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Life history and reproductive ecology of a tropical rock wallaby, *Petrogale assimilis*.

Thesis submitted by

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in March 1993

for the degree of Doctor of Philosophy

in the Zoology Department at

James Cook University of North Queensland.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Robyn M. Delaney
March 1993.

Preface

This thesis includes one paper, "Age estimation and growth rates of captive and wild pouch young of *P. assimilis*", *Australian Wildlife Research*, 1990, Vol. **17** pp. 491-9, by Robyn Delaney and Glenn De'ath, as Appendix 12. In addition, a second paper, "Age estimation in *P. assimilis*", by Robyn Delaney and Helene Marsh, has been accepted for publication by *Wildlife Research*.

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Robyn M. Delaney

March 1993.

Female #413
(Age : 12+ years)

"I come from the northern plains,
Where the girls and the grass are scanty,
Where the creeks run dry or ten feet high,
And it's either drought or plenty".

[refrain from "The Overlander" (Traditional Ballad)].

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The logistics of my project required help from many people. The management and staff (particularly Tony Gallagher) at Lyndhurst allowed access to Black Rock and their rainfall records. Numerous volunteers helped in the field, cheerfully complying with my requests for more data and longer hours. In particular, I would like to thank the overseas travellers for keeping alive my wonder with the dry tropical environment and the wildlife in it.

My uncle, Albert Bahr and my father, Jack Delaney built the bush hut at Black Rock in time for the searing heat of the first dry season and in hopeful anticipation of big wet seasons. John Hughes and Greenvale Nickel Pty Ltd., helped in the maintainence of the field program, fixing broken equipment and providing beds, phones and transport at short notice when all else failed.

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Abstract

The rock wallaby, *Petrogale assimilis*, is a small macropodid living in isolated colonies in rocky outcrops in the wet-dry tropics of northern Australia, a region where the onset, magnitude and duration of the wet season are unpredictable. Eighty individual *P. assimilis* were caught in traps between one and 42 times during more 4000 trap days over 44 monthly field trips to Black Rock (19° 05'S., 144° 07'E.) between June 1986 and June 1990, as part of a longitudinal study of this species.

Petrogale assimilis was a typical macropodid for its size, with regard to its life history and reproductive ecology. Both sexes were capable of reproducing continuously; gestation was about the same length as the oestrous cycle (approximately one month); a single young was born and, a post-partum oestrus and embryonic diapause probably occurred. Pouch young remained permanently attached to the teat until 110 - 143 days (n=11). Permanent exit from the pouch occurred at 180 - 231 days (mean=201 days, n=25), and weaning occurred between 267 - 387 days (n=5). Sexual maturity occurred at a minimum age of 17.5 months in females and 23 months in males.

The growth of pouch young of *P. assimilis* at Black Rock was compared with that of captive animals maintained in *ad libitum* conditions at Macquarie University, Sydney. No significant differences in pouch young growth were found between these two groups of young despite the potentially different nutritional conditions of their mothers. Individual pouch young of *P. assimilis* varied in their rate of growth, although the data were too limited to examine the potential causes. Exponential and Gompertz growth curves were described for the head and pes length respectively of pouch young and were used to predict the age of pouch young of *P. assimilis*.

Body measurements were of limited use for predicting the age of older rock wallabies and cannot be used accurately for sexually mature animals. *Petrogale assimilis* exhibited only limited sexual dimorphism in its external morphology and growth during adult life with males slightly larger than females in the average length of the head (4%), pes (4%), tail (7%) and ear (3%). Sexual dimorphism was most pronounced in upper limbs (and presumably in their associated musculature) (11%) and in weight (15%).

Radiographs were taken of the teeth of rock wallabies older than pouch young to measure the eruption stage and position of the teeth. Regression curves which were fitted to data from known age animals were used to estimate the age of rock wallabies older than pouch young. Available data, albeit limited, suggested that the rates of molar eruption and movement are similar in both wild and captive *P. assimilis*. Molar progression was mostly limited to movement induced by wear. This movement occurred too slowly and with too much variability to be useful in ageing animals in which the head had ceased growing or which had full molar eruption. The use of molar eruption for determining the age of macropodids was limited to animals with less than full molar eruption (estimated mean age = 7 years). As *P. assimilis* appears to have a maximum life span of approximately 12 years, molar eruption was a useful tool for ageing animals during a major proportion of their adult life.

The influence of the seasons on changes in the body condition of adult rock wallabies probably resulted from the availability of water and quality of forage.

Although below average annual rain fell in both years of my study (1987 and 1988) which could be fully examined, the pattern of rainfall was quite different during each of these years and this pattern of rainfall influenced the body condition of adult rock wallabies. In 1987 rock wallabies lost weight (mean loss = 10%) and the packed cell volume of their blood decreased as the dry season progressed. In 1988, when a higher proportion of the year's rain fell during the dry seasons and green forage was available throughout the year, rock wallabies maintained weight and the packed cell volume of their blood increased.

The seasons were also crucial to the survivorship of pouch young. Pouch young born in the late dry season were twice as likely to survive total lactational dependence than those born during the wet or early dry seasons. However, the length and harshness of the late dry season is dependent on when the unpredictable wet season arrives. This may explain some of the loss of 46% of pouch young during total lactational dependence. If the wet season does not arrive, the mother may lose her pouch young early in pouch life when her investment is low, in the expectation that the next pouch young is more likely to survive to take advantage of the wet season flush. The cause of the mortality of young pouch young is unknown, although anecdotal evidence suggests that components of the mother's diet may be crucial.

There was considerable variation between mothers in the survivorship of pouch young during both total lactational dependence and late pouch life. However, I was able to identify only one maternal correlate of pouch young survivorship: that smaller-framed females were more successful in rearing young in late pouch life than their larger conspecifics. I was unable to examine the influence of other factors (such as maternal age and position in the dominance hierarchy) which have been shown to influence the survivorship of young in other mammals.

There was a negative correlation between the mother's success at rearing a pouch young through total lactational dependence and her success in rearing pouch young through late pouch life, although data are limited. Despite the individual variation in reproductive success observed, the ultimate survivorship of pouch young born during my study was very low (15%). Almost no young born during this period survived to sexual maturity. This result and the recent improvement in offspring survivorship, particularly young at foot, with better seasons suggests that infant survivorship occurs in pulses with a higher proportion of young from most females surviving during more favourable years.

The age structure of the population provides supporting evidence for the hypothesis that infant survivorship occurs in pulses. Previous research at Black Rock during the above average rainfall years of the early 1970's suggested that there were a high proportion of pre-reproductive animals present in the population. During my study, the age structure of the population was skewed towards very young animals (pouch young) and very old animals (full molar eruption). Almost no sub-adults or young adults were present at Black Rock. While the older animals could not be accurately aged, I speculate that these animals may be part of a cohort which was born during the above average rainfall years in the late 1970's and early 1980's.

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Chapter 1

General Introduction

1.1 Life histories of mammals

Understanding the life history of a species involves knowledge of its patterns of birth, growth, maturity, reproduction and survivorship and the factors influencing these traits. Relatively few of the world's species are mammals, yet studies of this class constitute a disproportionately large number of studies of the evolution of life histories (Boyce 1988). Behavioural, physiological and anatomical adaptations (e.g. Armitage 1981, Calder 1984, Sibley and Calow 1983) have been used as the basis for comparative life history studies. However, from an ecological perspective, life history characters can be broken into two main categories: (1) the age-specific schedules of life and death, including such characteristics as gestation period, inter-birth intervals, age of weaning and age of first reproduction; and (2) and developmental characters such as size and developmental stage of young at birth, growth rates and body size.

In this review, I will firstly give a brief overview of the current theories and then examine life history strategies at the levels of species, populations and individuals. Particular emphasis will be placed on the life-histories of marsupials and other mammals in the wet-dry tropics. This is followed by an overview of the general life histories of the Family Macropodidae and the current knowledge of one genus, *Petrogale*, within this family. Finally, the aims of this study are outlined and a brief synopsis of other research at the same field site is given.

1.1.2 *An overview of current theories*

Several decades ago, studies of life history traits burgeoned to form a complex web of data, theories and ideas until Stearns (1976) found some order in the chaos and merged the literature into an argument of *r*- and *K*- selection versus bet hedging. *r*- and *K*- selected organisms can be seen as representing two extremes of a continuum ranging from organisms which mature early, have many small young, a short life and large reproductive efforts (*r*- selected organisms) to those with the opposite attributes (*K*- selected organisms). Bet-hedging is an alternative explanation for these observed trends and is based on the analysis of fluctuations in adult and juvenile mortalities (Stearns 1976). While many of these ideas have been somewhat discredited as being overly simplistic (or of having been over-simplistically interpreted) (Boyce 1988), Stearn's classic paper did serve to focus debate and channel subsequent research.

Current theories continue to follow Lack (1954, 1966, 1968) in considering variation in life histories as the consequence of natural selection. Most models of life history variation contain trade-offs which predict optimisation of life history traits. A basic premise of many of these models is that an individual has finite energy resources in its life-time which can be allocated to growth, maintenance or reproduction. Thus, an increase in the allocation of energy for reproduction reduces that available for growth or maintenance (Gadgil and Bossert 1970). Energy apportioned to reproduction includes that used in mating effort and post-natal care. Because such allocations are very difficult to measure, reproductive effort is often approximated by litter size, or weight of litter at birth or weaning (e.g. Stearns 1976, Russell 1982). Trade-offs may include variation in the age and size at first reproduction (Sadleir 1969) or in the size and number of offspring produced. The principle of energy allocation does not require that resource budgets are constant (although this is easier to model). Resources are highly variable both in time and space and fitness increases with the increasing abundance of a limiting resource such as food. However, physiologically, there must be an upper limit to fitness as measured by reproductive output.

Charnov and Schaffer (1973) developed a model which shows how the age-specific schedule of mortality can shape life histories. High juvenile mortality relative to adult mortality may push life history tactics towards iteroparity and reduced reproductive effort, whereas low juvenile relative to adult mortality favours high reproductive effort and semelparity. If the cost of reproduction is added, the model becomes an optimality model (Boyce 1988). Fitness is now balanced between rewards for current reproduction and costs to future reproduction. The idea that reproduction entails a cost to parental survival is known as the cost hypothesis (Bell 1984). For example, observations that breeding females have a higher mortality than non-breeding females in red deer, *Cervus elaphus* (Clutton-Brock, Guinness and Albon 1982) support this hypothesis. Schaffer (1974) notes that without such a cost, selection would be expected to favour the maximum reproductive effort that is physiologically possible.

However, such a cost may be difficult to detect because of confounding variables. For example, correlated components of fitness often occur particularly in territorial species (Bell 1984). Individuals or populations on high quality territories have better and more abundant resources available than those on low quality territories. These animals may grow larger, live longer and produce more surviving offspring than their less fortunate conspecifics. This hypothesis is quite difficult to test as the experimental design must limit confounding effects. It may be possible by manipulating the size of litters at birth for example, although this takes no account of pre-natal costs.

