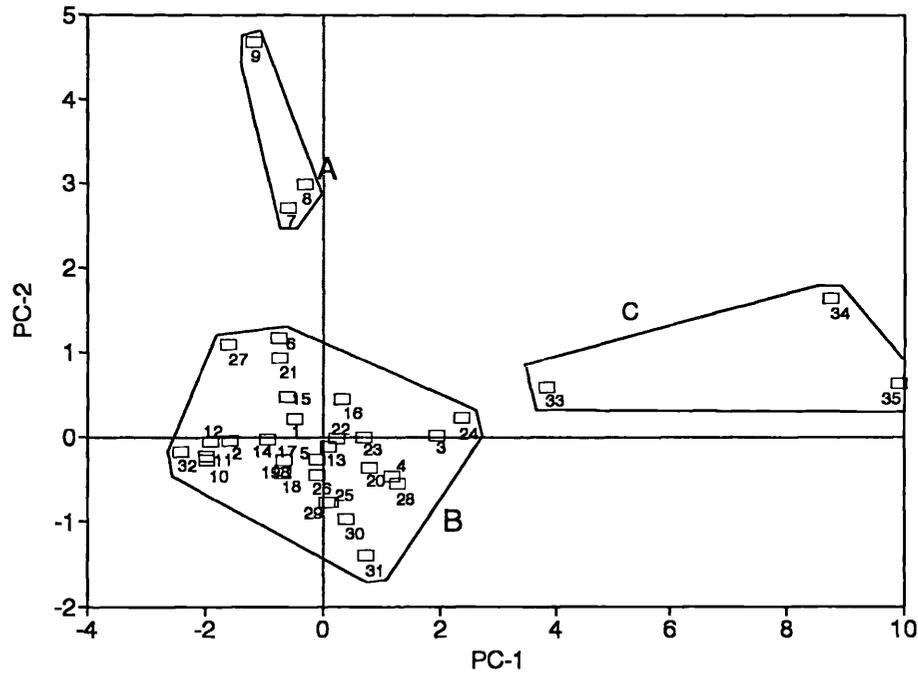


Figure 5.3 Plot of the first two principal components (PCs) of 35 mammal species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the order level have been removed. The polygons (A, B and C) denote groupings within the component space. 1 - *C. mesomelas*, 2 - *T. scriptus*, 3 - *P. leo*, 4 - *P. pardus*, 5 - *T. strepsiceros*, 6 - *C. adustus*, 7 - *R. norvegicus*, 8 - *L. pictus*, 9 - *S. scrofa*, 10 - *P. monticola*, 11 - *S. grimmia*, 12 - *A. marsupialis*, 13 - *P. cristatus*, 14 - *A. melampus*, 15 - *M. mungo*, 16 - *A. jubatus*, 17 - *D. dorcas*, 18 - *I. striatus*, 19 - *P. albinucha*, 20 - *H. brunnea*, 21 - *O. megalotis*, 22 - *C. civetta*, 23 - *C. taurinus*, 24 - *T. oryx*, 25 - *F. nigripes*, 26 - *M. albicaudatus*, 27 - *P. aethiopicus*, 28 - *C. crocuta*, 29 - *O. irroratus*, 30 - *P. cepapi*, 31 - *H. africae australis*, 32 - *E. burchelli*, 33 - *D. bicornis*, 34 - *H. amphibius*, 35 - *G. camelopardalis*.

PC-1 represents a positive gradient of adult weight and neonate weight which suggests a dimension describing the gradient from small to large mammals. PC-2 represents a negative gradient of litter size and a positive gradient of age at maturity which suggests a dimension varying from large litters with early age at maturity to small litters with a late age at maturity. PC-3 represents a positive gradient of gestation period suggesting a dimension representing a gradient from short to long gestation periods.

At the family level, PC-1 represents a positive gradient of adult body weight, litter size and neonate weight. This suggests a gradient varying from small mammals with small offspring and small litters to large mammals with large offspring and large litters. Here, a new gradient is observed illustrating that certain mammals do not conform to the classical continuum of life-history traits in that small mammals are usually associated with large litters and large mammals with small litters. Furthermore, the addition of litter size to PC-1 which accounts for most of the variation at the family level ($\pm 48\%$), suggests that this variable becomes more important when describing patterns of co-variation at the family level. PC-2 represents a positive gradient of gestation period while PC-3 is a positive gradient of age at maturity.

At the order level, PC-1 represents a positive gradient of adult body weight, neonate weight and age at maturity. PC-2 represents a positive gradient of litter size and PC-3 a positive gradient of gestation period. Thus, an interchange of variables (litter size, age at maturity and gestation period) occurred between the major PCs when comparing the order and family levels.

The PCA shows no groupings along PCs once the effects of phylogeny are removed at the genus level, only single isolated data points along both components. The PCA separates *T. scriptus* (2), *P. leo* (3), *T. strepsiceros* (5) and *P. pardus* (4) at opposite extremes relative to one another along PC-1 and *C. mesomelas* (1) and *C. adustus* (6) at opposite extremes along PC-2. This lack of groupings may be an effect of the removal of phylogeny at the genus level or alternatively, due to the drastic reduction in the number of data points. At the family level, a separation of 4 distinct groups along both PCs is evident (A,B,C,D). The litter size grouping of *L. pictus* (8), *R. norvegicus* (7) and *S. scrofa* (9) is evident (group A)

as is the antelope grouping (B). Groups C and D comprise a mixture of mammals with varying sizes and developmental periods along both PCs. Noteworthy is the outlier positions of *P. leo* (3), *C. taurinus* (23) and *T. oryx* (24) relative to groups A, B, C and D. Thus with the effects of phylogeny removed at the family level, these groupings do not comply with classical life-history groupings so that the patterns observed prior to the removal of phylogeny (see Chapter 4, Fig. 4.2(a)) suggests that at this taxonomic level phylogeny had a profound effect.

At the order level, only two major groupings are observed with group A a litter size grouping and group B a mixture of mammals. The persistent grouping of *L. pictus* (8), *S. scrofa* (9) and *R. norvegicus* (7) at the order and family level, suggests the strong impact that litter size has in grouping these mammals. Certain large mammals, *D. bicornis* (33), *H. amphibius* (34) and *G. camelopardalis* (35) are outliers to these groups following the removal of the effects of phylogeny at the family and order levels. Thus phylogenetic constraints seem to affect patterns of larger mammals more, which is consistent with the body size pattern observed for the larger mammals in chapter 4. Therefore, for these larger mammals, life-history patterns evident prior to the removal of phylogeny can probably be described in terms of phylogenetic constraints on size.

The results of the cluster analysis are presented in Figures 5.4, 5.5 and 5.6. At the order level there are 15 distinct groups of clusters (Fig. 5.6) compared with 12 distinct groups of clusters at the family level (Fig. 5.5) (see Material and Methods, Chapter 2 for distinguishing clusters). Note the classical carnivore groupings of clusters (group 3 and a subgroup of group 2) and the antelope grouping of clusters (group 6 and a subgroup of group 2) at the order level even though phylogenetic effects have been removed. Thus, life-history traits define these groupings irrespective of phylogenetic constraints. The reduction in the numbers of clustered groups from 15 to 12 (from order to family level) is a result of increased litter size effects in certain mammal groupings at the family level compared with the order level. The significance of certain traits such as litter size increases at different taxonomic levels for certain mammals which is consistent with the PCA results. This is especially evident within the antelope (litter size=1) and certain carnivores (*M. mungo*-4; *A. jubatus*-4; *C. civetta*-2; *P. pardus*-2,3.). Note the clustering of *L. pictus* (litter size 8,9), *R. norvegicus* (litter size

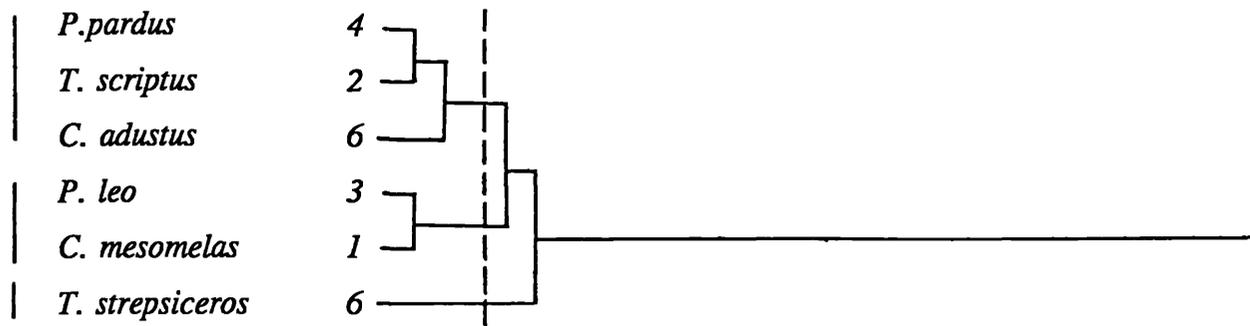


Figure 5.4 Dendrogram illustrating three clusters using five life-history variables (adult body weight, neonate weight, litter size, gestation period and age at maturity) of 6 mammal species in the southern African sub-region for which the effects of phylogeny have been removed at the genus level. Note the vertical bars on the left indicate groupings of clusters based on three convergences (illustrated by broken vertical line).

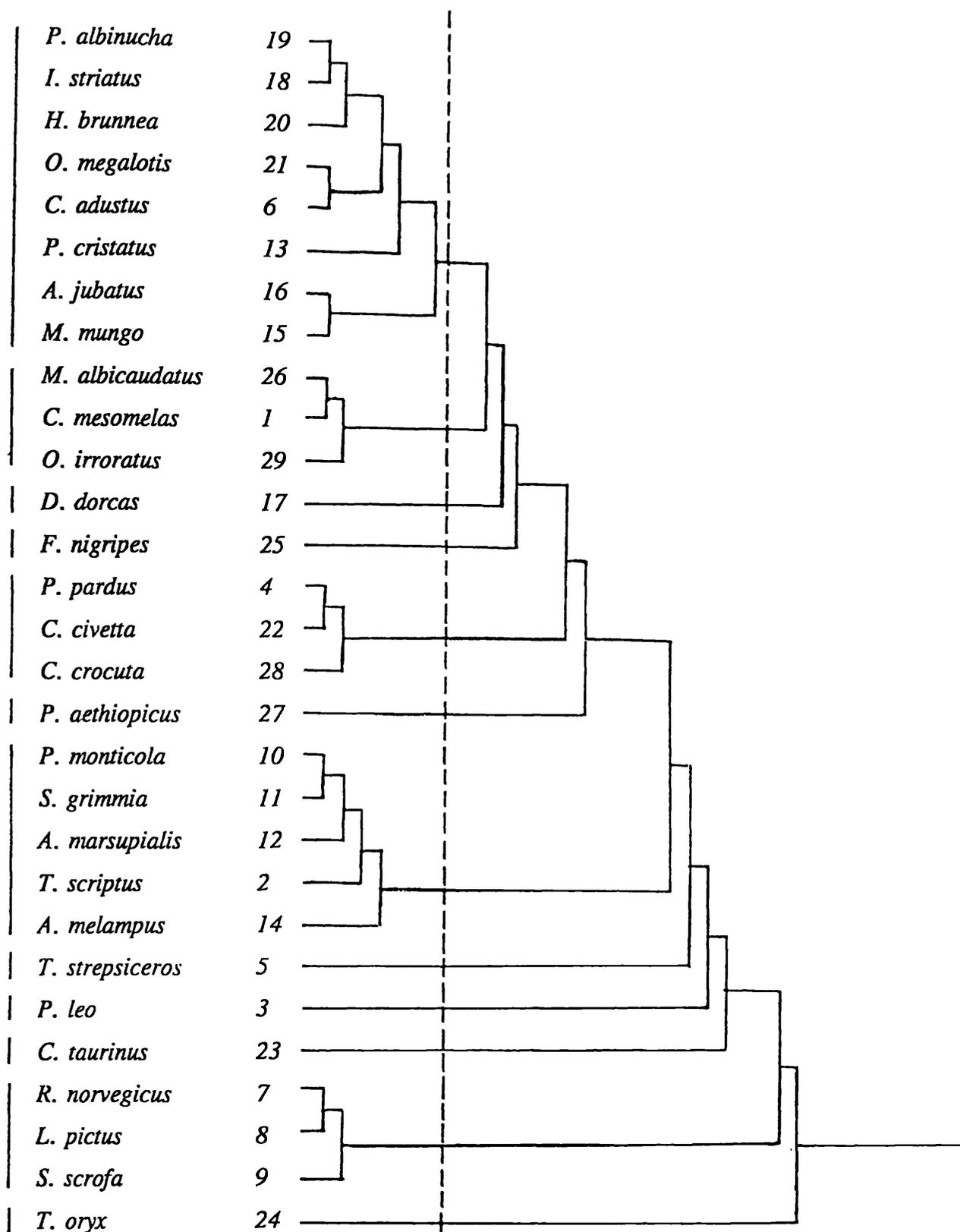


Figure 5.5 Dendrogram illustrating 12 clusters using five life-history variables (adult body weight, neonate weight, litter size, gestation period and age at maturity) of 29 mammal species in the southern African sub-region for which the effects of phylogeny have been removed at the family level. Note the vertical bars on the left indicate groupings of clusters based on seven convergences (illustrated by broken vertical line).

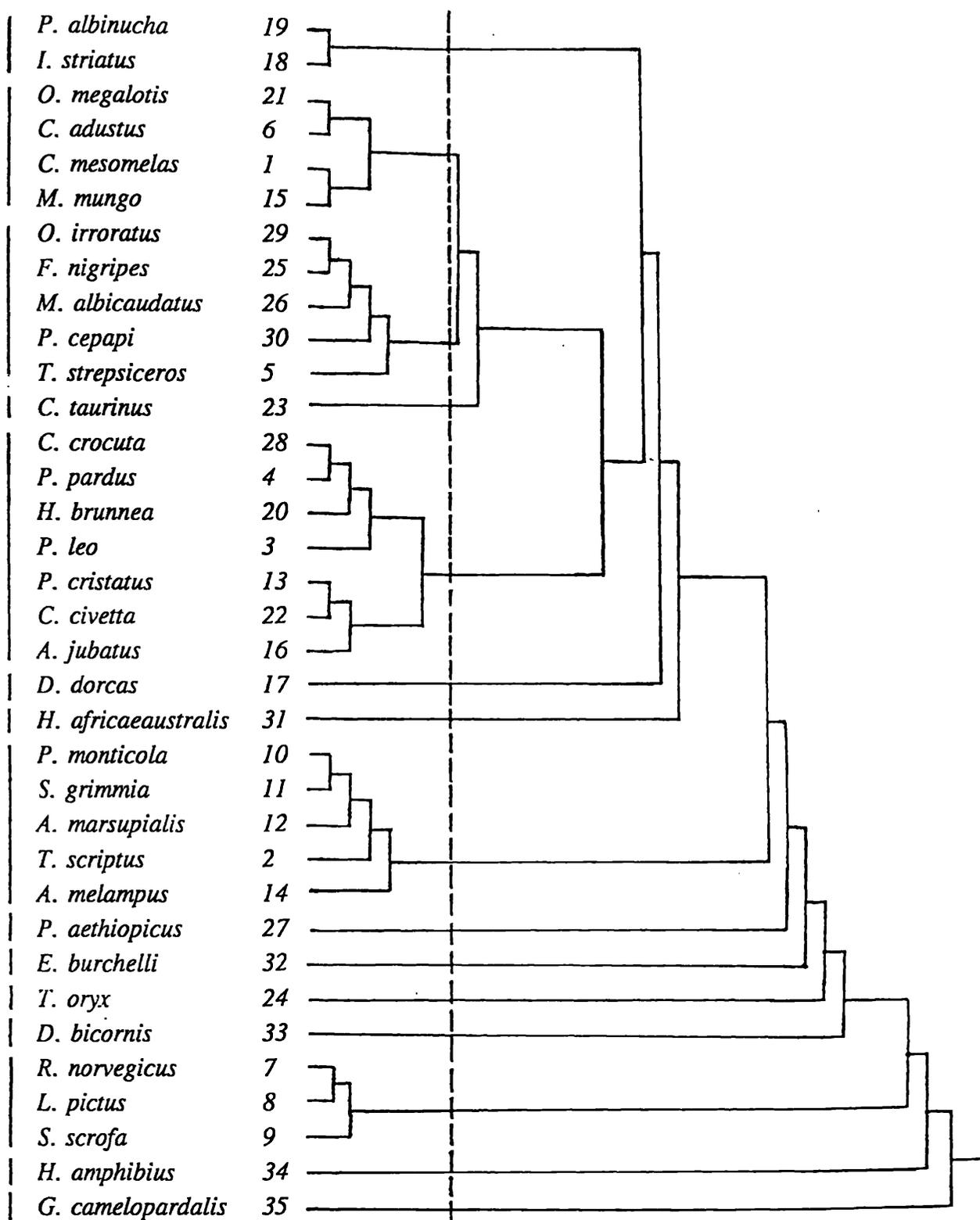


Figure 5.6 Dendrogram illustrating 15 clusters using five life-history variables (adult body weight, neonate weight, litter size, gestation period and age at maturity) of 35 mammal species in the southern African sub-region for which the effects of phylogeny have been removed at the order level. Note the vertical bars on the left indicate groupings of clusters based on seven convergences (illustrated by broken vertical line).

9,0) and *S. scrofa* (litter size 9,0) at all taxonomic levels. The pattern of clusters at the genus level may be influenced by the reduced number of species used at this taxonomic level and their inclusion could bias the final interpretation of life-history patterns.

Discussion

Phylogenetic constraints are important when describing patterns of life-history traits for mammals from the southern African subregion. These results are consistent with similar results obtained by Stearns (1980, 1983 and 1984) on the effects of phylogeny on correlations among life-history traits for mammals and reptiles when considering correlations after the removal of the effects of phylogeny at the family and order levels. Brown (1983) considered similar effects on snails and Felsenstein (1985) considered the effects of phylogeny in interspecific comparative analyses, obtaining similar results. Cheverud *et al.* (1985) proposed that 50% of the variation among primate species can be explained by phylogeny.

The description of southern African mammalian life-history patterns following the removal of phylogenetic effects, raises two points. First, the greatest impact of body size on life-history traits at different taxonomic levels was observed at the family level (see Chapter 4) whereas the greatest impact of phylogeny on life-history traits was found to be at the order level with the second-most significant impact of phylogeny being at the family level. Secondly, an additional dimension (3 PCs) is required when phylogeny is removed to explain the same amount of variation evident at each taxonomic level with the effects of body size removed (see Chapter 4). This raises two questions: first, why is the greatest impact of phylogeny at the order level, with a reduction in the impact of phylogeny occurring as one descends the taxonomic hierarchy, and secondly, why are more dimensions needed to explain life-history variation at each taxonomic level following the removal of the effects of phylogeny. The explanation of the patterns observed in terms of life-history evolution, requires an in-depth consideration of mammalian evolution.