In many mammalian species, reproduction may be optimised (unlike Schaffer *op. cit.*) by reducing the size of the litter (e.g. see Happold 1983, Lee and Cockburn 1985, Dobson 1988). The trade-off in this case is between the survival of young and litter size. In reality, it is unlikely that only one such trade-off occurs but rather, several together may determine 'optimal reproductive effort'.

The problem with such theories is that they assume either that reproduction is cost-free or that reproduction has a cost and an organism has finite energy resources over a lifetime. These alternatives assume that nature is either deterministic or that stochastic patterns of environmental influence on demography can be treated in terms of their mean effects on fitness (Geisel 1976).

Current theory concerning life history tactics is remarkably complex and as yet there is no single unifying hypothesis to explain the variation and evolution of life histories. One of the fundamental differences between current theories is in the different levels at which they analyse life histories. That is, life history evolution and strategies can be examined from the perspectives of variation between species, populations or individuals. As can be seen above, the questions asked and the potential answers are influenced by this level of analysis.

1.1.2 *Phylogenetic variation*

The life history traits discussed above are simultaneously correlated with and constrained by the phylogeny of the taxa involved (Stearns 1983, Boyce 1988). For example, all females in the Class Mammalia nurture their young via milk from their mammary glands. This production of milk in mammals necessitates maternal care and reduces the potential for paternal care. Stearns (1983) used the compilation of life history data of mammals provided by Eisenberg (1981) to examine the influence of phylogeny on variation in life history tactics. At the taxonomic levels of Order and Family, there are significant patterns of covariation of life history traits. Furthermore, there are identifiable phylogenetic constraints on the evolution of life history traits and these constraints vary between lineages. Thus once a lineage is separated, life history evolution is subsequently constrained within that lineage and the nature of these constraints varies between lineages. The principal component of Stearns' analysis (explaining 68-75% of covariation) was the distinction between taxa of early maturing, small, short-lived animals with short gestation, many small altricial young and long lactation, and taxa of animals with the converse characteristics. The distinction between altricial and precocial young was the second principal component and explained a further 12-20% of the covariation.

Much of the variation in life history traits can also be removed by scaling for adult body mass (Stearns 1983, 1992; Lee and Cockburn 1985; Lee and Ward 1989). When adjustments are made for phylogeny, the effect of adult body mass accounts for a significant proportion of the variation in life history traits (Stearns 1983). Calder (1984), and Lindstedt and Swain (1988) argue that rather than treating body size as 'noise' to be removed before examining other effects, we should accept that body size imposes its own constraints on life history parameters. Lindstedt and Swain (1988) also argue that comparisons of life history parameters should be in terms of physiological rather than chronological time. Their logic is that it is more likely that gestation length is shorter and body size smaller in shorter lived mammals and hence variation should be measured with respect to the life span of each species before comparisons are made.

In Australia, unlike the rest of the world, marsupial species are a dominant portion of the mammalian fauna. Historically, marsupials have been interpreted as 'primitive' and eutherians as 'advanced'. As further research evidence has accumulated on marsupials, this view has been shown to be erroneous (see review by Lee and Cockburn 1985). Anatomical differences occur between these two groups in the development and structure of the urino-genital system (Tyndale-Biscoe 1973) and in cranial and neural traits (Johnson, Kirsch and Switzer in Lee and Cockburn 1985), but these, and differences in life history strategies, are now viewed as equally successful alternatives.

Ecologically, the most important difference between eutherians and marsupials is in the relative maternal investment in gestation and lactation (Lee and Cockburn 1985). In most eutherians, relatively long periods of time and energy are invested in gestation and less in lactation (i.e. 'gestation specialists'). In contrast, marsupials invest relatively little time and almost no energy in gestation but have relatively long, and energetically demanding periods of lactation (i.e. 'lactation specialists') (Lee and Cockburn 1985). Other life history traits can be correlated with these phylogenetic constraints.

In both groups there is a correlation between the weight of a litter at birth and maternal body weight (Russell 1982, Lee and Cockburn 1985). In eutherians, the length of gestation is positively correlated with adult body weight (Millar 1981) and birth weight (Lee and Cockburn 1985). The gestation length of marsupials is variable by comparison (Tyndale-Biscoe and Renfree 1987) and weight of young at birth is independent of gestation length (Lee and Cockburn 1985). Here, phylogeny, rather than adult body weight, influences gestation length. The eutherian emphasis on gestation rather than lactation is reflected in their higher degree of general development and precocciality at birth when compared with marsupials. Marsupials have a very low birth weight (no marsupial weighs more than one gram at birth). Although some organs are extremely well developed, young are altricial in comparison with eutherians. The lactation specialisation of marsupials is also reflected in their possession of the most complex mammary glands of any mammalian group (Griffiths, McIntosh and Leckie 1972). Growth in marsupials is also slower than that of similar sized eutherians (Lee and Cockburn 1985).

The life history tactics which have evolved within these taxonomic groups are not necessarily optimal responses to particular selective pressures (or else species diversity as we know it would be severely restricted). At best, these tactics represent the evolution of the best compromise given the constraints of phylogeny (Stearns 1976). However, while knowledge of the phylogeny of a species is important in an understanding of its life history, the variability of a species' environment and the influence of that environmental variability on its life history tactics are also crucial.

1.1.3 *Population variation*

Environmental variability contains many selective forces which can act on life history patterns eliciting anatomical, physiological and behavioural adaptations (Stearns 1976, Boyce 1988). Responses to this environmental variability can have both genetic and non-genetic components. Life history characters that are genetically determined are usually the result of the interaction of many genes (Boyce 1988). Many life history traits such as body size and litter size may exhibit considerable phenotypic plasticity within a species. For example, teat number and litter size of some carnivorous marsupials, *Antechinus* spp., is highest in inland populations and at high elevations and lowest at low altitudes and on exposed headlands (Cockburn, Lee and Martin 1983). In several species of macropodid, the sex ratio at birth varies along an environmental gradient with a higher ratio of females born in regions of higher rainfall (Johnson and Jarman 1983). Litter size and body size often vary with variation in food availability. This very plasticity may itself be an adaptation. As J.B.S. Haldane pointed out, it is not the phenotype but the pattern of reaction to the environment that is inherited (Lewontin 1985).

Arguably the most important and common type of environmental variability in the evolution of life history patterns is seasonality (Boyce 1988, Eisenberg 1988, Zeveloff and Boyce 1988). The seasons are governed by abiotic factors and may have a relatively regular annual cycle (as occurs in the humid tropics and temperate regions) or may cycle more irregularly (as occurs in arid zones and the wet-dry tropics). The selective pressures involved may be direct or indirect through the seasonality of resources. Components of a species' life history may become adapted to the fluctuations in resources such as food, water and shelter which may become seasonally limiting (Zeveloff and Boyce 1988). For example, some mammals migrate to track favourable resources while other are sedentary and use the presence or absence of rainfall as a reproductive cue (Bourliere and Hadley 1983).

The wet-dry tropics is the climatic region that is of the most interest in this thesis. It is defined as that tropical sub-region with an annual rainfall of 600-1600mm spread over four to seven months (Landsberg *et al.* cited in Ridpath 1985) and includes many of the tropical savanna regions of the world (Bourliere and Hadley 1983, Johnson and Tothill 1984). Tropical regions differ from their temperate counterparts in that variation in day length is low (approximately 1.5hr/year) (McAlpine 1976) and temperatures are high. As a result, these environmental variables do not limit growth or reproduction as they do in higher latitudes. Other abiotic factors are a more important influence in the wet-dry tropics (Ridpath 1985). In particular, there is a pronounced seasonality in soil moisture with the annual variation in moisture varying between the extremes experienced in deserts and tropical rainforests (Nix 1983). Furthermore, the availability of soil moisture adequate for plant growth is temporally unpredictable and, in Australia, the fertility of soils is low in this region (Ridpath 1985). In essence, the seasonal cycles in higher latitudes are defined by day length whereas those in the wet-dry tropics are driven by moisture (Jones 1987) and are therefore more unpredictable.

While rainfall in southern Australia may also be very seasonal, there is often little inter-annual variation and most rain falls during winter when evaporation is low (Ridpath 1985). Thus, the increase in soil moisture per unit of rainfall is often higher in temperate regions than in the tropics. In contrast, in the wet-dry tropics, there is a large inter-annual variation in rainfall and most of this falls during summer when evaporation rates are extremely high. Most of the rain falls in intense, localised storms. The combined effects of low soil moisture retention, high run-off and high evaporation rates may effectively create drought periods even within a wet season (Ridpath 1985).

The spatial and temporal variability of soil moisture is the major determinant of the growth patterns of plants in this region (Taylor and Dunlop 1985, Tothill and Mott 1985). For example, in the Darwin region there may be up to 11 weeks variation between years in the date of commencement of pasture growth (McCown in Taylor and Tulloch 1985), and 22 weeks variation in the length of the period of useful pasture growth (McAlpine 1976). Even small aberrations in the rainfall pattern may have a strong effect on the availability of plant food, its seasonality and quantity (Wolda 1978). Dry season rains may break the annual drought which is the dominant feature of the wet-dry tropics (Taylor and Tulloch 1985).

The strong climatic seasonality of the wet-dry tropics directly (or indirectly) influences life history traits such as growth, reproduction and survival in mammals (Bourliere and Hadley 1970, Happold 1983). These seasonal changes in the life history characteristics of populations vary such that maximum energetic requirements occur at times of maximum quality or quantity of resources (Bourliere and Hadley 1970). Thus growth of many rodent species may be slowed during poor nutritional conditions such as often occurs at the end of the dry season, or enhanced during better seasons (e.g. Ojasti 1983, Redhead 1979). Similarly, agile wallabies, *Macropus agilis*, grew faster and matured earlier on improved pastures in the wet-dry tropics of northern Australia than on the native pastures in the same region (Bolton, Newsome and Merchant 1982).

For many species in the wet-dry tropics, reproduction is also timed to take maximum advantage of the period of highest resource availability. However, there is considerable phenotypic plasticity. Species which have large geographic ranges may exhibit a variety of reproductive patterns and small variations in rainfall can have a large effect on reproductive activity (Redhead 1979, Happold 1983). Most mammalian populations studied in the wet-dry tropics exhibit at least some reproductive seasonality (e.g. reviews on South American rodents, Ojasti 1983; African rodents and lagomorphs, Happold 1983; and African ungulates, Sinclair 1983). Litter sizes may also vary, with larger litters born in more optimal habitat (Happold 1983).