Mammals radiated about 70 million years ago at the beginning of the Cretaceous period (MacDonald 1984). This coincided with the extinction of dinosaurs which opened up numerous ecological niches for mammals giving rise to an explosion of divergent adaptations.



Mammals are believed to have usurped the dinosaurs as they evolved lactation and parental care. Dinosaur offspring are believed to have hatched (similar to modern crocodiles) as tiny replicas of their parents. Their minuscule sizes compared to the adults of their species, required a diet different from the adults. They grew at slow rates which depended on their foraging success and consequently reached adult sizes only after extended periods of development. In contrast, mammals evolved lactation which ensured rapid growth of offspring, increased survival due to parental care and reduced developmental periods. At independence, mammalian young are almost full-grown and enter more or less the same niche as the adult members of their species (MacDonald 1984).

During the Eocene, Oligocene, Miocene and Pliocene epochs of the Tertiary period (55 to 7 million years ago), mammals flourished and achieved their peak in terms of numbers (Hickman, Roberts & Hickman 1988) and probably in terms of varieties. This would have been reflected in a great diversity and variety of life-histories characterising mammals at that time. Subsequent extinction of mammalian species that has been observed during the Pleistocene (3 to 0.5 million years ago) could have resulted from one of two outcomes. First, mammals displaying similar life-history characteristics may have become extinct because these features were not conducive to adaptation during the Pleistocene, a period characterised by environmental changes (environmental cooling, ice-age, environmental warming). This would have resulted in convergent life-history patterns dominating present day mammals.

Secondly, mammals displaying similar life-history characteristics could have experienced selective extinction because only one or a few species displaying a particular suite of life-history traits were able to survive. This would have resulted in divergent life-history patterns which would be consistent with the large-scale variation observed for species at higher taxonomic levels, such as at the order level. Thus divergent adaptation of specific life-history traits may have occurred at a time when numerous other physiological and morphological characteristics were being-manifested in various species during the early stages of mammalian radiations. Developmental periods and other demographic traits may have evolved in response to selective pressures at a time when ancestral species displayed more variation which would have allowed them more flexibility in responding in an evolutionary

sense to selection pressures. Subsequent extinctions of numerous species having similar life-history traits resulted in fewer species displaying similar life-history traits with more species displaying divergent life-history traits. The outcome could be that present species may be constrained from responding in a similar way to these selection pressures (see Wootton 1987). This can be interpreted to mean that once a major group diverged from a related group, the subsequent scope of life-history evolution was constrained within that lineage.

The interspecific variation observed at lower taxonomic levels could suggest that although certain traits are constrained from lineage to lineage, the nature of the constraints could differ between lineages (Stearns 1983). Variation in life-history traits evident at higher taxonomic levels (e.g. at the order level), may simply have become randomly fixed in ancestral species and then been prevented from adapting further as a result of various other constraints (see Gould & Lewontin 1979). As a result, most of the variation displayed between species would be more evident at the order level with less variation evident at subsequent taxonomic levels as traits became fixed from lineage to lineage (see Stearns 1983). Therefore, the observation that different variables are more affected by the removal of phylogeny at different taxonomic levels, suggests that the nature of the constraints could differ from lineage to lineage.

Another consideration in describing the patterns of life-history traits in terms of phylogeny is one that has not been addressed thus far in this analysis, namely ecological factors. The patterns of variation explained in terms of body size, developmental periods (gestation period and age at maturity) or litter size may be related to ecological factors. For instance, primate species living in tropical rain forests have lower potential reproductive rates (Cole 1954) than species living in other habitats, such as savannah and secondary growth forest (Ross 1987). Much of the southern African subregion is savannah (Skinner & Smithers 1990) thus the advantages accruing from, for instance, an increase in reproductive output could have enabled ancestral species to invade these savannahs more successfully than those ancestral species with lower reproductive output.

Perusal of the species comprising the different orders shows a variety of adaptations which could have allowed them to meet all possible combinations of niche requirements. For



instance, a species may respond during natural selective processes (under various conditions), either by evolving to meet those requirements or by failing to persist in the specific environment or habitat (Wootton 1987). Life-history traits may control ecological characteristics by directly influencing the species composition found under certain ecological conditions, rather than selective forces driving the evolution of life-history traits. Under these conditions, life-history traits may determine whether a species successfully invades a new niche or habitat. Thus, life-history traits could dictate a species' ecology rather than ecological factors dictating the evolution of a species life-history traits. Ancestral life-history traits may therefore have dictated the habitat type that mammals invaded once diverse ecological niches opened up.

If life-history traits do not undergo rapid changes over ecological time in the face of selection (see Wootton 1987), then these traits could have dictated the response of species to ecological circumstances with these responses differing from lineage to lineage. Since mammals differ in their responses to environmental conditions, more than one variable or dimension is needed to explain the causal factors underlying these differences. Consequently, more dimensions will be needed at successive taxonomic levels to explain the importance of different traits at different taxonomic levels once the effects of phylogeny are removed because phylogeny will not be masking the true effect of these variables. The contribution of litter size and gestation period in addition to adult body weight, neonate weight and age at maturity in manifesting patterns of covariation is evident at the order level but the fixation of these variables and their relative importance, is evident at the family level. This is supported by the different representation of these variables along principal components at these taxonomic levels.

As the southern African subregion contains many diverse habitat types (Skinner & Smithers 1990), it would make sense to relate ecological factors to life-history traits in determining which causal factors account for most of the variation observed in mammalian life-history patterns within the subregion. Generally analyses of the causal basis of the variation observed for species' attributes has been explained in terms of the adaptation of forms to the external environment by means of natural selection (Wanntorp 1983), rather than adaptations allowing the exploitation of certain external environments. The fact that most of the

variation in life-history traits is observed at the order level, suggests that life-history traits were shaped in ancestors and that these traits have effectively constrained the response of species to past and current environmental conditions.

The persistent litter size grouping of *L. pictus*, *S. scrofa* and *R. norvegicus* at all taxonomic levels irrespective of which constraints are removed, suggests that this trait could have been shaped in the ancestors which may have enabled them because of their numbers (due to higher rate of natural increase) to exploit niches not possible had they had smaller litters. Rather than considered in the sense of a negative constraint, the litter sizes of these mammals could be conferring a selective advantage in enabling a response to environmental conditions not possible if these mammals had smaller litters. Thus litter size could be one of the major factors determining their responses, demographic or otherwise to environmental conditions. Note however, the explanation for larger litter sizes may be appropriate only to *L. pictus* since *S. scrofa* and *R. norvegicus* are species that were introduced into the southern African subregion. The persistent grouping of these three species is therefore a result of the similarity in the sizes of their litters ($\approx 9,0$) rather than anything else.

Conclusion

Phylogenetic constraints are important in describing patterns of covariation between life-history traits for mammals from the southern African subregion. Thus the most appropriate answer to why a certain mammal species in the southern African subregion displays a certain tactic would be because its ancestor exhibited a similar trait.

With the effects of phylogeny removed, a third dimension is needed to explain the variance observed between life-history traits across supraspecific taxonomic levels suggesting that the true contributions of these variables in explaining life-history patterns were masked by phylogenetic constraints. Thus other variables such as litter size or developmental periods could be having a profound effect on the patterns of life-history traits observed for mammals in the subregion. However, as phylogeny and body size are obviously having profound separate effects in constraining patterns of certain life-history traits for different groups of mammals, the combined effect of these two variables should be removed.



CHAPTER 6

THE COMBINED EFFECTS OF BODY WEIGHT AND PHYLOGENY ON PATTERNS OF COVARIANCE AMONG LIFE-HISTORY TRAITS

Introduction

Allometry and phylogeny are important aspects of life-history covariation (Harvey & Pagel 1991) and influence patterns of mammalian life-histories within the southern African subregion. The independent effects of size and phylogeny on patterns of covariation for life-history traits were evident in chapters 3, 4 and 5. No doubt, these variables influence the ordering of most mammals in the southern African subregion onto a "fast-slow" continuum, a phenomenon generally observed for mammals elsewhere (Read & Harvey 1989).

Given the effects that allometry and phylogeny have, it seems reasonable to expect a strong association between these two variables at different taxonomic levels since selection acting on specific traits such as gestation period or age at maturity at different taxonomic levels can only achieve limited change at any taxonomic level without causing readjustments in allometrically linked traits (see Western 1979). Conversely, predictions could suggest that adjustments in life-histories evolve through geometric changes in size rather than in allometric proportions. Conservatism in design is sufficiently great for the early radiation of taxa to initially have involved an ancestral size diversification with subsequent fixed specializations much later as one descends the taxonomic hierarchy.

To determine to what extent the relationship between allometry and phylogeny influence patterns of life-history covariation observed throughout this analysis, the aim of this chapter is to establish what the combined effect of these two variables are.

Material and Methods

A combination of two statistical methods were used. Stearns' (1983) phylogenetic-subtraction method (see chapter 5) was first used to remove the effects of phylogeny from all variables used. Residuals were obtained for each variable with the effects of adult body weight removed (see chapter 3) using a set of individual data points for which the effects of phylogeny had previously been removed. To this effect least squares regression analyses were used to obtain the relationship of each variable with adult body weight. These relationships were characteristically linear (see Table 6.1).

Covariance and correlation analyses were performed on three data sets characterised by the removal of the effects of phylogeny at the order, family and genus levels after the removal of the effects of adult body weight in each case. Principal components and cluster analyses were performed on these three data sets, comprising the same set of four variables (neonate weight, litter size, age at maturity and gestation period). Multiple discriminant analyses (MDA) were used to investigate differences between groups identified within the component space of PCA.

Results

Correlation and covariance analyses

The correlations and covariances between southern African mammalian life-history variables following the removal of the combined effects of phylogeny and adult body weight at the genus, family and order levels are presented in Tables 6.2, 6.3 and 6.4 respectively. Significant correlations and covariances are evident at all taxonomic levels. The highest percentage of significant correlations at supraspecific level is at the genus level (see Table 6.5). However, the highest percentage of significant correlations that increased in significance as well as the highest percentage of significant correlations that decreased in significance occurs at the order level. In addition, the greatest percentage of correlation coefficients that changed in sign were also evident at the order level. The changes in correlation coefficients from species to genus, family and order levels were most significant



Table 6.1 Relationships used to remove the effect of body weight following the removal of the effect of phylogeny at the genus, family and order level.

Genus	Relationship	r-value	df
Neonate weight	$y = 0,07x - 0,00004$	0,77	19
Litter size	$y = 0,002x - 0,00001$	0,08	73
Inter-litter interval	$y = 1,41x - 18,68$	0,86	3
Age at maturity	$y = 0,35x - 0,72$	0,23	9
Gestation period	$y = 0,29x - 0,85$	0,42	37
Lactation period	-	-	-
Age at weaning	$y = 2,89x + 0,01$	0,99	2
Age at first parturition	$y = -0,05x + 2,02$	-0,01	13
Juvenile mortality	-	-	-
Adult mortality	-	-	-
Adult lifespan	$y = -2,29x + 72,57$	-0,08	15
Reproductive lifespan	$y = -31,98x - 11,10$	-0,64	6
Family	Relationship	r-value	df
Neonate weight	$y = 0,08x - 0,49$	0,93	65
Litter size	$y = 0,002x + 0,03$	0,10	132
Inter-litter interval	$y = 0,52x - 7,62$	0,24	23
Age at maturity	$y = 2,36x - 17,17$	0,65	36
Gestation period	$y = -0,06x + 0,26$	-0,03	95
Lactation period	$y = 6,22x - 13,66$	0,69	3
Age at weaning	$y = 0,72x - 8,64$	0,65	25
Age at first parturition	$y = 1,75x - 14,95$	0,76	36
Juvenile mortality	$y = 0,01x - 0,69$	0,17	5
Adult mortality	$y = 24,85x - 24,01$	0,63	10
Adult lifespan	$y = 11,07x - 30,65$	0,64	33
Reproductive lifespan	$y = 1,49x + 675,61$	0,06	15
Order	Relationship	r-value	df
Neonate weight	$y = 0,07x - 0,95$	0,82	77
Litter size	$y = -0,0001x + 0,03$	-0,01	140
Inter-litter interval	$y = 0,33x - 14,48$	0,34	33
Age at maturity	$y = 1,32x - 44,21$	0,69	42
Gestation period	$y = 0,08x + 0,04$	0,09	105
Lactation period	$y = 0,05x - 1,34$	0,11	13
Age at weaning	$y = 0,06x - 2,81$	0,06	33
Age at first parturition	$y = 1,29x - 18,32$	0,80	42
Juvenile mortality	$y = 0,0009x - 0,69$	0,16	11
Adult mortality	$y = 41,56x - 816,19$	0,73	11
Adult lifespan	$y = 10,93x - 171,45$	0,86	40
Reproductive lifespan	$y = -0,68x + 220,05$	-0,06	19



Table 6.2 Correlations and covariances of life history variables of mammals in the southern African sub-region with the effects of phylogeny at the genus level and the effects of adult body weight removed. ** denotes significance at the 99% level and * at the 95% level. NEOWT -Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
NEOWT		-0,10 (18)	-0,92** (4)	0,71** (6)	0,40** (16)	-	-	0,17 (8)	-	-	0,69** (7)	-
LITSZ	0 (18)		0,93** (4)	-0,73** (10)	-0,13* (30)	-	-0,99** (3)	-0,03 (10)	-	-	0,05 (14)	0,89** (5)
INLTIN	-136 (4)	8 (4)		0,90** (3)	-0,99** (4)	-	-	-	-	-	-0,91** (3)	-
AGEM	-64 (6)	-34 (10)	2387 (3)		-0,38** (10)	-	-	-	-	-	-0,74** (8)	-0,88** (4)
GESP	11 (16)	-1 (30)	-777 (4)	-304 (10)		-	-	0,39** (13)	-	-	0,34** (16)	0,48* (7)
LACP	-	-	-	-	-		-	-	-	-	-	-
AGEW	0 (1)	-1 (3)	-	-	17 (2)	-	-	-	-	-	-	-
AGEPRT	20 (8)	-2 (10)	-153 (2)	-5714 (2)	849 (13)	-	-	-	-	-	0,15 (9)	-
JMORT	-	-	-	-	-	-	-	-	-	-	-	-
ADMORT	-	-	-	-	-	-	-	-	-	-	-	-
ADLIFE	1570 (7)	28 (14)	-80161 (3)	-47798 (8)	4951 (16)	-	-	9813 (9)	-	-		0,75** (7)
RELIFE	-167 (2)	702 (5)	2378 (2)	-69552 (4)	5193 (7)	-	-	-692 (2)	-	-	1 (7)	



Table 6.3 Correlations and covariances of life history variables of mammals in the southern African sub-region with the effects of phylogeny at the family level and the effects of body weight removed. ** denotes significance at the 99% level and * at the 95% level. NEOWT - Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPR - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPR	JMORT	ADMORT	ADLIFE	RELIFE
NEOWT		-0,23** (61)	-0,51** (19)	-0,07 (32)	-0,07 (57)	-	-0,29** (20)	0,06 (28)	-0,41 (5)	0,14 (9)	0,31** (25)	0,31** (10)
LITSZ	-1 (61)		0,03 (20)	-0,10 (34)	-0,06 (78)	-	-0,13 (24)	-0,12 (30)	-0,30 (5)	-0,68** (11)	-0,06 (30)	-0,01 (11)
INLTIN	-91 (19)	7 (20)		0,42** (13)	-0,07 (21)	-	0,69** (9)	0,01 (13)	-	0,10 (5)	-0,14 (14)	-0,36** (6)
AGEM	-26 (32)	-25 (34)	5042 (13)		0,05 (36)	-	0,52** (12)	0,42** (17)	-	0,70** (9)	0,17 (21)	-0,01 (6)
GESP	24 (57)	-2 (78)	-4532 (21)	1741 (36)		-0,79 (4)	0,22** (24)	-0,13* (36)	-0,04 (5)	0,21 (10)	-0,10 (34)	0,08 (15)
LACP	-2 (2)	1 (2)	-	0 (1)	-701 (4)		-	-	-	-	-	-
AGEW	-37 (20)	-9 (24)	4120 (9)	7795 (12)	491 (24)	-		0,60** (10)	-	0,67** (5)	0,53** (10)	0,27 (5)
AGEPR	-18 (28)	-19 (30)	74 (13)	9946 (17)	-3761 (36)	-	1566 (10)		-0,98* (3)	0,04 (3)	0,08 (26)	0,43** (9)
JMORT	-11 (5)	-2 (5)	509 (2)	-1048 (2)	-31 (5)	-	272 (2)	-1875 (3)		-	0,35 (3)	-
ADMORT	392 (9)	-531 (11)	10444 (5)	186280 (9)	3270 (10)	-725 (2)	150319 (5)	683 (3)	0 (1)		0,54** (6)	0,76** (3)
ADLIFE	1001 (25)	-91 (30)	-14631 (14)	35953 (21)	-24317 (34)	-	89417 (10)	13490 (26)	9517 (3)	1251230 (6)		0,76** (12) (6)
RELIFE	2533 (10)	-61 (11)	-42440 (6)	-3590 (6)	4960 (15)	-	6802 (5)	45862 (9)	-22409 (2)	1350110 (3)	1376560 (12)	



Table 6.4 Correlations and covariances of life history variables of mammals in the southern African sub-region with the effects of phylogeny at the order level and the effects of adult body weight removed. ** denotes significance at the 99% level and * at the 95% level. NEOWT -Neonate body weight; LITSZ - Litter size; INLTIN - Inter litter interval; AGEM - Age at maturity; GESP - Gestation period; LACP - Lactation period; AGEW - Age at weaning; AGEPRT - Age at first parturition; JMORT - Juvenile mortality; ADMORT - Adult mortality; ADLIFE - Adult lifespan; RELIFE - Reproductive lifespan. Figures in brackets represent sample sizes.

	NEOWT	LITSZ	INLTIN	AGEM	GESP	LACP	AGEW	AGEPRT	JMORT	ADMORT	ADLIFE	RELIFE
NEOWT		-0,13** (72)	-0,31** (27)	0,07 (38)	0,09* (68)	-0,49** (9)	-0,32** (28)	0,41** (35)	0,08 (10)	0,10 (10)	-0,24** (33)	0,10 (14)
LITSZ	-2 (72)		-0,13 (30)	-0,15** (40)	-0,33** (89)	-0,33** (11)	0,23** (31)	0,01 (36)	-0,23 (11)	-0,53** (12)	-0,22** (37)	-0,02 (15)
INLTIN	443 (27)	-49 (30)		0,70** (19)	-0,04 (30)	-0,17 (7)	-0,11 (11)	0,59** (20)	0,33** (8)	0,06 (7)	-0,36** (20)	0,15 (9)
AGEM	197 (38)	-88 (40)	29987 (19)		0,06 (42)	0,07 (6)	0,48** (17)	0,75** (24)	0,70** (7)	0,44** (10)	-0,01 (26)	0,37 (9)
GESP	118 (68)	-24 (89)	-1758 (30)	3405 (42)		-0,11 (14)	0,14* (31)	-0,01 (42)	0,10 (11)	0,54** (11)	-0,13* (41)	0,10 (19)
LACP	-1323 (9)	-33 (11)	-9519 (7)	4507 (6)	-693 (14)		0,99** (4)	-0,13 (4)	-	0,72 (4)	0,79** (7)	0,98* (3)
AGEW	-344 (28)	-39 (31)	-1411 (11)	22413 (17)	776 (31)	50257 (4)		0,36** (15)	-0,88** (5)	0,61** (5)	0,29** (15)	-0,36* (6)
AGEPRT	965 (35)	3 (36)	17591 (20)	57381 (24)	-464 (42)	-12500 (4)	14180 (15)		-0,33** (8)	0,71** (5)	-0,15** (30)	-0,08 (11)
JMORT	22 (10)	-2 (11)	455 (8)	3814 (7)	-84 (11)	1404 (2)	-738 (5)	-986 (8)		0,07 (3)	-0,18 (9)	-0,05 (4)
ADMORT	398 (10)	-1544 (12)	13644 (7)	203914 (10)	12742 (11)	212415 (4)	205864 (5)	221046 (5)	1987 (3)		0,63** (7)	0,79** (4)
ADLIFE	-3617 (33)	-434 (37)	-70099 (20)	-4211 (26)	-36519 (41)	305663 (7)	77457 (15)	-49536 (30)	-3933 (9)	1856110 (7)		0,69** (16)
RELIFE	2391 (14)	-98 (15)	39831 (9)	235448 (9)	5870 (19)	96310 (3)	-91657 (6)	-33133 (11)	-1942 (4)	2196590 (4)	2063010 (16)	



Table 6.5 Summary of the change in correlations between variables from the species level to genus, family and order level with the removal of body weight and phylogeny at these levels.

	Percentage significant correlations	Comparison level	Percentage that remained the same	Percentage that decreased	Percentage that increased	Percentage that changed sign	<i>z/T</i> -value (Wilcoxon matched-pairs signed-rank tests)
Species	67,5						
Genus	79,2	Species to Genus	0,0	18,2	12,9	12,9	$T_{24} = 106$ $p > 0,05$
Family	43,1	Species to Family	0,0	46,8	19,5	19,5	$z = -3,70$ $p < 0,05$
Order	58,5	Species to Order	0,0	54,5	29,9	24,7	$z = -3,73$ $p < 0,05$

at the order level ($z=-3,73$, $p<0,01$) followed by the family level ($z=-3,70$, $p<0,01$). This suggests that the combined effects of order and adult body weight and family and adult body weight are stronger than the combined effects of genus and adult body weight. Note that the number of observations used in the analyses are reduced at genus level which could bias the interpretation at this taxonomic level.

Adult lifespan was significantly correlated with most variables at all taxonomic levels following the removal of the combined effects of adult body weight and phylogeny. Adult mortality was also significantly correlated with most variables at the order level (Table 6.4) but only significantly correlated with litter size, age at maturity and age at weaning at the family level (Table 6.3). Litter size was significantly negatively correlated with neonate weight, age at maturity, gestation period, lactation period, age at weaning, adult mortality and adult lifespan at the order level but only negatively correlated with neonate weight and adult mortality at the family level. Thus, the number of significant correlations between litter size and most variables was drastically reduced from the order to family level. Noteworthy are certain variables that were not significant at one taxonomic level, but attained significance at another taxonomic level (age at weaning and interlitter interval; age at first parturition and interlitter interval; age at maturity and litter size; gestation period and litter size) which suggest that variables are differentially affected at different taxonomic levels by the removal of the combined effects of adult body weight and phylogeny. This is consistent with results obtained in previous chapters (chapters 4 and 5).

Principal Components and Cluster Analysis

The eigenvectors and eigenvalues for PCA using four life-history variables (neonate weight, litter size, gestation period and age at maturity) following the removal of the combined effects of phylogeny and adult body weight at the order, family and genus levels are presented in Tables 6.6, 6.7 and 6.8. In addition, the correlation coefficients between variables and principal components are shown in these tables. The first two principal components accounted for $\pm 93\%$ of the variance at genus level and $\pm 60\%$ of the variance at family and order levels. Plots of the first two PCs of the relevant mammal species at each taxonomic level using the same four variables for which the effects of phylogeny and adult



Table 6.6 Eigenvectors and eigenvalues for PCA using four life-history variables of which the effects of phylogeny at the genus level as well as the effects of adult body weight have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlations coefficients between variables and principal components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Litter size	-0,01	(-0,85)	0,21	(0,48)
Gestation period	(0,57)	0,21	(0,79)	0,04
Neonate weight	(0,61)	0,18	(-0,52)	(0,57)
Age at maturity	(-0,54)	0,45	0,24	(0,66)
Eigenvalues	58,93	34,11	6,67	0,27
Contribution to total variation (%)	58,93	34,11	6,67	0,27
Cumulative contribution (%)	58,93	93,05	99,72	100,00
Correlation coefficients				
Litter size	-0,02	-0,99	0,11	0,05
Gestation period	0,88	0,25	0,41	0,00
Neonate weight	0,94	0,22	-0,27	0,06
Age at maturity	-0,84	0,52	0,12	0,07



Table 6.7 Eigenvectors and eigenvalues for PCA using four life-history variables of which the effects of phylogeny at the family level as well as the effects of adult body weight have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlations coefficients between variables and principal components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Litter size	(-0,71)	-0,23	-0,02	(0,66)
Gestation period	-0,01	(0,63)	(0,74)	0,23
Neonate weight	(0,69)	-0,32	0,09	(0,64)
Age at maturity	0,09	(0,67)	(-0,66)	0,32
Eigenvalues	30,82	27,84	23,68	17,66
Contribution to total variation (%)	30,82	27,84	23,68	17,66
Cumulative contribution (%)	30,82	58,66	82,34	100,00
Correlation coefficients				
Litter size	-0,85	-0,27	-0,05	0,59
Gestation period	0,14	0,36	0,10	0,17
Neonate weight	0,79	-0,35	0,28	0,47
Age at maturity	0,08	0,87	-0,93	0,10



Table 6.8 Eigenvectors and eigenvalues for PCA using five life-history variables of which the effects of phylogeny at the order level have been removed. Principle contributions are indicated in brackets. Each component's contribution to the total variation as well as cumulative contributions are given. Note correlations coefficients between variables and principal components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Litter size	(-0,64)	0,16	0,34	0,19
Gestation period	(0,59)	-0,44	0,18	(0,65)
Neonate weight	0,36	0,21	(-0,91)	0,06
Age at maturity	0,34	(0,85)	0,34	0,19
Eigenvalues	36,46	23,85	23,25	16,44
Contribution to total variation (%)	36,46	23,85	23,25	16,44
Cumulative contribution (%)	36,46	60,31	83,56	100,00
Correlation coefficients				
Litter size	-0,82	0,13	-0,09	0,92
Gestation period	0,73	0,38	-0,28	-0,01
Neonate weight	0,58	0,27	-0,92	0,07
Age at maturity	0,47	0,92	0,27	0,16



body weight were removed at the order, family and genus level are presented in Figures 6.1, 6.2 and 6.3. At the order level, PC-1 represents a negative gradient of litter size and a positive gradient of gestation period and neonate weight whereas PC-2 represents a positive gradient of age at maturity. At the family level, the same composition of PC-1 and PC-2 exists. At the genus level, gestation period, neonate weight and age at maturity are loaded onto PC-1 thus representing a gradient varying from small neonates, short gestation periods and late ages at maturity to the opposite extremes of these traits along this axis. This component accounts for almost the same amount of variance ($\pm 60\%$) as the first two components at family and order levels. With removal of the combined effects of adult body weight and phylogeny, the amount of variation accounted for by the first component is reduced by $\pm 30\%$ at the order and family levels compared with the species level (see Chapter 3, Table 3.5) and genus level (Table 6.6).

Noteworthy are the positional representations of mammals within the component spaces. At the genus level (Figure 6.1), *T. scriptus* (2) and *P. leo* (3) are represented at the one extreme of PC-1 and *P. pardus* (4) and *T. strepsiceros* (5) at the opposite extreme. A similar phenomenon is evident along PC-2 with *C. mesomelas* (1) and *C. adustus* (6). However, the pattern may be biased by the reduction in number of data points as compared with the family and order level. At the family level, four major groups are evident (Figure 6.2) (MDA: $F_{12,55}=11,58$; $p<0,0001$), with several mammals spaced along primarily PC-1 but also along PC-2. At the order level (Figure 6.3), one major group is evident with several mammals scattered in the component space. Although groupings are evident, the fact is that following the removal of the combined effects of adult body weight and phylogeny, the groupings are not characterised by any specific factors at both family and order levels with mammals spread throughout the component space especially at the family level. This suggests that very little residual variation is left once adult body weight and phylogeny are removed from the picture. However, at the order level those mammals characterised by extreme litter sizes (*L. pictus* (8) - 8.9; *R. norvegicus* (7) - 9.0; *S. scrofa* (9) - 9.0) or extreme body sizes (*D. bicornis* (34) and *G. camelopardalis* (35)) are outliers to the major grouping. The extensive litter size effect for some mammals suggests that litter size could be an important component in addition to size and phylogeny in describing life-history variation in southern African mammals. The fact that certain large mammals are still outliers

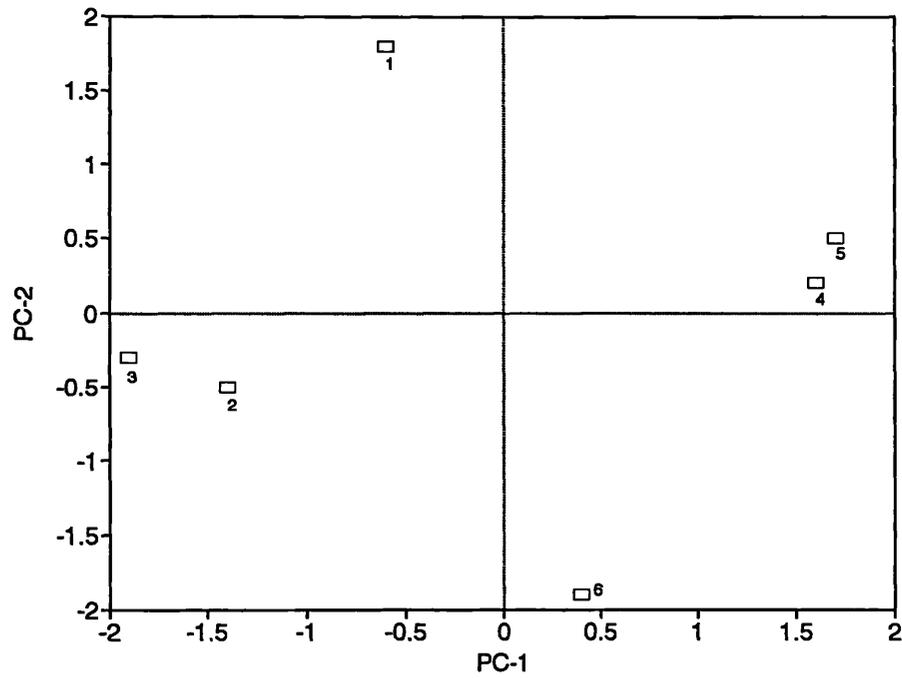


Figure 6.1 Plot of the first two principal components (PCs) of 6 mammal species in the southern African sub-region using four variables (neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the genus level as well as the effects of body weight have been removed. 1 - *C. mesomelas*, 2 - *T. scriptus*, 3 - *P. leo*, 4 - *P. pardus*, 5 - *T. strepsiceros*, 6 - *C. adustus*.

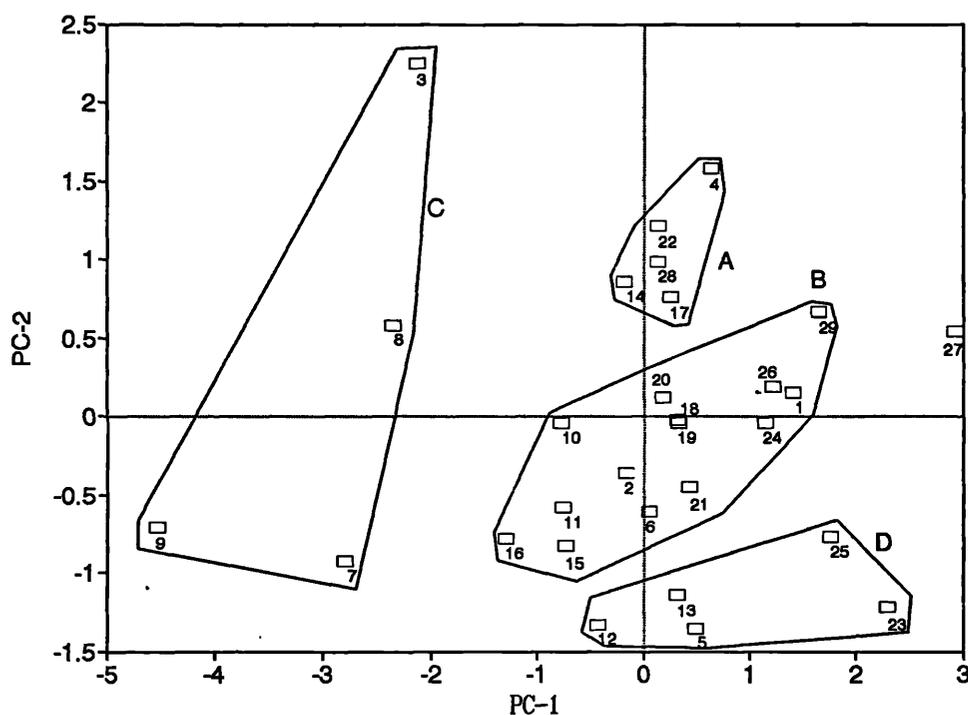


Figure 6.2 Plot of the first two principal components (PCs) of 29 mammal species in the southern African sub-region using four variables (neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the family level as well as the effects of body weight have been removed. The polygons (A, B, C and D) denote groupings within the component space. 1 - *C. mesomelas*, 2 - *T. scriptus*, 3 - *P. leo*, 4 - *P. pardus*, 5 - *T. strepsiceros*, 6 - *C. adustus*, 7 - *R. norvegicus*, 8 - *L. pictus*, 9 - *S. scrofa*, 10 - *P. monticola*, 11 - *S. grimmia*, 12 - *A. marsupialis*, 13 - *P. cristatus*, 14 - *A. melampus*, 15 - *M. mungo*, 16 - *A. jubatus*, 17 - *D. dorcas*, 18 - *I. striatus*, 19 - *P. albinucha*, 20 - *H. brunnea*, 21 - *O. megalotis*, 22 - *C. civetta*, 23 - *C. taurinus*, 24 - *T. oryx*, 25 - *F. nigripes*, 26 - *M. albicaudatus*, 27 - *P. aethiopicus*, 28 - *C. crocuta*, 29 - *O. irroratus*.

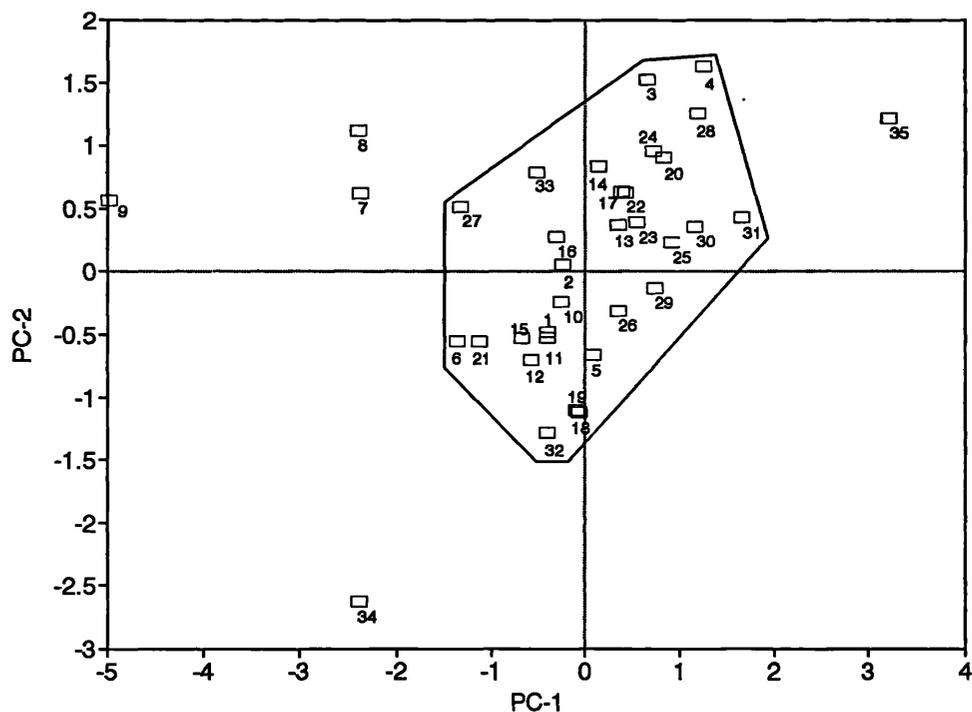


Figure 6.3 Plot of the first two principal components (PCs) of 35 mammal species in the southern African sub-region using four variables (neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the order level as well as the effects of body weight have been removed. The polygon denotes groupings within the component space. 1 - *C. mesomelas*, 2 - *T. scriptus*, 3 - *P. leo*, 4 - *P. pardus*, 5 - *T. strepsiceros*, 6 - *C. adustus*, 7 - *R. norvegicus*, 8 - *L. pictus*, 9 - *S. scrofa*, 10 - *P. monticola*, 11 - *S. grimmia*, 12 - *A. marsupialis*, 13 - *P. cristatus*, 14 - *A. melampus*, 15 - *M. mungo*, 16 - *A. jubatus*, 17 - *D. dorcas*, 18 - *I. striatus*, 19 - *P. albinucha*, 20 - *H. brunnea*, 21 - *O. megalotis*, 22 - *C. civetta*, 23 - *C. taurinus*, 24 - *T. oryx*, 25 - *F. nigripes*, 26 - *M. albicaudatus*, 27 - *P. aethiopicus*, 28 - *C. crocuta*, 29 - *O. irroratus*, 30 - *P. cepapi*, 31 - *H. africae australis*, 32 - *E. burchelli*, 33 - *D. bicornis*, 34 - *H. amphibius*, 35 - *G. camelopardalis*.



to the major groups even with size and phylogenetic effects removed suggests that a remaining size-related factor could be influencing the distribution of the larger mammals in the component space.