In the wet-dry tropics of Australia, the introduced ruminants, *Bos taurus* and *Bubalis bubalis* (Williams and Newsome 1991) and some native mammals, such as *Rattus sordidus colletti* (Redhead 1979), *Parantechinus* (formerly *Antechinus*) *bilarni* and *Dasyurus hallucatus* (Begg 1981a,b) breed seasonally. There is also some evidence of seasonal breeding in the macropodids, *Petrogale concinna* (Sanson, Nelson and Fell 1985, but see also Sanson in Lee and Cockburn 1985), and *M. robustus* and *M. antilopinus* (Russell and Richardson 1971, but see also Newsome 1975), although the data are poor.

In contrast, continuously breeding species usually occur in environments where resources are either relatively constant or very unpredictable (Sadleir

1969). This reproductive pattern appears to be less common than seasonal breeding as the strong seasonality of resources has constrained most mammalian species to a synchronised pattern of reproduction. In the wet-dry tropics of Australia, at least four native mammalian species are known to breed continuously: a rodent, *Mesembriomys gouldii* (Friend 1987), a dasyurid, *Planigale maculata sinualis* (Taylor, Calaby and Redhead 1982), a phalangerid, *Trichosurus arnhemensis* (Kerle 1985), and, a macropodid, *M. agilis* (Bolton *et al.* 1982). The largest of these species, *M. agilis*, reproduces opportunistically. The seasonal peak in births which occurs in native bushland is absent from animals grazing on improved pastures or in captivity (Merchant 1976, Bolton *et al.* 1982) and females may become anoestrus during prolonged periods of environmental stress (Bolton *et al.* 1982).

Despite the timing of reproduction to maximise survival for both parents and offspring, survivorship of all age groups may vary seasonally in the wet-dry tropics. Unfortunately, it is difficult to obtain data on seasonal effects of mortality from the literature as most mortality data are presented on an annual rather than a seasonal basis. However, evidence from a population of wildebeest in Kenya links the total mortality of young in 1961 with a failure of the wet season (Gosling in Sinclair 1983) and in Africa, the total population numbers of rodents and lagomorphs may fluctuate during the year, dependent on the length and timing of the wet and dry seasons (Happold 1983). The survivorship of all age groups decreases in years when there is a poor wet season or a prolonged dry season. The late dry season is often critical as water becomes scarce and forage decreases in quality and quantity, such that, animals lose weight and mortality increases

(Redhead 1979, Bolton *et al.* 1982, Ojasti 1983). Severe flooding also increased the mortality of *R. sordidus* (Redhead 1979) and *M. agilis* (Bolton *et al.* 1982), in northern Australia.

One of the problems of studying variation between populations in life history parameters in seasonally breeding species is the inability to separate the confounding effects of environmental and life history variables. In contrast, studies of species which have a continuous pattern of reproduction may help clarify some of the effects of environmental variables on life history parameters.

1.1.4 *Individual variation*

The generalisations espoused above for populations, are by definition, derived from an averaging of individual variation. Since selection ultimately occurs at the level of the individual, an understanding of individual variation is also crucial to our understanding of the evolution of life histories. Originally such information was obtained through cross-sectional samples of a number of individuals at one or a few points in time. More recently, there has been a trend towards repeated observations of the same individuals over their entire life-time. In this way the lifetime variation between individuals in life history variables can be compared. The latter studies have the following advantages: the total reproductive success of different categories of individuals can be compared; the proportion of variation in reproductive success which is actually due to environmental variation can be reduced; and information can be gleaned on why particular phenotypic traits affect components of reproductive success (Clutton-Brock 1988a). Furthermore, detailed questions such as those comparing different patterns of reproduction, and correlations between maternal age, optimal litter size and sex of offspring, can be asked.

These studies of individual variation have wrought a wealth of information, and in the process have changed our notions of how animal populations work. The outstanding studies of medium to long-lived mammals are those of red deer (Clutton-Brock *et al.* 1982), baboons (see Altmann, Hausfater and Altmann 1988), lions (see Packer *et al.* 1988), and elephant seals (see Le Boeuf and Reiter 1988). In Australia, these studies can only be equalled by those of *M. giganteus* by P. Jarman and *M. robustus* by D. Croft and their respective co-workers.

From these and other studies of individual variation of life history parameters, some generalisations can be made (Clutton-Brock 1988b). Consistent relationships exist between early growth and reproductive success in adults. Younger adults usually have a lower reproductive success than their older conspecifics. Individual differences in offspring survival (particularly after weaning) are one of the most important components of life-time reproductive success in female mammals. Female body size is positively correlated with fecundity, milk yield, and offspring weight and survival, while larger males commonly live longer and have better access to resources and mates. Some recent research also suggests that individual variation between females is more important in explaining variation in reproductive success than previously thought (Clutton-Brock 1988b). Most of this research has concentrated on large, sexually dimorphic, polygynous species and there is a dearth of information on monogamous species. However, to date, differences between monogamous and polygynous species are smaller than originally expected (see Clutton-Brock 1988b for review).

Chance seldom accounts for the observed variations in reproductive success in either sex, although short-term environmental changes can have a major effect (Clutton-Brock 1988b). Much of the individual variation in reproductive success may be due to climatic differences between years and, at least in long lived mammals, average breeding success in a life-time varies widely between successive cohorts. Selection is likely to favour flexible strategies for development and reproduction to help animals stay opportunistic. Species which have a continuous pattern of reproduction are ideal subjects for comparing individual variation in response to environmental parameters and hence further our understanding of life histories.

1.2 Family Macropodidae

The super-family Macropodoidea contains two monophyletic families: the Potoroidae and the Macropodidae, but I will restrict my discussion to the Family Macropodidae. Taxa of this family are ubiquitous in Australia, and species are also found in New Guinea and some adjacent islands. In Australia, the Family Macropodidae currently consists of 37 extant species in nine genera (Calaby and Richardson 1988), although the status of some taxonomic groups is under review (e.g. Dawson and Flannery 1985; Sharman, Close and Maynes 1990).

Historically, ecological research involving macropods has fallen into two major areas: captive studies (e.g. Sharman, Frith and Calaby 1964, Sharman and Pilton 1964, Kirkpatrick 1965a,b, Shield 1968, Merchant 1976, Johnson 1979, Poole *et. al* 1985), and samples from animals shot in the wild (e.g. Frith and Sharman 1964, Sadleir 1965, Newsome 1965, Kirkpatrick 1965b, Kirkpatrick and McEvoy 1966). Most of this earlier work concentrated on the larger, commercial species such as the red kangaroo (*M. rufus*) and grey kangaroos (*M. giganteus* and *M. fuliginosus*) or on species from more temperate regions of Australia such as the quokka (*Setonix brachyurus*). Smaller, tropical species have been largely neglected. A quarter of a century ago, Sadleir (1965: pp239-40) commented that "present knowledge of breeding in Australian marsupials is limited almost entirely to species occurring in the southern part of the continent, little being known of those in tropical or arid areas". While this bias particularly remains in the tropics (Lee and Ward 1989), the life history of many species of macropodid have been examined in at least some small way since Sadleir's comment. Indeed, reviews by Lee and Cockburn (1985) and Tyndale-Biscoe and Renfree (1987), argue that macropodids are the best known family of marsupials.

The macropodidae contains the largest extant species of marsupial and has species ranging in size from one to 85kg (Strahan 1983). As in other mammalian taxa, there is a strong correlation between body size and life history traits within the confines of their general life history (as outlined above and reviewed Russell 1982, Lee and Cockburn 1985, and Lee and Ward 1989). Much of the variation between species in their general pattern of growth and development can be accounted for by maternal body mass. There are strong correlations between the varying life history traits discussed above (except length of oestrous cycle and gestation), and adult body size, with larger species needing more time to develop and mature. In addition, significant positive correlations exist between maternal body mass, and mass of young at birth, pouch exit and weaning.

Sharman *et al.* (1964), Tyndale-Biscoe (1973, 1984, 1989), Russell (1974, 1982, 1984), Lee and Cockburn (1985), Tyndale-Biscoe and Renfree (1987) and Lee and Ward (1989) have reviewed the life history and reproductive biology of macropodids. The general pattern is that a single young is born after a relatively short gestation (27-37 days). While still altricial, the neonate is generally larger and more developed than those of other marsupials. Like other marsupials, the young finds its way to the mother's pouch immediately after birth and attaches to an available teat. Initially, the pouch young (PY) is permanently attached to this teat; later, it detaches and suckles at will. Macropodid young remain in the pouch for between six and eleven months. A short period of intermittent pouch usage is followed by permanent exit from the pouch (PEP). The young-at-foot may continue to suckle for an additional one to seven months until weaned.

No differences in size or growth rate of the sexes have been recorded in pouch young even in species which exhibit even the greatest sexual dimorphism as adults (Sharman *et al.* 1964; Ealey 1967; Poole, Carpenter and Wood 1982a,b). The patterns of post-pouch growth vary from those exhibited by the smaller species which reach a plateau early in adult life to those of the larger species where at least males may continue to grow throughout their life (Jarman 1989). Generally individual adult males are the same size or larger than their conspecific females. Males also tend to mature later, particularly in the larger dimorphic species (Tyndale-Biscoe and Renfree 1987, Jones 1989). The maximum life span of most macropodids is unknown, although in larger species it may extend up to 20 years (Russell 1982).

There are no major differences between species in the reproductive pattern of male macropodids. Physiological maturity (ability to inseminate females) occurs at between one and four years depending on body size although social maturity (access to mates) may be delayed a further one to four years in the larger dimorphic species (reviewed in Hume *et al.* 1989). Once sexually mature, males of all known species are capable of spermatogenesis throughout the year. However, spermatogenesis may be impaired during periods of drought or high temperature in *M. rufus* (Newsome 1973). Seasonal variation also occurs in males of *M. eugenii*; a species whose females show a marked seasonality. Peaks in testosterone levels and size of accessory reproductive organs in males occur in January-February when most females are undergoing oestrus and October when pre-parous females first enter oestrus (Inns 1982b, Curlewis 1991).

In contrast, the reproductive pattern in female macropodids varies both inter- and intra-specifically and has been the focus of much attention. The pattern of reproduction of female macropodids was first reviewed by Sharman, Calaby and Poole (1966). Since then the reproductive pattern of at least 15 macropodids has been examined at least in some way (Tyndale-Biscoe and Renfree 1987: p20-21), and reproduction in female macropods has been reviewed from the perspectives of physiology (Tyndale-Biscoe 1973, 1984, 1989 and Tyndale-Biscoe and Renfree 1987), evolution (Rose 1978, Lee and Cockburn 1985) and ecology (Tyndale-Biscoe 1973, Russell 1974, 1982, 1984, Newsome 1975, Lee and Cockburn 1985).

Since Sharman (1954) first described the phenomenon of embryonic diapause in *S. brachyurus*, much of the complexity of the physiological patterns of reproduction in female macropodids has been unravelled and several unique features of the endocrine system identified. These have been summarised by Tyndale-Biscoe (1989) as the "extension of the gestation period to occupy 80-110% of the oestrous cycle, the associated extension of the secretory phase of the corpus luteum and its bimodal rather than unimodal profile, the ability of the corpus luteum to become quiescent and for the associated embryo to enter diapause at the stage of the unilaminar blastocyst".