The dendrograms of the cluster analysis for four variables (neonate weight, litter size, gestation period, age at maturity) following the removal of the combined effects of phylogeny and adult body weight are presented in Figures 6.4, 6.5 and 6.6. The number of clusters increased from the order (11) to the family (19) level (Figures 6.5 & 6.6) which is consistent with the increased scatter data points for mammals at the family level in the PCA results (Figures 6.2 & 6.3). The number of clustered groups is smaller at the order level (5) than at the family level (6). A number of positional changes occurred within clusters from order to family level suggesting that different mammals were differentially affected by the removal of both phylogeny and adult body weight, a phenomenon consistent throughout these analyses.

There does not appear to be much change in the number of clusters from order to family level with certain groupings of carnivores and antelope remaining constant. However, relative positional changes of mammals within the clusters, frequently occurred.

Discussion

The results of the analyses which incorporate the removal of the combined effects of adult body weight and phylogeny suggest that most of the variation observed between mammalian life-history patterns within the southern African subregion can be described in terms of body size and phylogeny. However, different mammals and traits are affected differentially at all taxonomic levels which is consistent with the results obtained throughout these analyses (see Chapters 3, 4 and 5). The greatest effect on life-history traits evident at the order and family levels confirms the suggestion that much of the large-scale covariation between life-history traits for mammals within the subregion originates at these taxonomic levels which is consistent with previous findings (Pianka 1970, Stearns 1983).

Although adult body weight and phylogeny have profound impacts on patterns of covariation

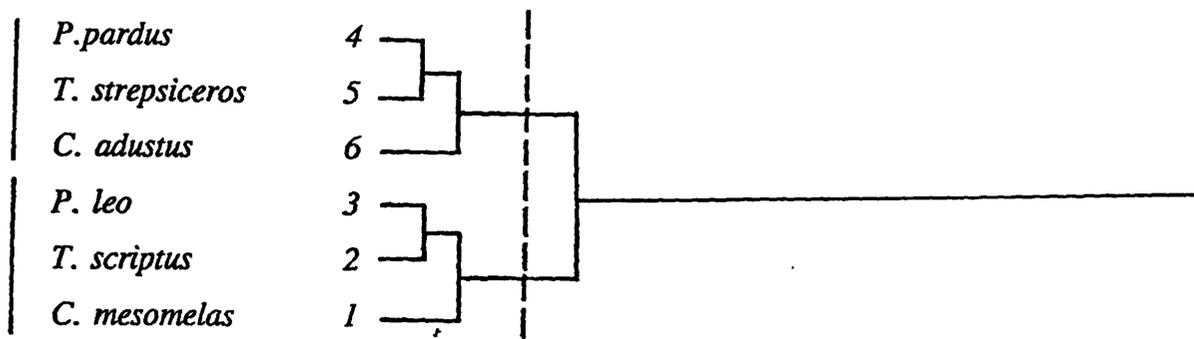


Figure 6.4 Dendrogram illustrating two clusters using four life-history variables (neonate weight, litter size, gestation period and age at maturity) of 6 mammal species in the southern African sub-region for which the effects of body weight as well as the effects of phylogeny have been removed at the genus level. Note the vertical bars on the left indicate groupings of clusters selected after three convergences (illustrated by the broken vertical line).

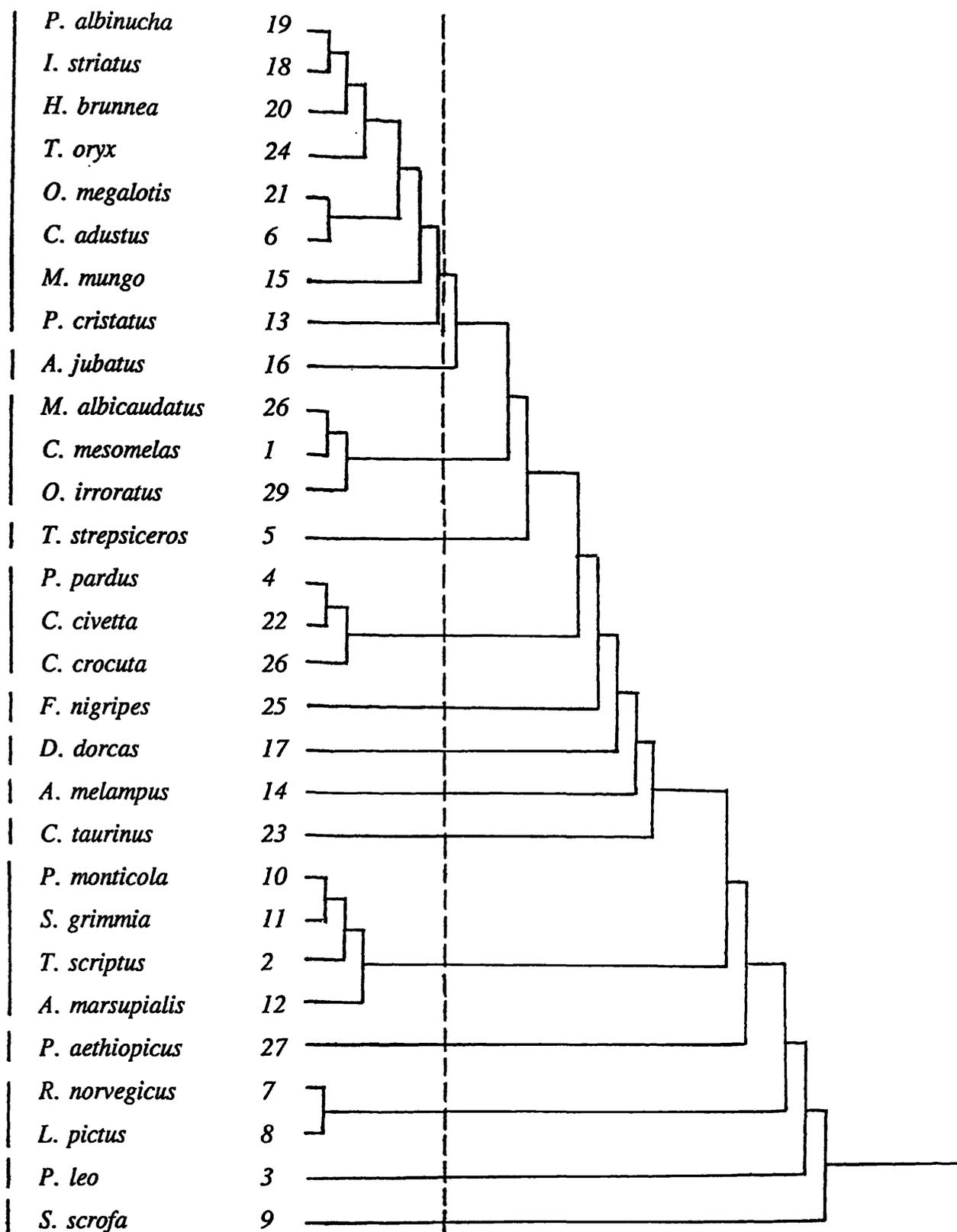


Figure 6.5 Dendrogram illustrating 14 clusters using four life-history variables (neonate weight, litter size, gestation period and age at maturity) of 29 mammal species in the southern African sub-region for which the effects of phylogeny have been removed at the family level as well as the effects of body weight removed. Note the vertical bars on the left indicate groupings of clusters selected after seven convergences (illustrated by the broken vertical line).



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through selective processes which may ultimately influence litter sizes.

Considering the life-histories of carnivores and artiodactyls, it is evident that there is considerable uniformity across artiodactyl life-history traits, social organization and mating systems (Eisenberg 1981). In contrast, the carnivores display much variance (Eisenberg 1981, MacDonald 1984). Assuming that the key to determining how natural selection shapes the evolution of life-history patterns, lies in the analysis of variations rather than similarities (see Eisenberg 1981), the focus of the next chapter will be on the carnivores.

Conclusion

The combined effects of adult body weight and phylogeny have a considerable effect on life-history covariation for southern African mammals but account for little more variation than either of these variables do independently. However, with the combined effects of these two variables removed, identifiable synergistic effects of other components such as litter size or developmental periods may be influencing certain groupings of mammals. This suggests that selective processes could be influencing litter size or one or more developmental periods directly. Consequently, adaptive strategies allowing these mammals to alter certain life-history features such as litter size or age at maturity may have been adopted. This may be the key to determining the adaptive responses of carnivores within a range of environments in the subregion.



CHAPTER 7

CARNIVORE LIFE-HISTORY PATTERNS IN THE SOUTHERN AFRICAN SUBREGION

Introduction

The patterns observed throughout the analyses thus far suggest that phylogeny and body size account for most of the variation observed in life-history patterns for southern African mammals (see Chapters 3, 4, 5 and 6). However, these are not the only factors influencing the ordering of mammals within this subregion onto the expected "fast-slow" continuum and this reservation seems especially pertinent to carnivores. Litter size effects appear to be particularly marked for certain groupings of mammals, specifically the carnivores (variance) and artiodactyls (conservatism) (see Chapter 6). Western (1979) found that amongst the carnivores and primates, life-history patterns in relation to size are remarkably similar to those established for the artiodactyls and that the regression slopes relating body weight to gestation time, age at first reproduction and lifespan were not significantly different from those of the artiodactyls. Furthermore, he concluded that the only differences between the carnivores and other orders are found in the intercepts of the regression equations where gestation period in carnivores is significantly shorter than in other orders for a given body weight. However, additional comparative life-history investigations among representatives of the Carnivora have revealed paradoxes within the hyaenids (Van Jaarsveld 1993; Van Jaarsveld, Richardson & Anderson 1995). These anomalies may not however, be restricted to the hyaenids but could be characteristic of the carnivores *per se*. This suggests that the carnivores may be a controversial order when comparative life-histories are considered.

The order Carnivora is represented by 33 terrestrial species in the southern African subregion. Members of this taxon display significant variance in their life-history features. The present chapter aims to further describe carnivore life-history patterns within the southern African subregion and to identify pertinent life-history traits which may characterise these patterns. This involves removing the effects of both body size and phylogeny in order to demonstrate what the impact of additional selective factors may be.



Material and Methods

Data for carnivore species were extracted from four data sets (see Chapters 3, 4, 5 and 6). These data sets were characterised as follows: data set 1 comprised observed values of five life-history variables (adult body weight, neonate weight, litter size, gestation period and age at maturity); data set 2 comprised values of four life-history variables (neonate weight, litter size, gestation period and age at maturity) for which the effects of adult body weight were removed; data set 3 comprised values of five life-history variables (adult body weight, neonate weight, litter size, gestation period and age at maturity) for which the effects of phylogeny at the family level were removed; data set 4 comprised values of four life-history variables (neonate weight, litter size, gestation period and age at maturity) for which the effects of both adult body weight and phylogeny at the family level were removed. Covariance, correlation, principal components (PCA) and cluster analyses (linkage distance method using Euclidean distances) (Ludwig & Reynolds 1988) were carried out on these four data sets separately (see Chapters 2, 3, 4, 5, 6 for detailed description of statistical procedures). Wilcoxon matched pairs signed-rank tests (Siegel 1956) were used to compare correlation coefficients resulting from the correlation analyses. Significance was taken at the 95% level.

Multiple discriminant analyses (MDA) were used to determine whether groups identified within the component space for the PCA were significantly different (Ludwig & Reynolds 1988). Similarly, MDA were used to investigate differences between families. Significance was taken at the 95% level. Clusters in the dendograms resulting from the cluster analyses were selected at a linkage distance of 50.

Results

Correlation analyses

The results of the correlations and covariances between five life-history variables for observed data (adult body weight, neonate weight, litter size, age at maturity, gestation period) for all species from the order Carnivora for which data could be obtained are presented in Table 7.1.



Table 7.1 Correlations (above the diagonal) and covariances (below the diagonal) between five life-history variables for carnivores in the southern African subregion for observed data. * denotes significance at the 99% confidence level. Figures in brackets represent sample sizes. ADWT - Adult body weight, NEOWT - Neonate weight, LITSZ - Litter size, AGEM - Age at maturity, GESP - Gestation period.

	ADWT	NEOWT	LITSZ	AGEM	GESP
ADWT		0,86* (18)	0,03 (32)	0,81* (18)	0,74* (25)
NEOWT	14 (18)		-0,15 (18)	0,85* (16)	0,76* (17)
LITSZ	1 (32)	-0,1 (18)		-0,16 (18)	-0,01 (25)
AGEM	10019 (18)	154 (16)	-102 (18)		0,92* (17)
GESP	460 (25)	8 (17)	-0,1 (25)	7588 (17)	

Positive correlations are evident between all variables except for those variables correlated with litter size. The results of the correlations and covariances between four life-history variables (neonate weight, litter size, age at maturity, gestation period) following the removal of the effects of adult body weight are presented in Table 7.2. The removal of body weight effects does not affect the correlations between variables except for litter size and age at maturity and litter size and gestation period, where the correlations were enhanced and attained significance at the 99% level (Table 7.2). Even though the positive correlation coefficient between age at maturity and neonate weight was reduced following the removal of the effects of adult body weight, it remained significant at the 95% level. Similarly, the positive correlation coefficient between age at maturity and gestation period was reduced but remained significant at the 99% level. The relationship between litter size and each of these variables showed a negative relationship both with and without the effects of adult body weight which could be indicative of a trade-off. Gestation period however, was not significantly correlated with neonate weight following the removal of body weight effects but did remain significantly correlated with age at maturity at the 99% level of significance.

The results of the correlations and covariances between the same five life-history variables following the removal of the effects of phylogeny at the family level is presented in Table 7.3. It is noteworthy that the relationships between the variables that were significantly correlated for the observed data (Table 7.1) were the same ones that remained significant at the 99% level once phylogenetic effects were removed (adult body weight/neonate weight; adult body weight/age at maturity; neonate weight/age at maturity; adult body weight/gestation period; neonate weight/gestation period; age at maturity/gestation period). Of interest is the enhanced correlation coefficient between gestation period and litter size as compared with the observed data (Table 7.1) even though the relationship did not attain significance as it did following the removal of body weight effects (Table 7.2).

The results of the correlations and covariances between four life-history variables (neonate weight, litter size, age at maturity, gestation period) following the removal of the effects of both adult body weight and phylogeny at the family level, are presented in Table 7.4. Although the relationship between most variables changed as compared with the observed data (Table 7.1), the correlation coefficient between gestation period and age at maturity remained



Table 7.2 Correlations (above the diagonal) and covariances (below the diagonal) between four life-history variables for carnivores in the southern African subregion for which the affects of adult body weight have been removed. ** denotes significance at the 99% confidence level. * denotes significance at the 95% confidence level. Figures in brackets represent sample sizes. NEOWT - Neonate weight, LITSZ - Litter size, AGEM - Age at maturity, GESP - Gestation period.

	NEOWT	LITSZ	AGEM	GESP
NEOWT		-0,21 (18)	0,36* (16)	0,18 (17)
LITSZ	-0,1 (18)		-0,46** (18)	-0,32** (25)
AGEM	163 (16)	-140 (18)		0,71** (17)
GESP	1 (17)	-5 (25)	1273 (17)	



Table 7.3 Correlations (above the diagonal) and covariances (below the diagonal) between five life-history variables for carnivores in the southern African subregion for which the effect of phylogeny at the family level has been removed. * denotes significance at the 99% confidence level. Figures in brackets represent sample sizes. ADWT - Adult body weight, NEOWT - Neonate weight, LITSZ - Litter size, AGEM - Age at maturity, GESP - Gestation period.

	ADWT	NEOWT	LITSZ	AGEM	GESP
ADWT		0,83* (18)	0,15 (32)	0,72* (18)	0,74* (25)
NEOWT	9 (18)		0,04 (18)	0,83* (16)	0,71* (17)
LITSZ	3 (32)	0,02 (18)		0,07 (18)	0,25 (25)
AGEM	4769 (18)	72 (16)	18 (18)		0,83* (17)
GESP	225 (25)	3 (17)	3 (25)	2178 (17)	



Table 7.4 Correlations (above the diagonal) and covariances (below the diagonal) between five life-history variables for carnivores in the southern African subregion for which the affects of adult body weight as well as phylogeny at the family level have been removed. * denotes significance at the 99% level. Figures in brackets represent sample sizes. NEOWT - Neonate weight, LITSZ - Litter size, AGEM - Age at maturity, GESP - Gestation period.

	NEOWT	LITSZ	AGEM	GESP
NEOWT		-0,18 (18)	0,58* (16)	0,19 (17)
LITSZ	-0,04 (18)		-0,01 (18)	0,20 (25)
AGEM	20 (16)	-1 (18)		0,60* (17)
GESP	0,30 (17)	2 (25)	687 (17)	

significant at the 99% level as did the correlation coefficient between age at maturity and neonate weight (Table 7.4). Again, the relationship between gestation period and litter size was enhanced but did not attain significance.

The results of comparisons between correlation coefficient matrices are presented in Table 7.5. The results illustrate that the biggest difference was observed between correlation coefficients based on observed data and correlation coefficients based on data from which the effects of body weight were removed ($T_6=0.00$, $p<0.05$).

Principal components analysis

The results of a principal component analysis using average values of five life-history variables (adult body weight, neonate weight, litter size, gestation period, age at maturity) for observed data of orders are presented in Figure 7.1. This analysis was necessary because the MDA in Chapter 3 indicated that there were significant differences between orders. PC-1 represents a positive gradient of body weight, neonate weight, gestation period and age at maturity, while PC-2 represents a positive gradient of litter size. Thus, the PCA shows the carnivores (1) and perissodactyls (5) to be outliers. However, with PC-1 being characterised by a positive gradient of adult body weight, neonate weight, gestation period and age at maturity, the representation of the perissodactyls within the component space is what would be expected of these mammals having large body sizes, large neonates, long gestation periods and late age at maturity. On the other hand, with PC-2 a positive litter size gradient, the carnivores appear to have larger litter sizes than expected for their body size.

The results of a principal component analysis showing the eigenvectors and eigenvalues using the observed data of 15 carnivore species for five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) are presented in Table 7.6. The graphic representation of these results is shown in Figure 7.2. The first principal component (PC-1) is characterised by adult body weight, neonate weight, age at maturity and gestation period whereas the second principal component (PC-2) is characterised by litter size. This does not however, explain how these variables are represented along these axes. A correlation analysis of each variable with the principal components (PC) was subsequently



Table 7.5 Summary of the change in correlations coefficients for carnivore species when adult body weight has been removed, phylogeny has been removed at family level and both have been removed.

	Percentage significant correlations	Comparison level	Percentage that remained the same	Percentage that decreased	Percentage that increased	Percentage that changed sign	<i>T</i> -value (Wilcoxon matched-pairs signed-ranked tests)
Species	60,0						
Weight	66,7	Species to weight removed	0,0	50,0	50,0	0,0	$T_6 = 0,00$ $p < 0,05$
Phylogeny	60,0	Species to phylogeny removed	10,0	20,0	70,0	0,0	$T_9 = 15,0$ $p > 0,05$
Phylogeny and weight	33,3	Species to phylogeny and weight removed	0,0	33,3	66,7	0,0	$T_6 = 5,00$ $p > 0,05$

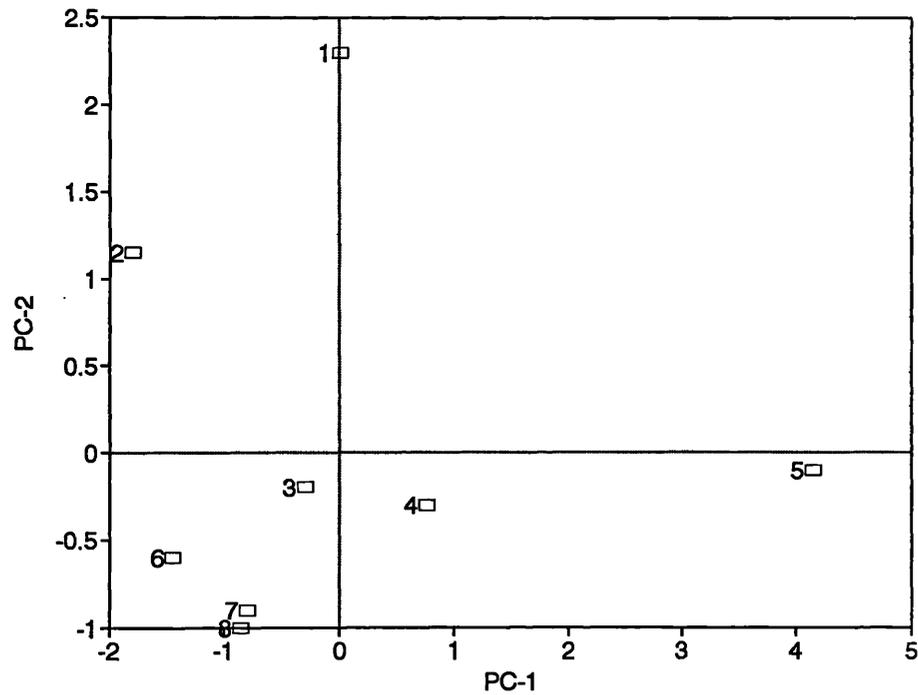


Figure 7.1 Plot of the first two components of eight orders using five variables (adult body weight, neonate weight, litter size, age-at maturity and gestation period). Average values were calculated for each order and used in the analysis. 1 - Carnivora, 2 - Rodentia, 3 - Hyracoidea, 4 - Macroscelidae, 5 - Artiodactyla, 6 - Perrissodactyla, 7 - Chiroptera, 8 - Primates.



Table 7.6 Eigenvectors and eigenvalues for PCA using five life-history variables of 15 carnivores. Principle contributions to each component are indicated in brackets. Each component's contribution to total variation as well as cumulative contributions are given. Not correlation coefficients between variables and principle components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult weight	(0,48)	0,09	(-0,62)	(0,61)	-0,04
Neonate weight	(0,80)	-0,01	-0,37	(-0,77)	-0,15
Litter size	-0,11	(0,99)	-0,03	-0,08	0,08
Age at maturity	(0,51)	0,01	0,36	0,01	(0,78)
Gestation period	(0,49)	0,14	(0,59)	0,15	(-0,60)
Eigenvalues	70,00	19,58	6,38	2,77	1,28
Contribution to total variation (%)	70,00	19,58	6,38	2,77	1,28
Cumulative contribution (%)	70,00	89,58	95,95	98,72	100,00
Correlation coefficients					
Adult weight	0,90	0,09	-0,35	0,23	-0,04
Neonate weight	0,93	-0,01	-0,21	-0,29	-0,15
Litter size	-0,21	0,98	-0,02	-0,03	0,08
Age at maturity	0,96	0,01	0,20	0,01	0,78
Gestation period	0,92	0,14	0,34	0,06	-0,60

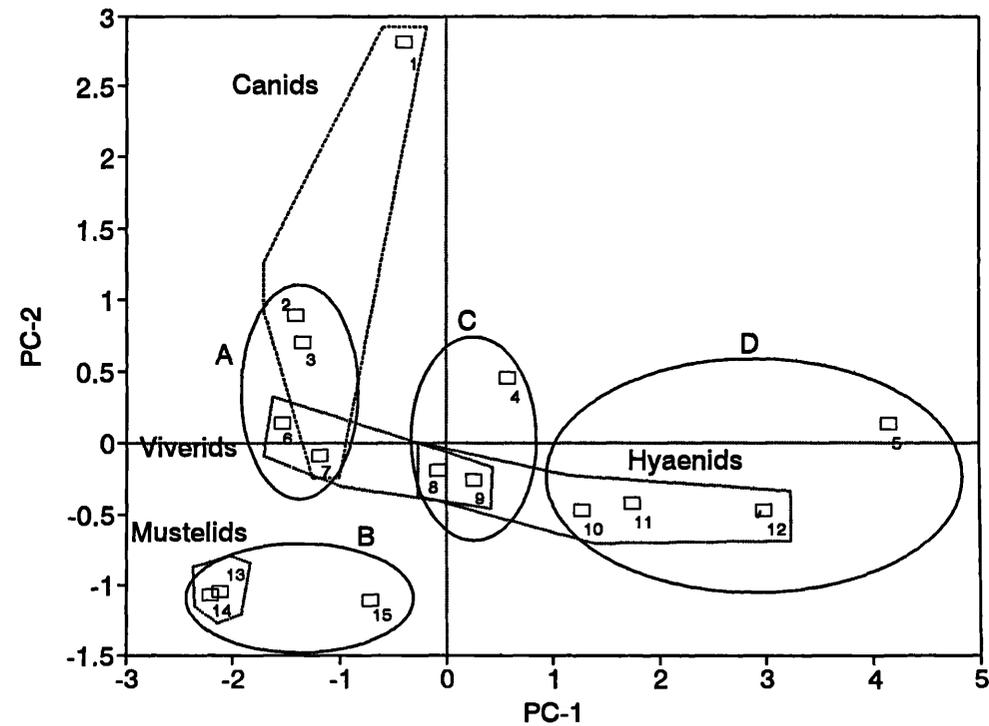


Figure 7.2 Plot of the first two principal components of 15 carnivore species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) of observed data. The elipses illustrate the major groupings within the component space, while the polygons illustrate conventional phylogenetic groupings (families). 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.



done which gave an indication of the relationships of these variables with the relative components (Joliffe 1986). Thus PC-1 represents a positive gradient of adult body weight, neonate weight, age at maturity and gestation period whereas PC-2 represents a positive gradient of litter size (Fig. 7.2). The PCA indicates that 89.58% (Table 7.6) of the variance within this order can be accounted for by the first two components, with PC-1 representing a gradient ranging from species with small body sizes, short gestation periods and early ages at maturity to large body sizes, long gestation periods and late ages at maturity. PC-2 represents a gradient ranging from species with small litters to large litters.

A scatterplot of the values for each species along PC-1 and PC-2 in Figure 7.2 using observed data indicated specific groupings (see polygons and ellipses). MDA revealed that the centroids of groups A, B, C and D (see Figure 7.2) were significantly different from each other within the component space ($F_{15,16}=4,35; p<0,0024$). These groups (ellipses) did not conform to classical phylogenetic groupings, but family groupings (polygons) did show significant differences (MDA: $F_{20,20}=3,20; p<0,0054$). On closer inspection, it is evident that considerable variation between the five life-history variables for the species within the different family groupings can be distinguished (see polygons of canids - 1,2,3,7; viverids - 6,9; mustelids - 13,14; hyaenids - 8,10,12). The individual species within these groupings occupy extreme positions relative to one another. It is noteworthy that no specific grouping of the felids (4,5,11,15) can be distinguished but they do vary considerably along PC-1. The hyaenids and viverids also vary along PC-1 with the mustelids occupying a concentrated position within the component space (13, 14). The canids on the other hand, vary considerably along PC-2 which is characterised by litter size, thus litter size may be particularly influential in this family. Interestingly, the classical phylogenetic groupings (polygons) are not supported within the obvious groupings (ellipses) evident within the life-history component space.

The eigenvectors and eigenvalues for PCA following the removal of adult body weight for four life-history variables (neonate weight, litter size, age at maturity and gestation period) are presented in Table 7.7. In comparing Tables 7.6 and 7.7, it is evident that an interchange of litter size and neonate weight occurred between PC-1 and PC-2. The graphic representation of the PCA results following the removal of the effects of adult body weight is shown in



Table 7.7 Eigenvectors and eigenvalues for PCA using four life-history variables of 15 carnivores for which the effects of body weight have been removed. Principle contributions to each component are indicated in brackets. Each component's contribution to total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principle components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Neonate weight	0,34	(0,92)	-0,02	0,18
Litter size	(-0,47)	,21	(0,85)	-0,10
Age at maturity	(0,60)	-0,06	0,26	(-0,75)
Gestation period	(0,55)	-0,32	0,45	(0,62)
Eigenvalues	55,86	21,53	16,23	6,37
Contribution to total variation (%)	55,86	21,53	16,23	6,37
Cumulative contribution (%)	55,86	77,40	93,63	100,00
Correlation coefficients				
Neonate weight	0,51	0,86	-0,02	0,09
Litter size	-0,70	0,19	0,69	-0,05
Age at maturity	0,90	-0,06	0,21	-0,38
Gestation period	0,82	-0,29	0,45	0,31

Figure 7.3. PC-1 represents a negative gradient of litter size but a positive gradient of age at maturity and gestation period. PC-2 represents a positive gradient of neonate weight. The amount of variation explained by the first two PCs has dropped by 12% following the removal of body size effects and therefore collectively account for 77.40% of the total variation. Recall from Figure 7.2 that litter size was represented on PC-2. The representation of life-history variables for each PC subsequently changed in Figure 7.3 with litter size now on PC-1. With body weight effects removed, the residual variation along PC-1 is explained in terms of the variation in litter size (negative gradient), age at maturity and gestation period (positive gradient) whereas the residual variation along PC-2 is explained in terms of the variation in neonate weight (positive gradient). Notably, following the removal of adult body weight effects, *Panthera leo* (5) and *Acinonyx jubatus* (4) have a relatively short gestation period and age at maturity as compared with *Panthera pardus* (11) and *Felis nigripes* (15). Each of the former two species have a larger litter size than the latter two species.

A pronounced variation in litter size is separating *Lycaon pictus* (1) and *Canis adustus* (2) from the other carnivores within the component space. Thus the variation in life-history characteristics is spreading the carnivores within the component space suggesting that the variation within certain variables is affecting the representation of certain carnivores more than others. For instance, the added effect of litter size to gestation period and age at maturity along PC-1 may be more influential in describing underlying life-history patterns in *L. pictus* (1) than in *P. pardus* (11) where gestation period or age at maturity may be more influential.

The family groupings remained significantly different from each other following removal of the effects of adult body weight (MDA: $F_{16,22}=3,32$; $p < 0,0050$ (polygons in Fig.7.3)), but were still not equivalent to the major groupings (MDA: $F_{8,10}=4,96$; $p < 0,0107$ (elipses in Fig.7.3)). This suggests that the differences between the major groupings and family groupings in Figure 7.2 were not a consequence of adult body weight.

In Figure 7.3, a similar variation in life-history features as in Figure 7.2 is evident within family groupings with the canids showing more variation along PC-1 (the litter size/age at maturity/gestation period component) than PC-2. The mustelids (13, 14) vary along PC-1, but to a lesser degree along PC-2. The hyaenids and viverids show distinct variation of life-

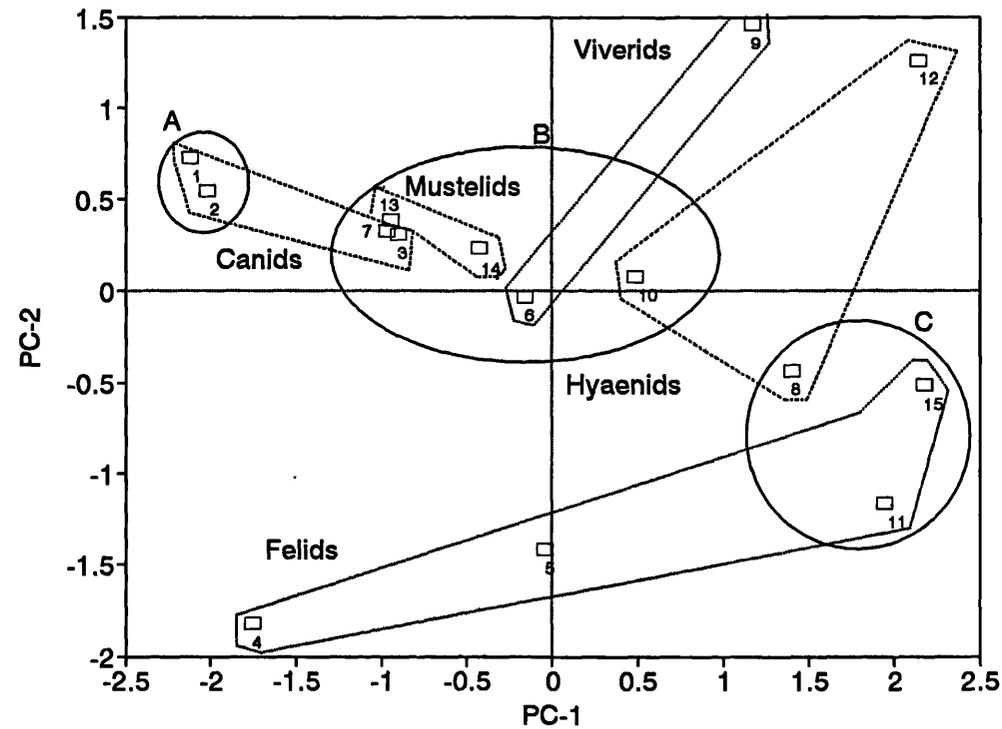


Figure 7.3 Plot of the first two principal components of 15 carnivore species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for which the effects of body weight have been removed. The ellipses illustrate the major groupings within the component space, while the polygons illustrate conventional phylogenetic groupings (families). 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.

history features along both PCs with the felids varying right across PC-1 (4,5,11,15). As PC-1 represents a negative gradient of litter size and a positive gradient of age at maturity and gestation period, this component reflects considerable variation in these felid life-history characteristics. Felids having large litter sizes with relatively short gestation periods and early ages at maturity are represented at one end of the gradient (4) contrasting with felids having relatively small litters with long gestation periods and late ages at maturity at the other end of the gradient (11,15). In addition, certain felids can be described as having intermediate litter sizes with intermediate gestation periods and age at maturity (5). Thus, considerable variation in these traits is displayed along PC-1 in Figure 7.3 within the felidae. The other families within the carnivora also show considerable variation in life-history traits along both components but to a lesser degree than the felidae.

The eigenvectors and eigenvalues for a PCA with the effects of phylogeny removed at the family level using five life-history variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) are presented in Table 7.8. The graphic representation of these results along the principal components is shown in Figure 7.4. Non-significant differences evident between family groupings (MDA: $F_{20,20}=0,44$; $p < 0,9620$) illustrate that phylogenetic constraints were effectively removed at the family level. PC-1 represents a positive gradient of adult body weight, neonate weight, age at maturity and gestation period whereas PC-2 represents a positive gradient of litter size. The composition of the major groupings in Figures 7.2 and 7.3 have changed slightly in Figure 7.4 in as far as the relative positions of the species comprising these groupings are concerned. The centroids of groups A, B and C are significantly different (MDA: $F_{10,8}=9,68$; $p < 0,0018$) in the component space illustrated in Figure 7.4. In addition, the variation of life-history characteristics for species in the polygons within the component space is more pronounced following the removal of phylogeny (see polygons). It is noteworthy that the hyaenid species (8,10,12) are represented at opposite extremes relative to one another along PC-1 and the canid species (1,2,3,7) at opposite extremes relative to one another along PC-2, more so than in either Figures 7.2 and 7.3. Just as important is the scatter in the positions of the felid species (4,5,11,15) relative to one another along PC-1. No distinct grouping of felid species can be distinguished but note their extreme positions relative to one another within the component space.



Table 7.8 Eigenvectors and eigenvalues for PCA using five life-history variables of 15 carnivores for which the effect of phylogeny has been removed at the family level. Principle contributions to each component are indicated in brackets. Each component's contribution to total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principle components.