The length of the oestrus cycle varies between species from 28 to 48 days. In all macropodids except *Wallabia bicolor*, the duration of the oestrus cycle is slightly longer than the gestation period and most species exhibit a post-partum oestrus and ovulation. Physiologically, a mature female macropod may be in one of six reproductive states: an infertile oestrous cycle, pregnancy, lactational or seasonal quiescence, or lactational or seasonal anoestrus (Tyndale-Biscoe 1989).

Lactational quiescence has been noted in most species of macropods examined (Tyndale-Biscoe and Renfree 1987). In these species, the birth of a young is typically followed within a few days by a post-partum oestrus and conception, although these may occur later in lactation. This embryo enters diapause after developing to a unilaminar blastocyst. The development of the blastocyst is controlled by the lactational status of the mother. Embryonic development is stimulated and the second young is soon born if the pouch young is lost or vacates the pouch. In the latter case, birth is timed to almost immediately follow permanent pouch exit (PEP) of the first young.

In two species, (*M. eugenii* and *M. rufogriseus rufogriseus*) quiescence extends beyond the period of lactation and becomes seasonal quiescence. In this case embryonic diapause is controlled by day length rather than lactation and occurs from winter until the summer solstice (Berger 1966, Tyndale-Biscoe 1984, Catt 1977).

Two types of anoestrous periods are now recognised: lactational and seasonal. Lactational anoestrous may occur regularly as in *M. fuliginosus* and *M. giganteus* (Poole and Catling 1974) and *M. parryi* (Lee and Cockburn 1985). *Macropus fuliginosus* has lost the capacity for lactational quiescence (Poole 1975). Seasonal anoestrus occurs in island populations of *S. brachyurus* (Sharman 1955, Shield 1964) and is thought to be due to the poor nutrition available during six months of the year. This is a facultative trait as animals brought into captivity and fed *ad libitum* gradually lose this pattern of seasonal anoestrus and breed continuously (Shield 1964). *Macropus rufus* may facultatively enter anoestrous during drought conditions (Frith and Sharman 1964, Newsome 1964).

Physiological patterns, such as those described above for reproduction in female macropodids, can be seen as responses to environmental conditions either past or present. Ecologically, species can be grouped into (1) continuous breeders, (2) opportunistic breeders or (3) facultative or obligate seasonal breeders (Lee and Cockburn 1985). Table 1.1 documents the relationship between these two perspectives of reproductive patterns. The ecological patterns of breeding can be related to the environmental conditions prevalent in a species' habitat.

Continuous breeding is now generally accepted as the ancestral trait and is the most common pattern of reproduction (Lee and Cockburn 1985, Tyndale-

Table 1.1 Comparison of the known physiological and ecological patterns of reproduction in female macropodids studied to date. Note that a species may be in more than one physiological category. ? denotes inference from the literature.

Physiological Pattern	Ecological Pattern			
	Continuous	Opportunistic	Seasonal	
			Obligate	Facultative
Lactational Quiescence	*M. r. banksianus*[1] *P. inornata*[2] *S. brachyurus* (mainland)[3] *W. bicolor*[4]	*M. agilis*[5,6] *M. robustus*[7,8] *M. rufus*[8]	*M. eugenii*[11] *M. r. rufogriseus*[3]	?*M. parma*[16]
Lactational Anoestrous		*M. robustus*[9] *M. rufus*[9,10]	*M. fuliginosus*[12] *M. giganteus*[12] ?*M. parryi*[13]	
Seasonal Quiescence			*M. eugenii*[14,15] *M. r. rufogriseus*[3]	
Seasonal Anoestrous				*S. brachyurus* (islands)[5] ?*M. parma*[16] ?*M. irma*[17]

[1]Merchant and Calaby 1981, [2]Johnson 1979, [3]Shield 1964, [4]Kirkpatrick 1970, [5]Merchant 1976, [6]Bolton *et al.* 1982, [7]Ealey 1963, [8]Sadleir 1965, [9]Newsome 1975, [10]Frith & Sharman 1964, [11]Berger 1966, [12]Poole & Catling 1974, [13] Lee & Cockburn 1985, [14]Berger 1966, [15]Renfree & Tyndale-Biscoe 1973, [16]Maynes 1973, [17]Tyndale-Biscoe 1989.

Biscoe 1989). The pattern of continuous breeding is most prevalent in species which live in habitats where the pattern of optimal conditions is either irregular or continuous (Sadleir 1969). Many macropodid species breed continuously both in the stable conditions experienced in captivity and in the more variable conditions of their natural habitat. For wild populations of the agile wallaby, *M. agilis* in the wet-dry tropics, young were born throughout the year with a peak of births in late wet/early dry season in one habitat (Bolton *et al.* 1982). Births also occur throughout the year in captive colonies (Merchant 1976, Kirkpatrick and Johnson

1969). Many temperate species breed continuously if conditions become more uniform such as occurs in captivity (Tyndale-Biscoe 1984, 1989). Species which breed continuously include *W. bicolor*, *M. rufogriseus banksianus*, *P. inornata* and mainland populations of *S. brachyurus* (Table 1.1).

At least two kangaroos occurring in more arid regions (*M. rufus* and *M. robustus*) are opportunists, breeding continuously when environmental conditions are favourable and entering a drought induced anoestrus during poorer conditions (Ealey 1963, Newsome 1966, 1975). The optimal time for pouch exit for these species cannot be predicted by any previous climatic variable and hence this strategy allows these kangaroos to take advantage of the irregular pulses of water and vegetative growth characteristic of arid Australia.

In temperate latitudes, there is a more regular annual seasonality of resources and breeding is also usually seasonal. The timing of births in species such as quokkas, *S. brachyurus*, on Rottnest Island, allows the young's exit from the pouch to coincide with the spring flush of fodder (Shield 1964).

In two species (*M. eugenii* and *M. rufogriseus rufogriseus*), this reproductive pattern has been taken to an extreme. These species have become obligate seasonal breeders, using photoperiod as a reproductive cue. They are adapted to living in temperate regions which show substantial annual variations in day length and have an annual climatic cycle which is highly predictable. Unlike the other seasonal breeding species, both appear inflexible in their response to changes in environmental seasonality (reviewed in Tyndale-Biscoe 1989). Individuals of *M. eugenii* transported to the northern hemisphere reversed their breeding season such that they were giving birth in the northern summer (Berger in Russell 1974).

By virtue of lactation, parental care in most mammals, including macropodids, is virtually restricted to females. Hence maternal body condition will play a greater role than paternal condition in the survival of offspring, particularly pouch young. Unlike most eutherians, the timing of births in macropodids does not relate to the optimal season for births *per se*, but rather to the optimal season for pouch exit.

In her review of the biology of kangaroos, Russell (1974) noted the significant relationships between environmental conditions and reproduction. Rainfall, ground cover, food availability or nutrition are the factors most commonly implicated. For example, sexual maturity in female red kangaroos may be delayed under poor nutritional conditions for up to eight months (Frith and Sharman 1964).

Since Sharman *et al.* (1964) first considered the pouch to provide a constant environment for the growth and development of young, many authors have considered that the mortality of pouch young in most conditions to be quite low (e.g. Frith and Sharman 1964, Poole 1973, Poole 1975). However, under extreme conditions such as prolonged drought, the mortality of young of *M. rufus* and *M. giganteus* may be as high as 100% (Frith and Sharman 1964, Kirkpatrick and McEvoy 1966). Mortality of young has been almost exclusively examined from the perspective of variation between populations, and there is little data on individual variation between wild females.

Most authors consider that mortality of young is highest around the time of pouch emergence when the drain on the mother's resources is the highest and when the change of environment for the young increases the number of deaths due to misadventure. The lack of literature discussing mortality during gestation implies either a lack of information on this aspect, or that such mortality is so low as to be considered negligible. Little mortality occurs during the travel of the new born young to the pouch (Russell 1982).

Poor environmental conditions as manifest through maternal nutrition are the usual reasons given for pouch mortality (e.g. Ealey 1963, Sadleir 1965, Newsome 1966, 1975). The methods of measuring the effect of environmental conditions on mortality of young have varied from changes in maternal body condition (e.g. Ealey 1963), indices of drought (e.g. Newsome 1965, 1966), and more recently, actual maternal intake of food (Higginbottom *pers. comm.*). The most spectacular effect of poor environmental conditions on maternal nutrition and hence on PY mortality occurs in the red kangaroo (Newsome 1966, Frith and Sharman 1964). Embryonic diapause follows conception at post-partum oestrus, and during good seasons re-activation occurs such that the birth of a new PY closely follows permanent emergence from the pouch by its sibling. In the early stages of drought, PY mortality increases and the quiescent blastocyst develops to replace a lost PY rather than one vacating the pouch voluntarily. If the environmental conditions worsen, females become anoestrus. Within 14 days of drought-breaking rain, when green forage becomes available, females return to oestrus and the normal cycle starts again (Newsome 1966).

1.3 *Petrogale*

While the genus *Petrogale* is only one of nine extant genera within the family Macropodidae, it contains almost as many species as the better known *Macropus*

(Calaby and Richardson 1988). There were 23 taxa of rock wallabies in 11 species recognised in 1990 (Sharman *et al.* 1990) although the taxonomy is still under review (see Eldridge *et al.* 1988, 1989, 1990, 1991a,b, Sharman *et al.* 1990). Briscoe *et al.* (1982) hypothesised that rock wallabies arose on the Precambrian (Western) Shield of the continent, expanding and diversifying from their point of origin to occupy their present, almost Australia-wide range.

Members of this genus are currently found in several major habitat types and all biogeographic zones within mainland Australia, including the arid interior (e.g. *P. lateralis*, *P. xanthopus*), the southern extremities of the Great Dividing Range (*P. penicillata*) and tropical vine forest (*P. persephone*). By far the greatest diversity is found in the drier areas of the tropics with at least six species represented (*P. assimilis*, *P. brachyotis*, *P. burbidgei*, *P. concinna*, *P. godmani*, *P. inornata*, and the Mareeba and Mt Claro races of *P. assimilis*, and the Cape York race of *P. godmani*) (Briscoe *et al.* 1982). No species is present in Tasmania although smaller off-shore islands in Western Australia are important genetic refuges for *P. lateralis* and *P. rothschildi* (Briscoe *et al.* 1982).

On a local scale, the distribution of *Petrogale* is more patchy as they are typically associated with steep, rocky slopes, boulder outcrops, and cliffs and gorges (Briscoe *et al.* 1982). Such habitats are often disjunct, restricted and island-like. For rock wallabies, optimum habitats occur where suitable shelter sites in the rocks are close to well-vegetated feeding areas. The colonies of rock wallabies inhabiting these outcrops range in size from a few animals to many hundreds (Briscoe *et al.* 1982), with the maximum size of a colony probably limited by the number of suitable resting or cave sites available.