	Eigenvectors				
	PC-1	PC-2	PC-3	PC-4	PC-5
Adult weight	(0,49)	-0,04	(-0,69)	0,29	0,44
Neonate weight	(0,50)	-0,18	-0,24	(-0,56)	(-0,59)
Litter size	0,11	(0,98)	-0,07	-0,09	-0,09
Age at maturity	(0,50)	-0,01	(0,55)	-0,38	0,56
Gestation period	(0,50)	-0,01	0,40	(0,67)	-0,38
Eigenvalues	67,86	17,72	6,07	4,68	1,66
Contribution to total variation (%)	67,86	17,72	6,07	4,68	1,66
Cumulative contribution (%)	67,86	87,58	93,65	98,34	100,00
Correlation coefficients					
Adult weight	0,90	-0,04	-0,38	0,14	0,13
Neonate weight	0,92	-0,18	-0,13	-0,27	-0,17
Litter size	0,21	0,98	-0,04	-0,04	0,03
Age at maturity	0,92	-0,01	0,30	-0,18	0,16
Gestation period	0,91	-0,01	0,22	0,33	-0,11

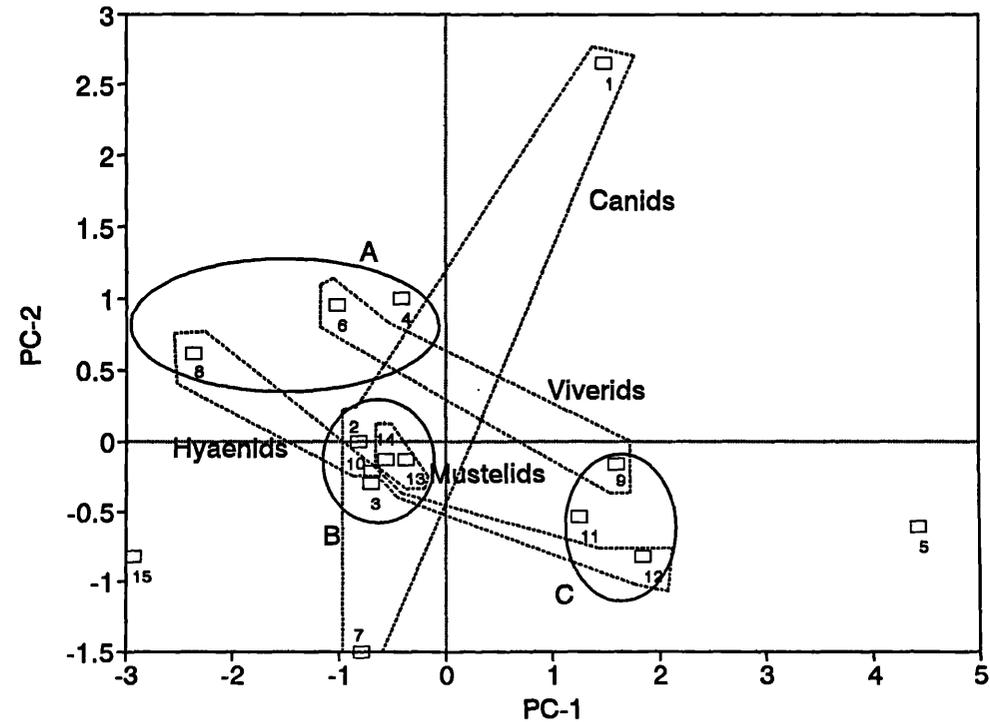


Figure 7.4 Plot of the first two principal components of 15 carnivore species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the family level have been removed. The ellipses illustrate the major groupings within the component space, while the polygons illustrate conventional phylogenetic groupings (families). 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.

The eigenvectors and eigenvalues for PCA with the effects of both phylogeny at the family level and adult body weight removed using four life-history variables (neonate weight, litter size, age at maturity, gestation period) are presented in Table 7.9. PC-1 represents a positive gradient of neonate weight, age at maturity and gestation period and PC-2 a positive gradient of litter size. Noteworthy is the increase in the contribution to the total variation of PC-2 by almost 30% (Table 7.9) as compared with 17-21% in Tables 7.6, 7.7 and 7.8. Thus the added effect that litter size may have is evident with almost 30% of the total residual variation contributed by PC-2, the component characterised by litter size. A concomitant decrease in the contribution to the total variation of PC-1 is evident with the removal of both phylogeny and adult body weight (49.80%) when compared with the observed results (70%), the results of the removal of adult body weight (55.86%) and the removal of phylogeny at the family level (67.86%). Consequently, the amount of residual variation that potentially can be explained by factors other than body size and phylogeny, is reduced.

The graphic representation of the results of the PCAs with the effects of both adult body weight and phylogeny removed at the family level is shown in Figure 7.5. As expected, no significant differences were evident between family groupings (MDA: $F_{16,20}=0,36$; $p<0,9805$). Although two major groupings are evident within the component space which differ significantly from each other (A, B; MDA: $F_{4,4}=17,74$; $p<0,0082$), the relative positions of the species relative to one another within each of these groupings has changed. The canids vary across PC-2 which is characterized by a positive gradient of litter size thus the variation in litter size of canid species may underly patterns of life-history variation for these species whereas the combined effects of age at maturity, gestation period and neonate weight may be more influential in describing underlying sources of variation in the hyaenids and viverids. The mustelids (13, 14) vary to a lesser degree along PC-1 but occupy a concentrated position within the component space. The felids (4, 5, 11, 15) vary considerably along PC-1 and to a lesser degree along PC-2 with changes in their positions relative to one another as compared with Figure 7.2 for the observed data.



Table 7.9 Eigenvectors and eigenvalues for PCA using five life-history variables of 15 carnivores for which the effects of body weight as well as the effect of phylogeny at the family level have been removed. Principle contributions to each component are indicated in brackets. Each component's contribution to total variation as well as cumulative contributions are given. Note correlation coefficients between variables and principle components.

	Eigenvectors			
	PC-1	PC-2	PC-3	PC-4
Neonate weight	(0,56)	0,06	(-0,81)	-0,12
Litter size	-0,09	(0,95)	-0,04	0,28
Age at maturity	(0,57)	0,25	0,50	(-0,60)
Gestation period	(0,59)	-0,15	0,29	(0,74)
Eigenvalues	49,80	28,08	16,37	5,75
Contribution to total variation (%)	49,80	28,08	16,37	5,75
Cumulative contribution (%)	49,80	77,88	94,25	100,00
Correlation coefficients				
Neonate weight	0,73	-0,44	-0,45	-0,22
Litter size	0,04	0,92	-0,38	-0,08
Age at maturity	0,93	0,08	-0,05	0,36
Gestation period	0,77	0,26	0,53	-0,22

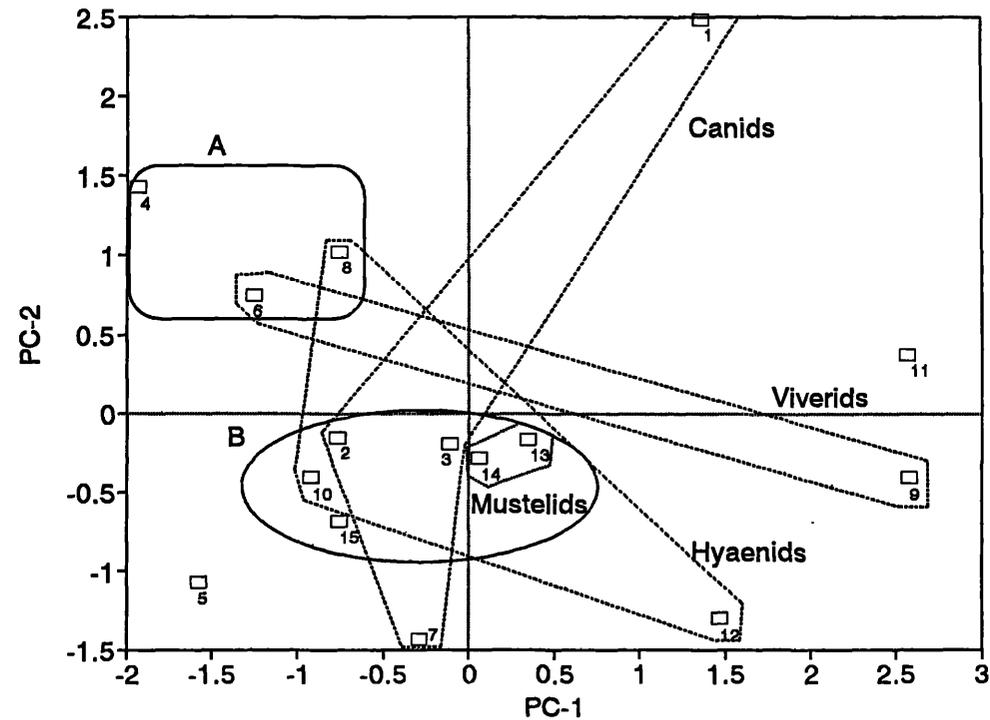


Figure 7.5 Plot of the first two principal components of 15 carnivore species in the southern African sub-region using five variables (adult body weight, neonate weight, litter size, age at maturity and gestation period) for which the effects of phylogeny at the family level as well as the effects of body weight have been removed. The ellipses illustrate the major groupings within the component space, while the polygons illustrate conventional phylogenetic groupings (families). 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.

The cluster analysis

The dendrogram resulting from cluster analyses using observed data illustrates seven clusters at a linkage distance of 50 (Figure 7.6) compared with six once the effects of body weight have been removed (Figure 7.7). Following the removal of phylogenetic constraints at the family level (see Figure 7.8), six clusters were observed at a linkage distance of 50, while four clusters remained once both the effects of body weight and phylogeny at the family level were removed (Figure 7.9). Evident from the reduction in total linkage distance is that with the removal of allometric constraints, phylogenetic constraints and the combined effects of these constraints respectively, species are being successively grouped closer together. This suggests that allometric and phylogenetic constraints underly life-history patterns observed within carnivores and that the variation between species within this order diminishes once these effects are removed. However, residual variation does remain which may be described by variation in litter size, gestation period and age at maturity.

Discussion

These analyses confirm earlier reports that significant correlations exist between life-history variables for observed data of mammals, with the effects of adult body weight removed (Harvey & Zammuto 1985; Read & Harvey 1989; van Jaarsveld 1993) and with the effects of phylogeny removed at the family level (Stearns 1983). Furthermore, significant correlations exist between these variables at the order level (see chapter 6). However, although allometry and phylogeny may underly life-history variance of carnivores, these results suggest that life-history variance is not merely a consequence of either allometric or phylogenetic relationships but may also be a consequence of variation in relationships of litter size, neonate weight, age at maturity and gestation period (see PC-1, Table 7.7; PC-1 & PC-2, Table 7.8; PC-1 & PC-2, Table 7.9).

Although the positive covariations between age at maturity and gestation period suggest an *r-K* continuum from those carnivores with short gestation periods and early ages at maturity to those with long gestation periods and late ages at maturity, the negative covariation between litter size and each of these variables suggests that small litters are associated with long

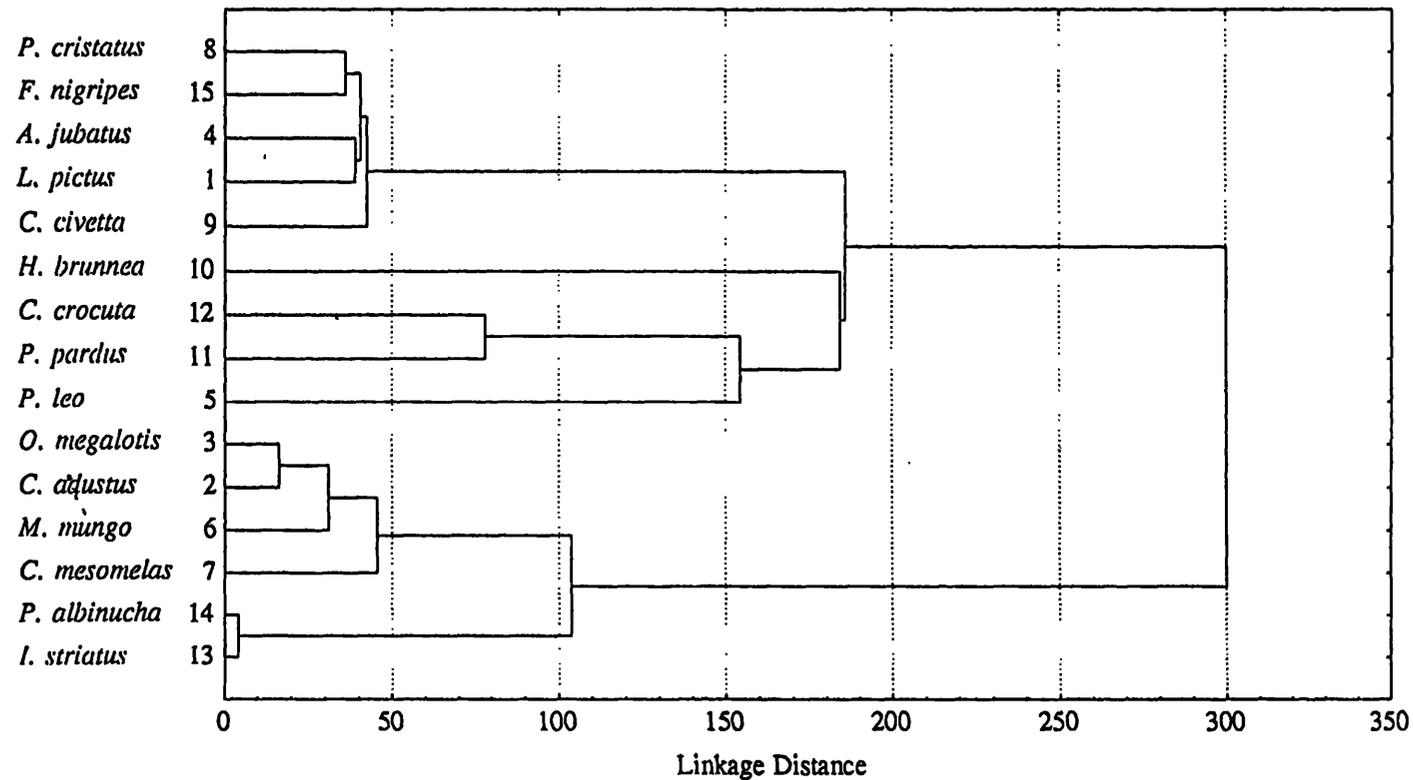


Figure 7.6 Dendrogram (euclidean distances) illustrating clusters selected at a linkage distance of 50 using five life-history variables (adult body weight, neonate weight, litter size, age at maturity, gestation period) of 15 carnivore species in the southern African sub-region. 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.

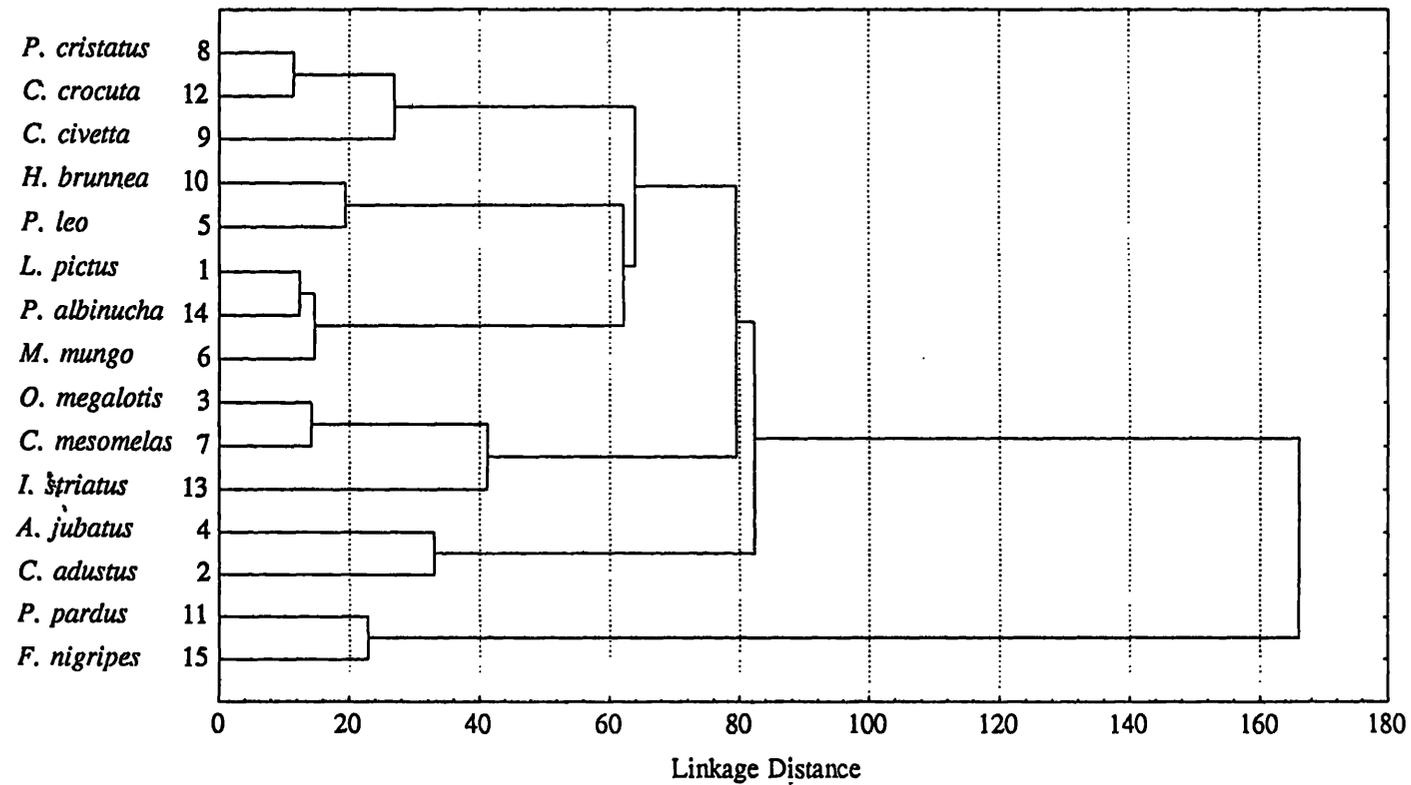


Figure 7.7 Dendrogram (euclidean distances) illustrating clusters selected at a linkage distance of 50 using four life-history variables for which the effect of body weight has been removed (neonate weight, litter size, age at maturity, gestation period) of 15 carnivore species in the southern African sub-region. 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.

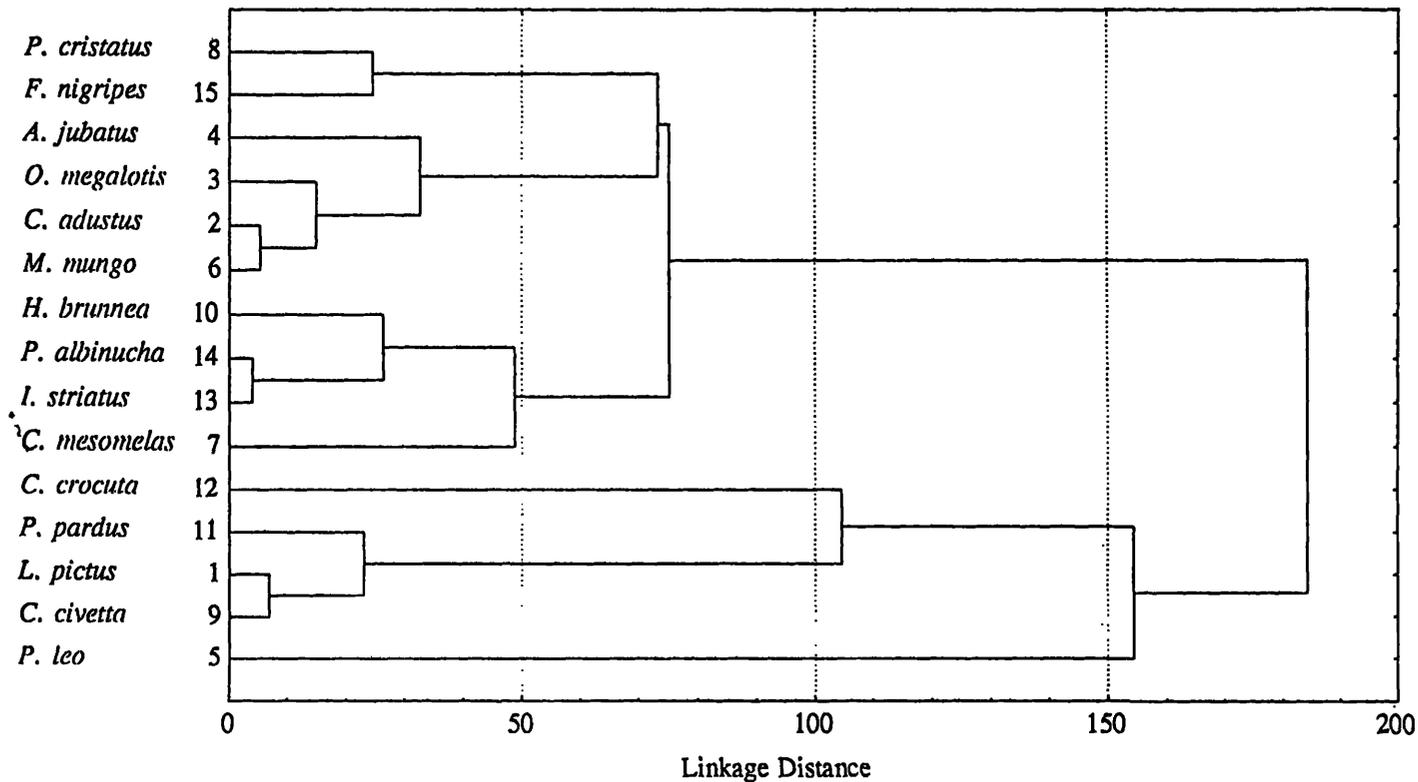


Figure 7.8 Dendrogram (euclidean distances) illustrating clusters selected at a linkage distance of 50 using five life-history variables for which the effect of phylogeny at the family level has been removed (adult body weight, neonate weight, litter size, age at maturity, gestation period) of 15 carnivore species in the southern African sub-region. 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.

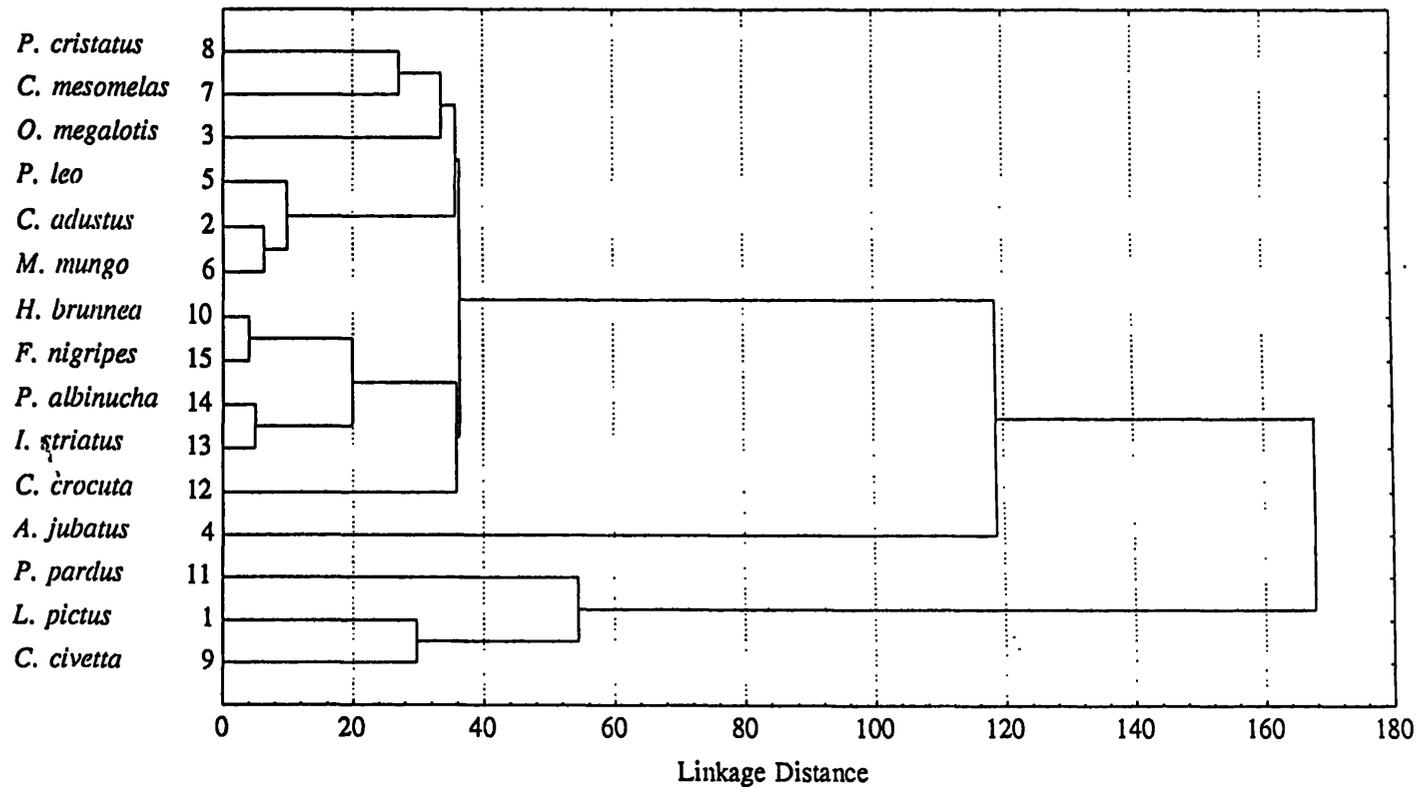


Figure 7.9 Dendrogram (euclidean distances) illustrating clusters selected at a linkage distance of 50 using four life-history variables for which the effect of body weight as well as the effect of phylogeny at the family level have been removed (neonate weight, litter size, age at maturity, gestation period) of 15 carnivore species in the southern African sub-region. 1 - *L. pictus*, 2 - *C. adustus*, 3 - *O. megalotis*, 4 - *A. jubatus*, 5 - *P. leo*, 6 - *M. mungo*, 7 - *C. mesomelas*, 8 - *P. cristatus*, 9 - *C. civetta*, 10 - *H. brunnea*, 11 - *P. pardus*, 12 - *C. crocuta*, 13 - *I. striatus*, 14 - *P. albinucha*, 15 - *F. nigripes*.



gestation periods and late ages at maturity and large litters with short gestation periods and early ages at maturity. However, following the removal of both allometric and phylogenetic effects, all variables covaried positively so that small litters are associated with short gestation periods and early age at maturity and large litters with long gestation periods and late ages at maturity, phenomena contrary to the expected r - K continuum.

If life-history traits of carnivores are considered separately rather than collectively, the variation in developmental periods and litter sizes is elucidated. Members of the genus *Lycaon* have very large litters following a relatively short gestation period, short lactation period and subsequent early ages at maturity (suggesting a short period as independent juvenile), thus litter size in addition to these developmental periods may be especially meaningful in describing underlying life-history patterns for this taxon. Despite the short gestation periods, short periods as independent juveniles and early ages at maturity of members of the genera *Crocuta* and *Proteles*, they have extended lactation periods. Extended lactation periods have been associated with accelerated juvenile growth and reaching sexual maturity prematurely which is considered to be particularly meaningful in understanding paradoxical life-histories of these two genera (van Jaarsveld 1993; van Jaarsveld *et al.* 1995). In addition, members of the genus *Hyaena* have relatively long gestation periods, short lactation periods and late ages at maturity (with long periods as independent juveniles). Members of the genus *Poecilogale* have small litters following an extremely short gestation period (32 days) whereas members of the genus *Aonyx* have small litters following a relatively long gestation period (60 days). Despite the small litters of the genus *Genetta*, they have a relatively long gestation period (70-77 days). Members of the genus *Canis* have relatively large litters following relatively short gestation periods (± 60 days) but with a delayed age at first parturition, up to three years for *Canis mesomelas* (Rowe-Rowe 1992). Members of the genus *Panthera* are characterised by contrasting life-history features. *Panthera leo* have larger litters than *P. pardus*, a longer gestation period (220 days compared with 100 days for *P. pardus*), earlier age at weaning but a longer period as dependent juvenile.

When considering size-related life-history patterns, certain carnivores have larger litters than expected for their body size and either shorter or longer developmental periods than expected for their size which suggests that they do not conform to expected allometric relationships.

Western (1979) found size-related carnivore life-history patterns to be similar to size-related artiodactyl and primate life-history patterns. These results are consistent with Western (1979) when considering certain developmental periods such as gestation period which he found to be significantly shorter for carnivores in comparison to other orders. In addition, Oftedal & Gittleman (1989) suggest that reproductive output in carnivores is mainly related to allometric and phylogenetic constraints and once these are accounted for, to other factors such as dietary and parental factors. Similarly, PCA and cluster analyses in the present study illustrate that variation in life-history features of carnivores within the sub-region is influenced by allometric and phylogenetic constraints. However, residual variation in developmental patterns together with litter size may contribute to describing anomalies apparent in representatives of this order. These anomalies may be the reason for the outlier position of the Carnivora relative to other orders (disregarding the Perrissodactyla) within the component space (see PCs of Figure 7.1) and could be a result of the considerable variation displayed across this order in litter sizes (1.5-8.9), ages at maturity (4.5 months-3.5 years) and gestation periods (32-110 days) in addition to adult- and neonate body weights. These traits may therefore be particularly meaningful in describing underlying life-history patterns within this taxon.

Considering the enhanced relationship between certain life-history variables of the carnivores, for instance litter size and age at maturity as well as litter size and gestation period with the removal of adult body weight, it is conceivable that body weight could have been masking the true relationship between litter size and each of these variables. The significant negative relationship between these variables with the removal of adult body weight suggests there may be a significant trade-off between these variables. One such trade-off could be increasing litter size at the expense of maternal investment in individual young. Theoretical models suggest that the significance of this trade-off (Gaillard *et al.* 1989) lies in attempting to increase the number of potential young produced by delaying reproduction (to an age where the mother is more mature) or dying while waiting to do so (Harvey & Keymer 1991). In contrast, some carnivores appear able to increase their litter sizes, yet override this general mammalian trade-off by decreasing the time to reach reproductive maturity (Van Jaarsveld 1993).

Noteworthy, is that the negative relationship between litter size and age at maturity changed to a positive one following the removal of body weight effects. The apparent trade-off

between litter size and age at maturity for the observed data may therefore have been the result of body size effects. However, the fact that age at maturity and gestation period remained highly significantly correlated even with the effects of both phylogeny and body weight removed, coupled with the enhanced relationship between litter size and gestation period, suggests that these variables may still be relevant in describing life-history patterns within this order. An in-depth discussion of carnivore biology may therefore serve to elucidate the possible influence that these variables have in shaping carnivore life-histories.

The most noticeable feature of carnivore biology is the variation in social systems (asocial to extended sociality) and a feature that can be associated with degree of sociality, is breeding biology. It is well-known that several carnivores within the subregion, *P. leo*, *Mungos mungo*, *Crocuta crocuta*, *L. pictus*, *Helogale parvula* and *Hyaena brunnea* occur in large, cohesive groups, clans or packs which afford protection for the group as a whole (Schaller 1972; Skinner & Smithers 1990). In contrast, *Ictonyx striatus*, *Genetta genetta*, *P. pardus* and *F. nigripes* are considered to be solitary. *Panthera leo* has the advantage of birth synchrony with several females breeding (Schaller 1972) whereas *L. pictus* is a seasonal breeder with generally the dominant female in the pack that breeds (Skinner & Smithers 1990). Both species display communal suckling. Alpha and beta females of *L. pictus* suckle each others pups but alpha females have priority in suckling over beta females (Mills, pers. comm.). Consequently, indiscriminant suckling of pups occurs and if the biological female is away hunting or even dies, other females in the group or pack will suckle the young (Skinner & Smithers 1990). This feature is not only limited to *L. pictus*, but is ubiquitous in canids which may suggest that it was present in a common ancestor (Packer, Lewis & Pusey 1992). This trait is also common in taxa with larger litter sizes. However, communal suckling in *L. pictus* only occurs if both alpha and beta females breed and considering the large litter sizes of this species, if only the alpha female breeds (and therefore is the only female lactating), this would be energetically very expensive for the breeding female. However, the social structure of this species opened up an alternative option, *viz.* regurgitation, a feature unique to canids which may explain why extremely large litters can be accommodated even though these mammals have relative short lactation periods. This behaviour bridges both sociality and breeding biology for this species and provides a means of increased energetic investment in both the breeding female and the pups.



Increased energetic investment in young has been considered to be accomplished in one of two ways, either prenatally (increased litter size through investment by helpers through mother) or postnatally (through increased growth rate of offspring) (Creel & Creel 1991). Positive correlations have been found between the number of helpers and the number of offspring raised in most species with communal care (coyotes, Bekoff & Wells 1982; lions, Bygott, Bertram & Hanby 1979; wild dogs, Malcolm & Marten 1982; jackals, Moehlman 1979; dwarf mongooses, Rood 1989; badgers, Kruuk 1989). In addition to communal suckling, a meat-supplemented diet in certain species such as *L. pictus*, suggests an accelerated growth spurt which could ensure that juveniles cross the vulnerable period between birth and reaching sexual maturity, prematurely. Canids are considered to have high rates of litter growth (Oftedal & Gittleman 1989), a consequence of regurgitation of food by pack members for the young. Gittleman 1985 also suggests that carnivore species with biparental or communal (alloparental) care have higher litter weights and litter growth rates than species with maternal care only. Although little growth data is available, the present analysis suggests accelerated post-natal growth in certain carnivores when considering the short gestation period yet early age at maturity scenario. Thus sexual maturity is reached relatively early despite the short relative gestation period, a phenomenon evident in a number of carnivore species, but particularly so in members of the canids (*Otocyon megalotis*, *Vulpes chama*, *C. adustus*, *C. mesomelas* and *L. pictus*). In this respect, these species do not conform to the expected *r-K* continuum in mammals which dictates that a short gestation period is usually associated with a later age at maturity (Read & Harvey 1989). Combining a relatively short gestation period with an early age at maturity shortens the vulnerable period as an independent juvenile. The suggestions that *C. crocuta* (van Jaarsveld 1993; van Jaarsveld *et al.* 1995) and *P. cristatus* (van Jaarsveld 1995) reach sexual maturity prematurely as a result of accelerated growth which is a means of counteracting juvenile mortality, may be pertinent to the canids. Accelerated growth prior to sexual maturity may also be a feature of other carnivores but additional growth data is needed before extrapolations can be made. However, the question does arise as to why accelerated growth rates may be necessary for carnivores within the subregion?

Considering that reproductive tactics may reflect two points of view, the degree of iteroparity and the degree of reproductive investment, and that the potential for a complex social structure



is high if the reproductive system tends toward iteroparity (Eisenberg 1981), then those iteroparous species that produce very large litters may approach a condition of semelparity. Taking cognisance of the subjective nature of the iteroparous/semelparous dichotomy, it appears that canids have combined both an iteroparous life-style (relatively early reproduction with a short gestation period and relatively many young) with semelparous characteristics (extensive maternal investment in the form of helpers). However, carnivores are generally perceived to be iteroparous and iteroparity is usually considered to be a response to some other life-history variable such as high juvenile mortality (Partridge & Sibly 1991). This suggests that carnivores may be especially susceptible to juvenile mortality.

It is well documented that many carnivores have high juvenile mortalities: *P. leo* (Schaller 1972; Bryden 1976), *A. jubatus* (Laurenson 1994), *L. pictus* (Maddock & Mills 1994) and *M. mungo* (Sadie 1983). Juvenile mortalities in *C. mesomelas* are recorded to be more than 50%; *O. megalotis* \pm 50%; *M. mungos* more than 50 %; *Helogale parvula* about 50%; *P. cristatus* \pm 30-50%; *L. pictus* 20-50%. *Poecilogale albinucha* and *Ictonyx striatus* are known to lose all juveniles in a litter but are capable of having a second litter during the same season (Rowe-Rowe 1992). *L. pictus* start weaning their pups from 3-4 weeks thus having a reduced lactation period which would, in effect, extend the vulnerable juvenile period and increase the chance of juvenile mortality. This also applies to *C. adustus* and *C. mesomelas*. *L. pictus* is known to be susceptible to diseases, specifically canine distemper virus (Alexander & Appel 1994) and diarrhoea (Skinner & Smithers 1990). Selection could have resulted in one of two outcomes: either increasing the lactation period or evolving co-operative behaviour. Increasing the lactation period in a species such as *L. pictus*, could prove energetically too expensive for a single lactating female, with a litter size that may already be large. This could however, be an option open to a species which does not have such large litters. For instance, *P. cristatus* appears to have adopted this strategy combining an extended lactation period with intensive biparental care which allows an accelerated growth spurt. Consequently, adult body size is reached premature to sexual maturity, thus reducing the vulnerable period during which juveniles may be susceptible to mortality. (van Jaarsveld *et al.* 1995). Extended lactation may not have been possible for *L. pictus* with large litters but another option, regurgitation, was.