The close association of *Petrogale* with rocky outcrops indicates that these outcrops are an important habitat requirement for this genus. Such outcrops act as refuges both from predators and more importantly, from the physiological extremes of the surrounding environment. This is particularly striking in central Australia where the mammalian fauna tends to consist of the larger species (e.g. *M. rufus* and *M. robustus*) which are more able to cope with the extreme temperatures, or the smaller mammals (e.g. species of the families of Rodentia, Dasyuridae and Thylacomyidae) which are 'hiders', escaping from the heat in burrows or in spinifex clumps. Where suitable rocky outcrops occur, the rock wallabies are by far the largest of the species to employ such an avoidance strategy. Localised rocky microhabitats often exhibit a microclimate distinct from the surrounding region. Such outcrops may ameliorate the effects of the local environment and develop a distinctive flora and fauna (Dwyer 1972; Wilson, Gerritsen and Milthorpe 1987; Mares and Lacher 1987; Freeland, Winter and Raskin 1988). Mares and Lacher (1987) suggest that rockpiles may provide a specialised environment that is distinctive in climate, structure, vegetation and fauna from the surrounding area. They predicted that rocky habitats will be important mesic refuges in areas that are characteristically dry, have marked wet and dry seasons, and year-round high temperatures leading to high evaporation potential and hence lower effective rainfall. Freeland *et al.* (1988) noted that in Australia, the diversity of rock-adapted mammals was greatest in the drier regions of northern Australia. This region approximately coincides with that of the wet-dry tropics described earlier. The rock-adapted mammals in this region include the rock rats (*Zyzomys*) and the rock ringtail and scaly-tailed possums

(*Pseudocheirus dahli* and *Wyulda squamicaudata* respectively). The greatest diversity of rock wallaby species is also found in this tropical region. Indeed, this is the only area where rock wallaby species occur sympatrically (*P. concinna* and *P. brachyotis* in the Northern Territory; and *P. burbidgei* and *P. brachyotis* in the Kimberleys) (Kitchener 1983, Sharman and Maynes 1983c, Sanson *et al.* 1985).

Despite the relatively high proportion of species of macropodid within the genus *Petrogale*, research on these rock wallabies is almost as patchy as their distribution, with the evolutionary and taxonomic status within the genus providing the main thrust. The phylogeny and taxonomy of the 23 taxa of rock wallabies described between 1827 and 1982 (reviewed by Briscoe *et al.* 1982) have been re-assessed in recent years (e.g. Eldridge *et al.* 1988, 1989, 1990, 1991a,b; Sharman *et al.* 1990, Eldridge and Close 1992). The inter-relationships between these taxa are complex and have been studied using a wide variety of techniques from skull morphometrics, to chromosomal re-arrangements, allozyme electrophoresis and ecto- and endo-parasites (see Eldridge *et al.* 1991b for review).

The genus *Petrogale* exhibits a chromosomal diversity that is unusual in marsupials (Sharman *et al.* 1990). Briscoe *et al.* (1982) placed the species of *Petrogale* in three major groups: (1) the *xanthopus* group containing the yellow footed rock wallabies (*P. xanthopus* and *P. x. celeris*) and *P. persephone*; (2) the *brachyotis* species group in the Timorian biogeographic region including *P. brachyotis*, *P. burbidgei* and *P. concinna* (formerly *Peradorcas* (Calaby and Richardson 1988)); and (3) the *lateralis-penicillata* species group including three taxa of *P. lateralis*, and the remaining taxa from eastern Australia (*P. assimilis*, *P. godmani*, *P. inornata*, *P. penicillata*, *P.p. herberti*, and the Cape York, Mareeba and Mt Claro races) (see also Figure 1.1; Figures are located at the end of each Chapter). These three races have recently been proposed for elevation to specific status (*P. coenensis*, *P. mareeba* and *P. sharmani* respectively) by Eldridge and Close (1992).

While the specific conclusions reached have often been somewhat contradictory, it appears that *Petrogale* has undergone complex or reticulate speciation (Sharman *et al.* 1990, Eldridge *et al.* 1991b). The distribution of rock wallaby taxa is thought to be controlled by climatic factors, with their speciation primarily a response to environment (Sharman *et al.* 1990). A bioclimatic prediction system delineated a more or less unique bioclimatic profile for each of the taxa in eastern Australia. It is assumed that individuals carrying the ancestral karyotype invaded new habitats with resultant selection for randomly occurring changes of adaptive significance in the new habitat (Sharman *et al.* 1990).

This complex speciation is particularly evident in the tropical region of north eastern Australia (Briscoe *et al.* 1982; Eldridge *et al.* 1988, 1989, 1990, 1991a,b; Sharman *et al.* 1990). Briscoe *et al.* (1982) argues that *Petrogale* offers an opportunity to study the genetic mechanisms which underlie this fundamental evolutionary phenomenon. However, before speciation and intra-specific variation can be fully understood knowledge of the life history and ecology of these species is also required.

Lesser attention has been paid to these aspects of their biology, with research to date concentrated on captive studies and a small subset of species of *Petrogale*. The growth and development of *P. inornata* (Johnson 1979), *P. xanthopus* (Poole *et al.* 1985) and more recently *P. assimilis* (Bell, Close and Johnson 1989, Close and Bell 1990) in captivity has been examined. Only Poole *et al.* (1985) was able to fit whole-of-life growth curves. Both Johnson (1979) and Close and Bell (1990) presented data for pouch life only. Sanson (1978, 1989) suggested that the browsing diet of most *Petrogale* spp. precludes the usual methods of molar eruption and progression from being useful to determine age in these species. However, molar eruption and molar progression have been used to determine the age of post-pouch young of *Petrogale* (Poole *et al.* 1985, Bell *et al.* 1989). Poole *et al.* noted that the accuracy of prediction was restricted to determining the year and possibly the season of birth. They also observed a lack of sexual differences in the growth of pouch young.

The degree of sexual dimorphism of a species has been linked to its overall size, behavioural ecology and mating system (e.g. Jarman 1983, Kleiman 1977). Little dimorphism is expected as the genus *Petrogale* contains some of the smallest species of macropod with no species exceeding ten kilograms in body weight. No colour dimorphism has been recorded (Sharman and Maynes 1983a) and no sexual dimorphism before pouch exit for *P. xanthopus* or *P. assimilis* (Poole *et al.* 1985, Close and Bell 1990). Both *P. concinna*, one of the smallest rock wallabies (data from Sanson in Jarman 1989), and *P. xanthopus*, the largest rock wallaby (Poole *et al.* 1985), stop growing early in adult life, although Jarman (1989) classified *Petrogale* as medium sized macropodoids whose females continue rapid growth past middle age. Sharman and Maynes (1983a), however, noted that adult males were up to 30% larger than females and Jarman (1989) recorded that where sexual dimorphism exists, males were slightly larger than females.

Until recently rock wallabies were considered to have a polygynous mating system with males having a stable linear dominance hierarchy (Dwyer 1974, Barker 1982, 1990, Horsup 1986). Horsup (1989 and unpublished) and Barker (1990) now consider that *P. assimilis* form long-term pair bonds although pairing does not necessarily determine paternity (P. Spencer *personal communication*).

The reproductive ecology of *Petrogale* has been examined in some detail for captive populations of *P. inornata* and *P. xanthopus* (Johnson 1979, Poole *et al.* 1985), while lesser information now exists for *P. assimilis* (Bell *et al.* 1989) and wild populations of *P. lateralis* (Kinnear, Onus and Bromilow 1988) and *P. xanthopus* (Lim *et al.* 1987). The pattern in these species suggests that *Petrogale* fits into the group 2 pattern of marsupial reproduction described by Sharman *et al.* (1966) *i.e.* the gestation period is extended to almost the full length of the oestrous cycle, so that parturition is followed by an oestrus and mating with a consequent lactational quiescence and development of the dormant blastocyst will continue at any time of the year with the loss or removal of the pouch young. Sexual maturity is attained from 18 months in both sexes (Johnson 1979, Poole *et al.* 1985, Bell *et al.* 1989). The length of the oestrous cycle is between 30 and 37 days and the gestation period is 31 to 33 days. Parturition is usually followed by oestrus and mating with a consequent lactation controlled embryonic quiescence. Pouch life lasts 189 to 227 days and young are weaned a maximum of 90 days after PEP (Poole *et al.* 1985, Johnson 1979). Thus females are capable of producing one offspring every seven months (Johnson 1979). Breeding occurs throughout the year in these captive populations, although there is a suggestion that *P. concinna* (Sanson *et al.* 1985) and possibly other species of rock wallaby may be seasonal breeders (Sharman and Maynes 1983a). Poole *et al.* (1985) noted a male bias in offspring in *P. xanthopus*, with a tendency for older mothers to produce male offspring (Lim *et al.* 1987).

Information on the population biology of *Petrogale* is scant. Colonies of *P. xanthopus* appear to contain equal numbers of both sexes (Lim *et al.* 1987). Some movement between closer colonies (one to two km apart) has been recorded, although there is a high site fidelity (Lim *et al.* 1987). Populations of *P. lateralis* in the Western Australian wheat-belt are adversely affected by fox predation (Kinnear *et al.* 1988) and by drought.

1.3.1 *Why study P. assimilis?*

Petrogale assimilis is a medium-sized rock wallaby (2.5 - 5 kg) found within the wet-dry tropics of north eastern Queensland (Figure 1.1). Its distribution is parapatric with *P. inornata* to the south and *P. godmani* to the north (Eldridge *et al.* 1988). The Mareeba and Mt. Claro races of *P. assimilis* are found to the north and east of the nominate race (*P. mareeba* and *P. sharmani* respectively, Eldridge and Close 1992). This species complex forms part of the *Petrogale lateralis-penicillata* species group. Indeed, *P. assimilis* is morphologically indistinguishable from *P. inornata* and was previously given subspecific status within *P. inornata* (Sharman and Maynes 1983b). *P. assimilis* and *P. inornata* are now separated into distinct species based on chromosomal evidence (Calaby and Richardson 1988, Sharman *et al.* 1990).

Examination of the life history and reproductive ecology of a wild population of *P. assimilis* in the light of current knowledge would allow comparisons to be made with other macropod species and other mammalian species living in the wet-dry tropics. Such research into the life history and reproductive ecology of *P. assimilis* could partially fulfil the need for research into the life histories of smaller, tropical species of macropods in the wild as noted by Sadleir (1969), Lee and Cockburn (1985) and Lee and Ward (1989).

While there are several species of macropodid that could be used to fill these needs, *P. assimilis* has the added advantage of being part of a taxonomic group which is considered to be undergoing complex speciation. Much is known of the evolutionary and taxonomic status of this genus, and debate and research into the genetic mechanism into this topic still continues, yet there is little understanding of the ecological mechanisms involved. Knowledge of the life history of such a species could lend substance to, or postulate ecological mechanisms for the proposed rapid evolution of rock wallabies. In particular, it was hoped that detailed information could be gathered on a subset of individuals such that some insight could be gained into individual variation in reproductive success by females.