In a highly specialized social rearing system, a potential benefit of communal rearing of young



(as opposed to uni-, or biparental care) is that more time and energy can be invested in offspring that would otherwise be impossible without helpers (Creel & Creel 1991) with direct investment in young through care by feeding them (jackals, Moehlman 1979; wild dogs, Malcolm & Marten 1982), lactation (dwarf mongooses, Rood 1983; lions, Schaller 1972; wild dogs, Mills, pers. comm) or feeding the mother (wild dogs, Malcolm & Marten 1982; silverbacked jackals, Moehlman 1989). *Lycaon pictus* females for instance, only have to suckle their pups for the first few weeks after parturition because other adults in the pack aid in feeding them by regurgitation of food. Pup survival has been found to be positively correlated with the number of females in a pack (Maddock & Mills 1994). The close-knit nature of wild dog packs is evident in that adults will share food with sick members who did not participate in the hunt (Kruuk 1972) as well as return straying pups other than their own, to the protection of the pack (Skinner & Smithers 1990). Another canid, *V. chama*, has the adult male provisioning the lactating female while she remains with the newborn (Rowe-Rowe 1992). Although pup-survival rate is not known, this may be to ensure that the female can invest more time and energy with the young which would ensure a better chance of juvenile survival.

Juveniles of the viverrid *M. mungos*, are also highly susceptible to mortality with less than 50% of them surviving to the age of 3 months (Sadie 1983). Pack life is of adaptive significance directed to the protection of the young. When threatened, the group aggregate around the young while moving to the nearest cover. They display highly advanced social behaviour as they are vigilant over invalids in the group, warning and grooming them and allowing them preferred access to food (Sadie 1983; Skinner & Smithers 1990).

In contrast to the more social species, the felids (with the exception of *P. leo*) are solitary. High juvenile mortality is however known to occur in most felids, especially *A. jubatus* whose young are prone to predation by lions and hyaenas (Laurenson 1994). *Acinonyx jubatus* males occur in highly cohesive, albeit somewhat small social groups of three to six (Grobler, Hall-Martin & Walker 1984) but the young are looked after by the single mother (Laurenson 1994). The extent of maternal care has been shown to mirror cub susceptibility to mortality which highlights the importance of patterns of parental care on juvenile mortality (Laurenson 1994). *Panthera pardus* is solitary except during the mating season when a male consorts with



an oestrus female or when a female has cubs. There is no seasonality in their reproductive pattern and although not much is known about juvenile mortality in this species, they appear to have evolved effective anti-predator behaviour by continually moving their cubs from one hiding place to another (Schaller 1972) which would effectively counteract juvenile mortality. As they are not social animals, there is no opportunity for communal care. A major difference however, between *P. pardus* and *A. jubatus* is litter size. The mean litter size of *P. pardus* is known to be smaller than both *A. jubatus* as well as *P. leo* with a relatively short lactation period (Skinner & Smithers 1990). However, *P. pardus* and *A. jubatus* are similar in that neither has alloparental care. Juvenile mortality of the highly social *P. leo* whose group members extend communal care to juveniles, is known to be lower than that of *A. jubatus*. No mortality data on *P. pardus* is available. Before the degree of sociality and parental care can, however, be related to juvenile survival in these species, more reliable mortality data as well as growth data is needed.

When considering social carnivores with communal rearing systems in which members are considered to be helpers and juvenile mortality is high, larger litters than average may be a response to high juvenile mortality. Thus, the more extended a rearing system is with a greater number of members considered to be helpers, the greater the number of offspring that can be accommodated as well as the greater the number of potentially surviving young. Thus, species having extended social systems with extensive maternal investment in large litters (not necessarily their own), may provide a reinforcing (positive feedback) mechanism to aid juvenile survival. Extensive energetic investment of members in breeding/lactating females as well as juveniles within social species with large litters, would ensure accelerated growth of juveniles, consequently reducing the vulnerable juvenile period. If this strategy increased the chances of juveniles surviving, then it would effectively release the constraint of having large litters. Therefore, extensive maternal investment in large litters does not pose a restrictive evolutionary constraint but rather a selective evolutionary advantage because the costs of individual maternal investment is not as high for species occurring in large social groups with communal care as it may be for species with maternal investment by single or both parents. Packer *et al.* 1992 suggest that, across species, the costs of nursing offspring other than your own decreases with increasing litter size and it follows, possibly with increasing group size. This ensures accelerated growth and consequently, reaching sexual

maturity earlier which would increase the chances of juvenile survival. Accelerated growth would therefore be a measure of counteracting juvenile mortality.

Even though life-history characteristics may be considered to be relatively conserved, the variability in carnivore life-history features suggests that these mammals have the ability to alter these features under differing circumstances. Packer *et al.* (1992) suggest that variability in litter size, for instance, in species which produce multiple offspring is one feature that reflects differing optima under different conditions. It would appear that the social structure of certain social carnivores is a specific factor that has allowed these species to invest as much as possible in offspring, through communal care. The co-operative social behaviour displayed by certain cohesive groups within the Carnivora has therefore allowed the evolution of a complex breeding biology. Those carnivores which have not evolved extended social systems however, have optimised alternative life-history strategies (eg. the extended lactation in *P. cristatus*). Thus, carnivores have adopted different strategies to overcome what may be similar constraints (such as juvenile mortality) under differing conditions. It is therefore important to consider life-histories of representatives of this order separately, rather than collectively, as species-specific differences in life-history strategies may be overlooked.

Conclusion

These analyses suggest that unexpected life-history patterns persist within the carnivores. The evolution of larger litter sizes in certain carnivores with concomitant adjustments in the gestation period and reduction in age at maturity (suggesting accelerated growth) could be a response to juvenile mortality in certain species within this taxon. The social structure of several carnivores may be a factor that could alleviate constraints of juvenile mortality on their life-histories. For those carnivores that are solitary and have high juvenile mortalities, alternative strategies have been adopted. Thus, it appears that carnivores have several options open to them which allows them to adopt different strategies to overcome similar constraints. However, mortality data as well as growth data is needed to evaluate both the assumptions and predictions of this chapter and caution should be exercised in generalizing these speculations to all carnivores as there is a real danger that species-specific differences may be overlooked.



CHAPTER 8

SYNOPSIS

Although DNA sequencing data as well as paleontological data suggest that eutherian radiation occurred near the end of the Mesozoic (about 80 million years ago), the branching orders of the major eutherian lineages remain highly controversial (see Li, Gouy, Sharp, O'Huigin & Yang 1990). Classifying mammals according to life-history traits appears to be just as controversial. This could be because attempts to categorically classify mammals according to life-history traits are generally fraught with difficulty. Living creatures generally, with mammals not the least among them, display a rather perverse tendency to defy precise classification (see Eisenberg 1981). In this analysis, the carnivores within the southern African subregion represent a good example of this "perversity".

DNA sequencing data has established that the rodents branched off before the Lagomorpha, Primates, Artiodactyla and Carnivora. However, the traditional taxonomic view based on paleontological and morphological data is that the Artiodactyla and Carnivora are regarded as having branched off before the divergence between primate and rodent divergence (Novacek 1982). McKenna (1975) and Szalay (1977) have placed the Rodentia as an outgroup to the Primates, Artiodactyla and Carnivora. Carnivores are perceived to be closer to the ungulates than other mammals are to them (Li *et al.* 1990). This analysis strongly supports DNA sequencing data of Li *et al.* (1990) as far as the grouping of the Primates, Artiodactyla and Carnivores are concerned. However, the life-history data of this analysis places the rodents in between the artiodactyls and carnivores. This is a persistent grouping evident even after the effects of adult body size and phylogeny are accounted for and is suggested to be a function of litter size seeing that the rat remains grouped with the wild dog (both litter sizes ± 9.0).

The problem associated with attempting to classify mammals according to life-history traits is one of generalization. Assuming a random distribution, only the most generalized of mammals will conform to these life-history patterns and only if classified in terms of averages, modes or medians (which are abstractions) rather than individual data points



representing the complete spectrum of species life-history characteristics (Eisenberg 1981). As statistical abstractions, averages, modes or medians do not completely represent the reality of individual dimensions. However, they may be of heuristic value in identifying trends. The major problem, therefore, lies in attempting to reconcile theory with reality.

This analysis gives an insight into the classification of mammalian species within the southern African subregion according to life-history traits which do not necessarily reflect conventional trends. The effects that certain variables such as litter size and developmental phases may have in explaining residual variation throughout this analysis (following the removal of body size effects), exemplifies the importance of possibly maximising fecundity within this subregion. For instance, litter size at birth has been found to profoundly influence developmental time (Eisenberg 1981) and within this subregion, there may be a number of reasons for this.

Given the diverse habitat types within the subregion from savanna woodland and grassland, fynbos, desert scrub and sand to forest (see Skinner & Smithers 1990) the evolution of mammalian life-history traits could be intimately linked with adaptations to unpredictable environments. This would influence major adaptive trends leading to specific specializations for certain mammals, which may differ depending on the species requirements. If the environment is difficult to predict from one year to the next, then selection could favour an increase in investment in the young. If offspring survival is unpredictable, this could lead to selection for increased litter sizes. Together, this would entail an increase in the percentage of reproductive investment as well as parental time spent on the young to ensure survival, maintenance and learning. This may be more easily achieved in species with high social complexity compared with asocial species. However, much would depend on how each species is able to adapt to specific conditions. Thus covariation among life-history traits within the subregion may be considered to be adaptive with species-specific features reflecting different circumstances. The primary selective force could strive to optimize fecundity or other features which would positively influence their ability to cope with unpredictable environments. Consequently, this may involve co-adaptive adjustments of other life-history features such as litter size and developmental phases.

The influence of size at higher taxonomic levels is evidenced in the decrease in the amount of variation explained by the first component once size effects are removed. However, as one progresses down through the taxonomic hierarchy, size becomes less important. Thus this analysis could be interpreted as suggesting that selection may first of all have operated on adult size early on in evolutionary time but was subsequently followed by co-adaptive adjustments in other traits (see Stearns 1983). This may be especially pertinent to the artiodactyls and carnivores.

The African bovids are adapted to a continuum of varying habitat types with the larger grazing herbivores adapted to open savanna generally existing in large herds that can repel predators through communal defense mechanisms (Eisenberg 1981). They are however, rather uniform in their body plan, physiology and feeding adaptations and most are characterized by a litter size of one. Thus similar selective forces appear to have resulted in similar adaptive responses (conserved litter size). On the other hand, the carnivores, also inhabiting the savannas had to become more specialized in their social behaviour, evolving various hunting tactics to secure prey from these larger herbivore groups. Selection favoured the smaller carnivores for foraging on the smaller denizens of the grassland (Eisenberg 1981). These diversified into a number of specialist social groups which required effective antipredator behaviour against larger carnivores. Thus sociality is a significant feature in certain carnivores. However, other carnivores are distinctly asocial, thus much variability is displayed in life-history features within this taxon. They appear to differ considerably not only in their physiology and feeding adaptations, but in all aspects pertaining to their life-histories. For instance, they display a wide range of litter sizes, ages at maturity and gestation periods. Thus within a taxon, different adaptive responses resulted in optimization of different traits. However, comparisons between different taxa such as the artiodactyls and carnivores suggest that similar selective forces may have resulted in different adaptive responses of carnivores (variation) and artiodactyls (conservatism) under differing conditions. The key to explaining differences in life-history patterns will more likely lie in the analysis of variations that considers different adaptive responses (see Eisenberg 1981).

In order to understand adaptive syndromes, demography can be used but more complete field data and life-tables on individual species derived from field studies are a pre-requisite. One



of the shortcomings this project has identified is that there is sporadic and incomplete documentation of data for all species and across all demographic variables specifically a paucity of mortality and growth data. Secondly, models should be designed to take species-specific life-history features into account as well as constraints imposed on these features rather than trying to implement universal models which tend to generalise explanations of mammalian life-histories. Studies integrating all aspects pertaining to a species life-history coupled to its interactions with its environment are imminent. Life-history traits of individual species or groups of species cannot be studied in mutually exclusive groups of covariations but should rather be considered in relation to the complete spectrum of ecological/demographic conditions that could prevail. A failure to do this may result in the individual parts adding up to far less than the whole.

Furthermore, from a phylogenetic view-point, different adaptive responses are more probable in explaining dissimilarities in life-history features within certain orders such as the carnivores. The present study reveals that a paradoxical increase of litter size in certain carnivores is associated with a shorter gestation period than expected and a concomitant extensive investment in individual young which in turn reach maturity at an early age. It is suggested that social behaviour such as regurgitation allows large litter sizes of certain carnivores to be accommodated (allowing accelerated juvenile growth) which may be a response to high juvenile mortality. Other carnivores who are not social have optimised other features such as extended lactation (also allowing accelerated juvenile growth) to counteract what may be similar constraints of juvenile mortality.

Generally, the data seem to support the notion that specific life-history characteristics/demographic traits for mammals within the subregion are influential in explaining the variation in life-histories observed within this geographic region (see Hypothesis 1, Chapter 1). However, demographic traits for mammals in the southern African subregion are dominated by an allometric component, as for mammals elsewhere, so that tactics are more severely constrained by body size rather than by any other feature. Because body size affects life-history features of mammals within the subregion severely, variation in body-size related traits will inevitably result in variation of other life-history features. In addition, the impact of size-related demographic traits in explaining life-history



variation seems to hold across taxonomic groupings (see Hypothesis 2, Chapter 1). However, species that are grouped within life-history categories do not represent established taxonomic groupings based on morphological characteristics but rather reflect species-specific life-history adaptations to specific constraints on their demographic traits (see Hypothesis 3, Chapter 1). Disregarding taxonomic groupings, mammals in the southern African subregion can generally be arranged along a "fast-slow" life-history continuum which reflects potential selection gradients (see Hypothesis 4, Chapter 1). However, caution should be exercised in attempting to group any mammals within the subregion, or elsewhere for that matter, into categories, as species-specific differences may be overlooked. This may be especially pertinent to the carnivores.

Finally, the merits of this project are two-fold. First, one practical application would be when considering the degradation or fragmentation of habitats with consequent loss of biodiversity. In this context, it becomes important to identify the most salient components of a species' life-history so that areas most suitable for optimising survival can be accommodated. Life-history features can therefore be a criterium, a qualitative measure of how suitable an area is. Such areas may then be set aside for game/nature reserves if of conservation value. Thus, life-histories should represent an additional dimension worthy of consideration in any game-management/planning strategy and we would be guilty of malpractice if we attempt to implement any management programme without first considering the spectrum of each species' life-history characteristics.

Secondly, life-history considerations are important for single species conservation actions, for *e.g.* in captive breeding programmes of endangered species or game management/species introductions. One could strive to reduce juvenile mortality by altering juvenile vulnerability by reducing the time to reach sexual maturity and consequently lengthening the adult reproductive period. Another strategy could be to shorten interlitter intervals, increasing the number of litters produced during the reproductive lifespan. However, the impact of such alterations on other life-history features should be taken into account when such manipulations are attempted. In this respect, manipulating life-history features may be influential on an ecological time scale for selected localised populations, but may not have any long-term evolutionary implications.



In conclusion, when considering mammals generally, larger mammals appear to be more prone to extinction. However, extinction is part and parcel of evolutionary processes and a reality of natural processes. More problematic is the rate of extinction due to unnatural causes, specifically human interference and ignorance. Thus, knowledge of as many of the life-history tactics of as many species as possible, not only of those which become endangered, would be of paramount importance in influencing the rate at which extinction occurs.



SUMMARY

The principal objective of this analysis was to determine what factor(s) may be influential in the evolution of common life-history patterns of terrestrial mammals within the southern African subregion. To do this, it was necessary to define those features that may be influential in shaping life-history patterns. Thirteen life-history variables across 293 species were considered and statistical procedures carried out on those species for which data was available. Statistical procedures included correlation and covariance analyses as well as multivariate analyses (Principle Component Analyses, Multiple Discriminant Analyses and Cluster Analyses).

A number of hypotheses were formulated which proposed that: specific life-history characteristics could be influential in describing most of the variation observed in mammalian life-histories within the same geographic region; certain variables could describe specific life-history patterns within certain taxonomic groupings; species could be delineated within life-history groupings which would reflect established taxonomic groupings and the arrangement of southern African mammals along life-history continuums would reflect potential selection gradients.

The results suggested that allometry and phylogeny underly most of the life-history patterns observed for terrestrial mammals within the southern African subregion, but that additional selective factors such as developmental periods and litter size may also conceivably influence these patterns, more so for certain mammals than others. As size appears to be the most important component in constraining mammalian life-history patterns within the subregion and phylogeny the second most important constraint, the notion is that selection operated on size early on in evolutionary time but was subsequently followed by coadaptive adjustments in other traits. These traits then became increasingly constrained within each successive lineage. The influence of these co-adaptive adjustments on life-history traits are particularly pronounced in carnivores which do not conform to expected life-history patterns. Variation in these co-adaptations may go some way to explaining the diversity of life-history strategies within this order.

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Appendix 1

Common and Latin names of mammals in the southern African subregion referred to in the thesis.

Common names	Latin names
African weasel	<i>Poecilogale albinucha</i>
Striped polecat	<i>Ictonyx striatus</i>
Vleirat	<i>Otomys irroratus</i>
White-tailed mouse	<i>Mystromys albicaudatus</i>
Little free-tailed bat	<i>Tadarida pumila</i>
Springbuck	<i>Antidorcas marsupialis</i>
Tree squirrel	<i>Paraxerus cepapi</i>
Bushbuck	<i>Tragelaphus scriptus</i>
Porcupine	<i>Hystrix africaeaustralis</i>
Blue duiker	<i>Philantomba monticola</i>
Common duiker	<i>Sylvicapra grimmia</i>
Kudu	<i>Tragelaphus strepsiceros</i>
Small spotted cat	<i>Felix nigripes</i>
Impala	<i>Aepyceros melampus</i>
Bonte/blesbok	<i>Damaliscus dorcas</i>
Hippopotomus	<i>Hippopotamus amphibius</i>
Aardwolf	<i>Proteles cristatus</i>
Civet	<i>Civetticis civetta</i>
Warthog	<i>Phacochoerus aethiopicus</i>
Spotted hyaena	<i>Crocuta crocuta</i>
Leopard	<i>Panthera pardus</i>
Brown hyaena	<i>Hyaena brunnea</i>
Lion	<i>Panthera leo</i>
Cheetah	<i>Acinonyx jubatus</i>
Bat-eared fox	<i>Otocyon megalotis</i>
Side-striped jackal	<i>Canis adustus</i>
Black-backed jackal	<i>Canis mesomelas</i>
Banded mongoose	<i>Mungos mungo</i>
Blue wildebeest	<i>Connochaetes taurinus</i>
Eland	<i>Taurotragus oryx</i>
Rock hyrax	<i>Procavia capensis</i>
Zebra	<i>Equus burchelli</i>
Wild dog	<i>Lycaon pictus</i>
Feral pig	<i>Sus scrofa</i>
Rat	<i>Rattus norvegicus</i>
African elephant	<i>Loxodonta africana</i>
Black rhinoceros	<i>Diceros bicornis</i>
Giraffe	<i>Giraffa camelopardalis</i>