Since this project was also hoped to be the start of a long-term study into the biology of this species, I tried to establish a population of individuals of known age and reproductive history on which to base these future studies. In doing so, the methodology and techniques required for this needed to be developed. Based on information available for other rock wallaby species and the general macropodid pattern, I expected individuals of *P. assimilis* to be gregarious and easily re-locatable, to have a gestation period of about a month, a pouch life measurable in months and a life-span of years rather than decades.

Therefore, the broad aims of this project were to examine the life history of a wild population of the allied rock wallaby, *Petrogale assimilis* in the wet-dry tropics of Australia. Specifically, the aims were to:

(1) develop the methodology to estimate accurately the age of individuals;

(2) examine growth and development of both young and adult animals;

(3) determine the pattern of breeding;

(4) examine the effects of seasonality on reproduction and body condition; and

(5) examine the survivorship of offspring born during the study period and hence the variation in maternal success during this time.

A study of the individual variation in life-history tactics of a species in this rapidly speciating genus would complement the genetic studies and provide further insights into the evolutionary process. Additionally, *P. assimilis* lives in an unpredictable, tropical environment which would allow me to examine the environmental influences on the life history traits of this species and provide some comparisons between a wild, tropical population and studies of both captive populations and species from deserts and more temperate climes. If *P. assimilis* also had a continuous pattern of reproduction as I expected, I may be able to clarify some of the effects of environmental variables on life history parameters.

1.3.2 *Other research at Black Rock*

This study is one of several that have, and are being conducted on the same colony of *P. assimilis* at the study site, Black Rock. This rock wallaby colony was originally investigated by Wally Davies (University of Queensland) to examine the behavioural ecology of this species with particular emphasis on mother-young behaviour. Field work was carried out between 1972 and 1976 and an unknown number of adults were tagged. Unfortunately this study was never completed, and no results are available for comparisons.

In 1986, Alan Horsup and I commenced research into different aspects of rock wallaby biology at the Black Rock field site. Originally an Honours project (Horsup 1986), Alan's work was expanded into a doctoral project encompassing the behavioural ecology of these animals. The focus of his research examines the relationships between the diet (Horsup and Marsh 1992), social organisation, home range and movement of individuals. It was originally hoped that both Alan and I would be able to gather detailed information on the same individuals. Unfortunately there was little overlap between the regularly re-trapped animals from my study and the animals intensively observed by Alan Horsup and much of this work is not yet completed. As a result, less has been made of the connection between the projects than otherwise envisaged. Peter Spencer has also investigated parameters of the blood in animals in this colony (Spencer and Speare 1992) and the effect of a feral cat on the population (Spencer 1991).

The monthly sampling trips initiated by this study are being continued by Peter Spencer and Helene Marsh, to maximise the information on life history, reproductive ecology, survivorship and mortality of the population and in particular, aspects of maternal investment. Some of their data (18 months) has been used to supplement my own to examine individual variation between females in rearing pouch young (Chapter 8). More recently, research into the lactation energetics of individuals of this colony has been started by Helene Marsh, with Jim Merchant and Brian Green of CSIRO, Canberra (Merchant and Marsh 1992). Peter Spencer, while collecting the ecological data mentioned above, is also collecting data to examine genetic variation and maternity/paternity within this colony via the use of DNA fingerprinting (Odorico, Spencer and Miller 1992). Most of the above mentioned work is still in progress and as yet there is little which can be drawn upon for this study.

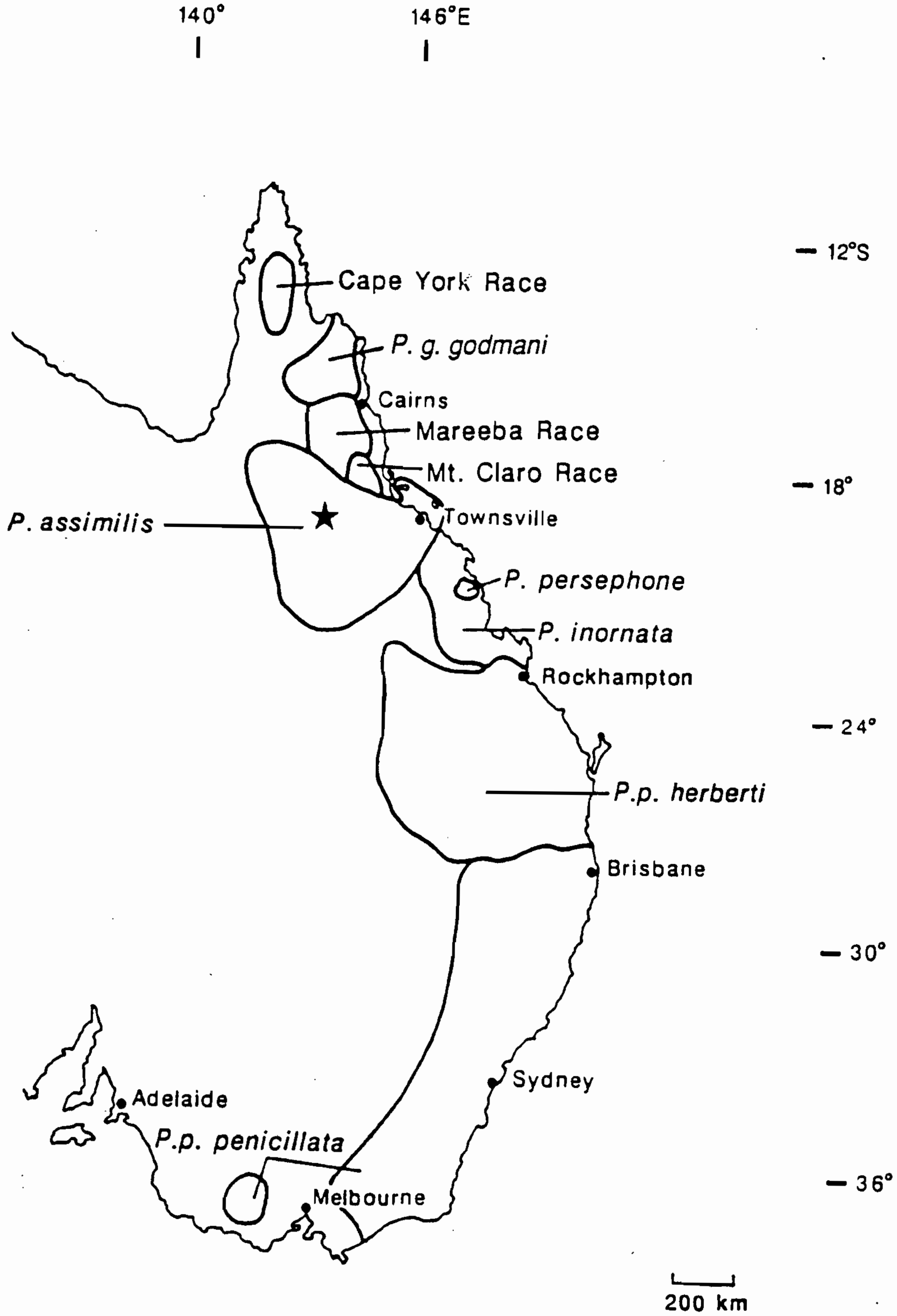


Figure 1.1 Distribution of *Petrogale spp.* in eastern Australia. Note the distribution of *P. assimilis* and the presence of three races, *P. assimilis* Mareeba, *P. a.* Mt. Claro and *P. godmani* Cape York. ★ marks Black Rock (Map courtesy of M. Eldridge).

Chapter 2

Description of Study Site and General Methods

2.1 Study site

2.1.1 *Location*

The study was located at Black Rock (19° 05'S., 144° 07'E.), situated on 'Lyndhurst' Station, about 265 km west-north-west of Townsville at an altitude of 620m. The rock wallaby colony at Black Rock is in the approximate centre of the distribution of *P. assimilis* (Figure 1.1). Black Rock is an isolated sandstone bluff which dominates the surrounding landscape of parallel low sandy ridges separated by shallow clay pans. The outcrop is approximately 800 x 400m. The main axis runs north-south with an eastern cliff face rising some 20m above the surrounding countryside (Figure 2.1). The bluff slopes gently away to the west. On the outcrop, the highest density of rock wallabies is found sheltering around the large rock fall (approximately 100m long) on the southern end of the cliff face (Figure 2.2). Breakaway gullies and smaller rock falls around the rest of the outcrop also form additional shelter sites.

2.1.2 *Habitat*

The surrounding country is medium height (approximately 10-15m) open woodland dominated by sclerophyllous species (Geographic Section, Department of National Development map 1972). The soil is sandy and low in organic matter.

Four major vegetation zones have been identified at the study site (Horsup and Marsh, 1992):

1. the outcrop complex dominated by the shrubs *Tephrosia filipes* and *Melhania oblongifolia*;
2. mixed woodland (typical of the slopes) dominated by *Brachychiton*, *Grevillea*, *Petalostigma* and *Eucalyptus* species;
3. open woodland dominated by *Eucalyptus* species; and
4. low-lying areas dominated by *Melaleuca* and with a lush ground cover of forbs, herbs and sedges.

Rock wallabies generally shelter during the day in and around the rock fall, moving out at night to feed on the surrounding vegetation. No vegetation zones were particularly favoured as feeding areas by the rock wallabies (Horsup and Marsh 1992).

2.1.3 *Climate*

The study site lies in the Wet-Dry tropics of northern Australia. Rainfall is extremely seasonal. Most rain occurs in the summer wet season with little falling in the longer dry season (Figure 2.3a). Rainfall in this region of Australia is also unpredictable in both time and space. In particular, the onset, length and intensity of the wet season vary between years and locations (Ridpath 1985, Jones 1987). This was evident in the very large variation in annual rainfall (Figure 2.3b) recorded at Lyndhurst homestead (16km south-south-west of Black Rock). Rainfall has been recorded at this homestead since 1886 (n=99) and totals (measured July to June so as not to divide wet seasons between two calendar years) have ranged from 189mm to 1612mm (mean=738mm; C.V.=40%). Thus, there is more than an eight-fold variation in annual rainfall.

It seemed critical to take this temporal variability into account when defining the seasons. Hence, following Jones (1987), the wet season was defined as beginning in the first of two consecutive months that averaged 75 mm rainfall per month (approximately 10% of average rainfall at Lyndhurst) and lasting for as long as two consecutive months averaged 75 mm per month. The onset and duration of the wet season is variable (Figure 2.4). The wet season usually starts in December, but may start as early as October or as late as February and its duration has ranged from one to six months (Figure 2.4). In one year (1925/6) the wet season failed completely.

Rainfall was measured at Black Rock when field workers were present (12-15 days per month) from January 1988 to June 1990. The monthly rainfall records from Lyndhurst homestead (obtained from the station and from the Australian Bureau of Meteorology) were compared with Black Rock data (Appendix 1). There was a strong linear relationship between the measured monthly rainfall at Lyndhurst homestead and Black Rock: (Black Rock = 0.746 + 0.793 * Lyndhurst; r^2 = 0.91) indicating that Lyndhurst records are a reliable index of rainfall at Black Rock. As the Lyndhurst records were more complete, they have been used in the analyses in this thesis, except for the 1990/91 wet season when the Black Rock records were more complete.

Lyndhurst records (1886 to 1990) provide a long term perspective of the climate for the trapping area (Figure 2.3b). In only two years during the 1970's was there below average rainfall (1977/78 and 1979/80). In contrast, most of the

1980's were drought years with less than average rain falling during six years (Figure 2.3b). The trapping period (June 1986 to June 1990) was part of a time of below average rainfall (mean=600 ± 53.9 mm S.E.; n=8 years), which had persisted since the 1981/82 wet season except for 1983/84 (Figure 2.3b). The monthly rainfall totals for the months just prior to, and until the end of the study period (October 1985 to June 1990), are shown in Figure 2.5. The next above average rainfall year was in 1989/90, after the major part of my field work had ceased. Comparison of the average monthly rainfall with the monthly rainfall for the last 20 years, also indicates that in general the 1970's were wetter than the 1980's (Figure 2.6).

The seasonal changes throughout the year were quite marked (Figures 2.3 - 2.7), and for the analyses in this study, I divided the months between the wet seasons arbitrarily and approximately equally into early and late dry seasons (Table 2.1). A weather year was defined from the start of one wet season until the

Table 2.1 Lengths of seasons at 'Black Rock' during the study period (June 1986 - June 1990).

		Season (# months)	
Year	Wet	Early Dry	Late Dry
1985/86	Nov - March (5)	April - July (4)	Aug - Dec (5)
1986/87	Jan - April (4)	May - August (4)	Sept - Jan (5)
1987/88	Feb - March (2)	April - July (4)	Aug - Dec (5)
1988/89	Jan - March (3)	April - June (3)	July - Oct (4)
1989/90	Nov - Dec (2)	Jan - June (6)	July - Dec (6)

beginning of the following wet season, and unless otherwise specified, will be referred to simply as a year throughout this study.

Daily minimum and maximum temperatures were recorded at Black Rock when field workers were present. Daily minimum and maximum winter (June) and summer (December) temperatures averaged 10°C/24°C and 21°C/35°C respectively (Figure 2.8). The lowest temperature recorded was 4°C in July 1987 and the highest 41°C in November 1987. Horsup (1986) measured the temperatures and relative humidity in the rock wallaby shelter sites in May 1986. The range of temperatures measured was much narrower than ambient (range: 18°-23°C *cf* 19°-33°C). The relative humidity in the shelter sites averaged 5.1% higher than the external environment, particularly during the hottest part of the day. Thus shelter sites ameliorate the extreme environmental conditions encountered at Black Rock.

2.1.4 *Other rock wallaby colonies near Black Rock*

A second and much smaller sandstone outcrop lies approximately two km north west of Black Rock. This small outcrop supports a small colony of *P. assimilis* (probably no more than five adults). Beyond this, the nearest known suitable rock wallaby habitat surrounds a permanent waterhole at the junction of Bundock Creek with the Einasleigh River, 6km due west of Black Rock. Although these sites (particularly the second with its permanent water) were checked regularly (approximately every month for the waterhole site and six monthly for the small outcrop site) but somewhat haphazardly with binoculars, no tagged animals from Black Rock were sighted at either of these colonies. One juvenile caught initially at the colony 2km west of Black Rock was sighted once at Black Rock less than one month later (A. Horsup, *personal communication*).

2.2 Field techniques

2.2.1 *Capture of rock wallabies*

Individuals of *P. assimilis* were trapped during field trips held at approximately monthly intervals between June 1986 and October 1988 (Appendix 2). Two additional sampling trips were held in February and June 1989. This resulted in a total of 3764 trapping days over 30 monthly field trips. In addition, I made limited use of data collected by Peter Spencer between November 1988 and June 1990 (Chapter 8 only). A trapping day was from midday of that day until midday of the following day. Field trips were reduced from seven to five nights in September 1987 and then to four nights in January 1988, as the rock wallabies became habituated to trapping, and new animals for the trip were rarely caught after the second night.

Rock wallabies were captured in wire cage, treadle-release traps ranging in size from 50 x 35 x 35 cm to 90 x 40 x 40 cm. Initially the traps were wired open between trips so that the animals could become habituated to them. Later, when the majority of rock wallabies which were frequently caught were accustomed to the traps, the traps were closed at the end of each field trip.

The number of traps set increased from 12 to 33 during the study period as more traps became available. This and the habituation probably account for the increased number of animals caught per month during the study period (Appendix 3). Traps were set in one to three irregular trapping lines and were placed around the main section of the colony to maximise (rather than randomise) the number of captures. After the third trip, traps were left in position between trips. Those traps which were consistently unsuccessful in capturing animals were moved to more suitable positions.

The traps were set prior to dusk with a bait of mixed peanut butter, rolled oats, oil and honey. They were checked once during the night (and cleared and re-set if necessary) and again in the early morning when they were closed until re-opened in the late afternoon. Thus the number of trapping opportunities (>7,500) was approximately twice the number of trapping days. Individual traps were closed in winter if they were exposed to strong winds. All traps were cleared of animals and closed if it rained during the night.

Rock wallabies were removed from traps and retained in labelled hessian bags. Animals were usually released on removal from the trap if recaptured during a trip. Rock wallabies caught during the night were suspended in their bags until the next day. In winter, these suspended bags were covered for warmth and to reduce wind chill. All animals were released at their trapping site as soon as practicable on the same trapping day they were captured.

Standard 25mm packaging tape was used to tape closed the pouches of females with large pouch young to prevent them from "throwing" the young when released. The mother removed the tape when she reached a safe place, by which time she had reformed the pouch by contracting the appropriate muscles.

2.2.2 *Marking the animals*

Emergent pouch young and older animals were tattooed when first captured. Older animals were tattooed with a unique, three digit number in each ear. A single letter was tattooed in one ear only, of emergent pouch young so that a full tattoo could be added later as the animal reached adult size. When initially caught, adults (n=79) and sub-adults (n=1) were also tagged in both ears using individually numbered monel metal fingerling tags (No. F3, Salt Lake Stamp Co., Salt Lake City, Utah).

2.2.3 *Routine data collection*

Two volunteer field assistants were taken on almost all field trips. Although these people were usually untrained, non-biologists, they adapted readily to the work with on-site tutoring. In order to standardise observer error, all body measurements on the rock wallabies were taken by myself or in later trips by Peter Spencer, a part-time research assistant in the Black Rock project.

Rock wallabies were restrained in hessian bags during examination. All adult animals were weighed to the nearest 50g as soon as possible after capture on the first occasion they were caught on each trip. Standard body measurements of the head, pes, arm, leg and tail lengths (±0.5mm) of post-pouch young animals were taken using vernier calipers or a ruler following Sharman *et al.* (1964). Each measurement was taken twice on each occasion. While only the first measurement was used in subsequent analysis, the second measurement was used as a check on the repeatability of the first measurement. If the second measurement was different by more than one millimetre of the first, both measurements were repeated. In most cases the second measurement was within 0.5mm of the first. The frequency of measurements varied with the age class of each animal: juveniles and sub-adults were measured each month; adults approximately every six months.

Special care was taken during handling of pouch young (PY) to minimise stress and mortality, as an important facet of the project was to determine accurate survivorship curves for wild animals. Pouch young were examined and measured within their mother's pouches while they were permanently attached to the nipple. Each PY was measured once per trip until it was no longer trapped with its mother. Measurements (as described above) of the head, pes and tail of small pouch young were taken opportunistically to lessen the potential loss of such young due to handling. These three measurements were considered the most critical as they were the ones measured most often for other macropodids (e.g. Shield and Woolley 1961, Sadleir 1963, Sharman and Pilton 1964, Kirkpatrick 1965a, Ealey 1967, Kirkpatrick and Johnson 1969, Murphy and Smith 1970, Catt 1977, Johnson 1979, Pearse 1981, Rose and McCartney 1982, Close and Bell 1990). The head measurement is usually considered the most accurate body measurement for measuring growth in macropodids (Poole, Carpenter and Wood 1982a,b; see also Chapter 3). The lengths of the arm and leg were measured and the body weight recorded once the young began growing body hair. PY were weighed correct to the nearest 5g. External developmental stages were recorded as per Kirkpatrick (1985).

Information on the body condition of each animal was obtained using several indices including weight and an index of fatness (see Chapter 8). Blood samples were taken from the lateral tail vein to obtain the packed cell volume (PCV). The blood was placed in three micro-haematocrit tubes and centrifuged at 4000rpm for at least three minutes. The readings for the three tubes were averaged.

Any dead animals found were collected and identified if possible. Evidence of the cause of death was also noted.

2.2.3.1 Female reproductive status

The pouch of each female was examined as outlined in Poole and Catling (1974). The following details were recorded: general appearance; presence of covering secretion/scale; the size, form, and lactation status of each teat; the presence of pouch young; and the teat of attachment. Enlargement of the pouch and eversion of all the teats was taken as evidence of sexual maturity (Merchant and Calaby 1981). On several occasions, I attempted to collect blood for progesterone assays which would have been useful in resolving any anomalies in reproductive condition but the stress induced in the animals by holding them at high temperatures (up to 40°C) under basic field conditions was deemed unacceptable as it threatened to increase mortality and interfere with the major aims of the project.

The sex of each PY more than approximately ten days old was also recorded. The sex of neonates younger than this was not determined to minimise stress and mortality. Thus young dying soon after birth were not sexed and were subsequently omitted from any analyses requiring this datum.

2.2.3.2 Male reproductive status

The total length (including epididymis), width (both testes together) and depth (±0.5mm) of the testes of each male were measured using vernier calipers. A testes index was calculated as the cube root of the product of the testes dimensions. Evidence of sexual maturity and sperm production was determined by the presence of sperm in the urine rather than via testes biopsies to avoid the risk of causing long-term damage. Testosterone assays would also have been useful in determining male sexual maturity and seasonality. However, as for the collection of blood for progesterone assays, the stress on the animals induced by holding them for the number of hours required, in the basic and often very hot field conditions was deemed unacceptable.

Each male was stimulated to urinate by massaging the area around the urogenital opening. The resulting urine was collected in a test tube and centrifuged at 4000rpm for at least three minutes. The supernatant was drawn off and discarded and the residue preserved in 10% formalin. The sample was later re-spun in the laboratory and a droplet of the sediment placed in an Improved Neubauer Haemocytometer, stained with gentian violet and examined under low power (40x) using a binocular microscope. Counts of the numbers of whole spermatozoa and separated heads and tails were made in five fields of the haemocytometer (corresponding to a total volume of $0.4mm^3$). Because of the variation in the volume of urine collected, data on the presence or absence of spermatozoa only were used in subsequent analyses.

2.3 Captive animal techniques

Data from two groups of captive *P. assimilis* were used in the chapters concerning growth and age determination (3, 4 and 5). The first group of captive animals was housed at Macquarie University, Sydney by Robert Close and Jane Bell (see Bell, Close and Johnson 1989, and Close and Bell 1990 for details). Data from some of the PY from these animals were used to help construct PY growth curves and for comparisons between growth rates of captive and wild PY (Chapter 3).

The second group comprised three female and one male PY of *P. assimilis* which were orphaned during field work at Black Rock or, in one case, in a road accident at Mt. Stuart, near Townsville (Table 2.2). The dates of birth of two of these (#079 and #M/310) were known to within a few days (from capture records of their mothers, #054 and #008 respectively). When orphaned, both PY were fully furred and the first incisors had erupted. One animal had already started leaving the pouch (#M/310), the other (#079) was only days from leaving it for the first time. A third animal (#R/311) was also orphaned at Black Rock but its mother was unknown and the date of birth was calculated from measurements taken at this late stage of pouch life. The developmental stage of the last PY (#W) at the time when its mother was killed is unknown although it is likely that it was at least furred. Its age could be calculated only from measurements taken when it was first brought to personnel at Queensland National Parks and Wildlife Service (Q.NPWS) at Palleranda, Townsville.

All PY were hand-reared until independence. Two females (#079 and #W) were then permanently housed at Q.NPWS, Palleranda. No males were available for the females to mate with at this facility. Female #079 died at the age of 927 days, while the other female was transferred to Macquarie University at more than 700 days of age. The two remaining animals (#M/310 and #R/311) were maintained in similar enclosures at James Cook University by Alan Horsup and Peter Spencer until their release or death (Table 2.2).

My irregular access to these orphaned animals coupled with the non-standard conditions under which they were reared made it impossible or inappropriate for me to use their bodily measurements for fine scale age determination (such as in Chapter 3). However, it seemed appropriate to use data from those orphans which were more frequently measured and whose history and rearing regime was better known, to help describe post-PY growth and sexual maturity (Chapter 4) and to calculate the rate of molar eruption and progression (Chapter 5).

2.4 Experimental ethics

This study was conducted under the guidelines of the James Cook University Experimentation Ethics Review Committee. Since the primary aims of this study were to investigate the survivorship and reproductive success of a free-living population of *P. assimilis*, all steps were taken to minimise stress on animals and their young. In some cases, these actions precluded the use of techniques that would provided greater insights. For example, I refrained from sexing pouch young less than ten days old as I believed that the additional intervention necessitated by this procedure would have jeopardised the primary aims of my study.

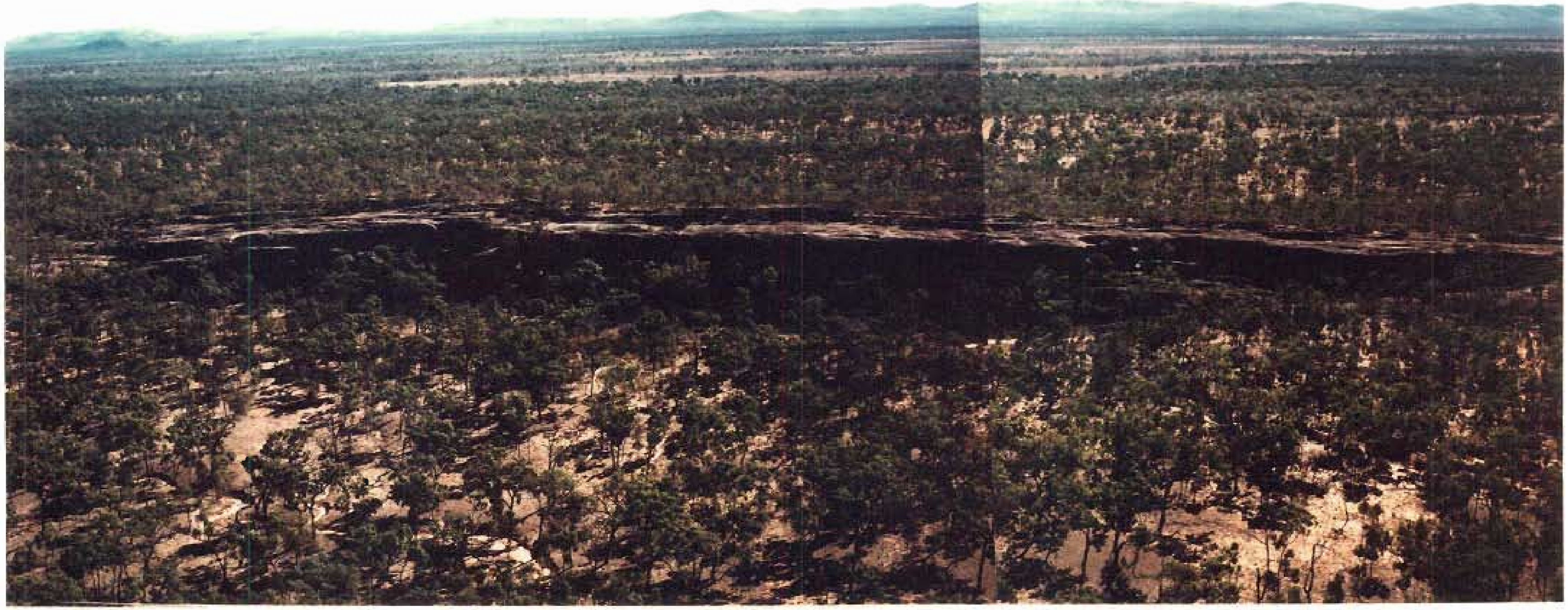
2.5 Statistical analysis

The database program DBASE III+ was used to store the data and for initial data manipulations. Statistix 3.0 and SAS were used for statistical analyses as appropriate. Non-standard biometrical techniques have been outlined in the Methods Sections of the relevant chapters.

Table 2.2 Identity and history of orphaned pouch young held in captivity at Townsville.

#	Sex	Location	Date orphaned	Age orphaned	Subsequent history	Eventual fate
079	F	Black Rock	17-2-87	173 days	Hand-reared until weaning, taken to Q.NPWS, and kept in enclosures there.	Died in captivity 12-3-89, age 927 days.
W	F	Townsville	<2-10-87	<293 days	Hand-reared until weaning by unknown people, eventually given to Q.NPWS, and kept in enclosures there.	Transferred to Macquarie University.
M/310	F	Black Rock	5-2-88	186 days	Hand-reared until weaning, and eventually kept in enclosures at JCUNQ.	Died in captivity 27-8-88, age 387 days.
R/311	M	Black Rock	30-1-88	183 days	Hand-reared until weaning, and eventually kept in enclosures at JCUNQ.	Released at Black Rock Dec 1988, found dead Jan 1989.

Figure 2.1 Black Rock, an isolated sandstone outcrop surrounded by open savanna woodland 265km WNW of Townsville in north eastern Australia.



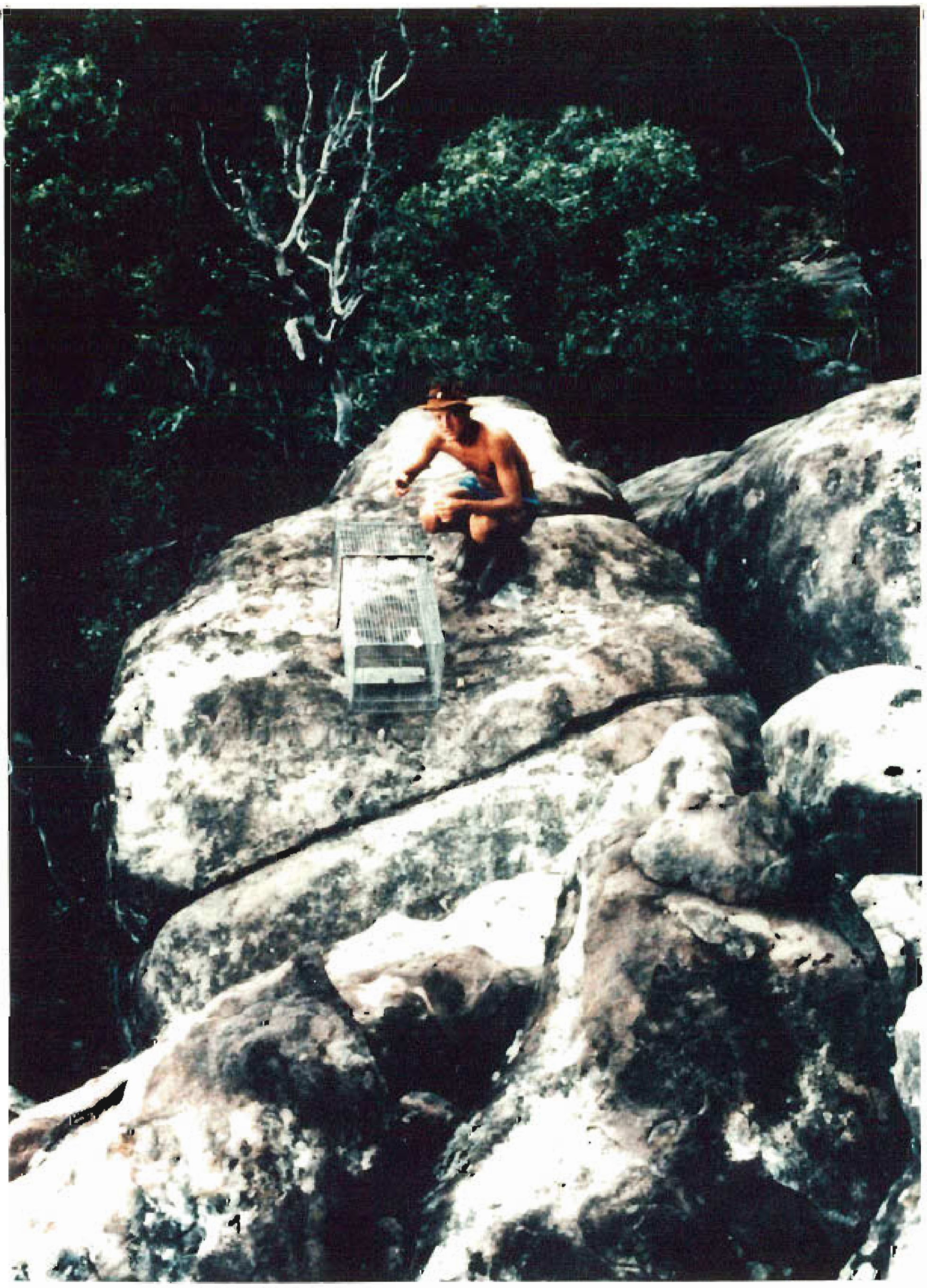
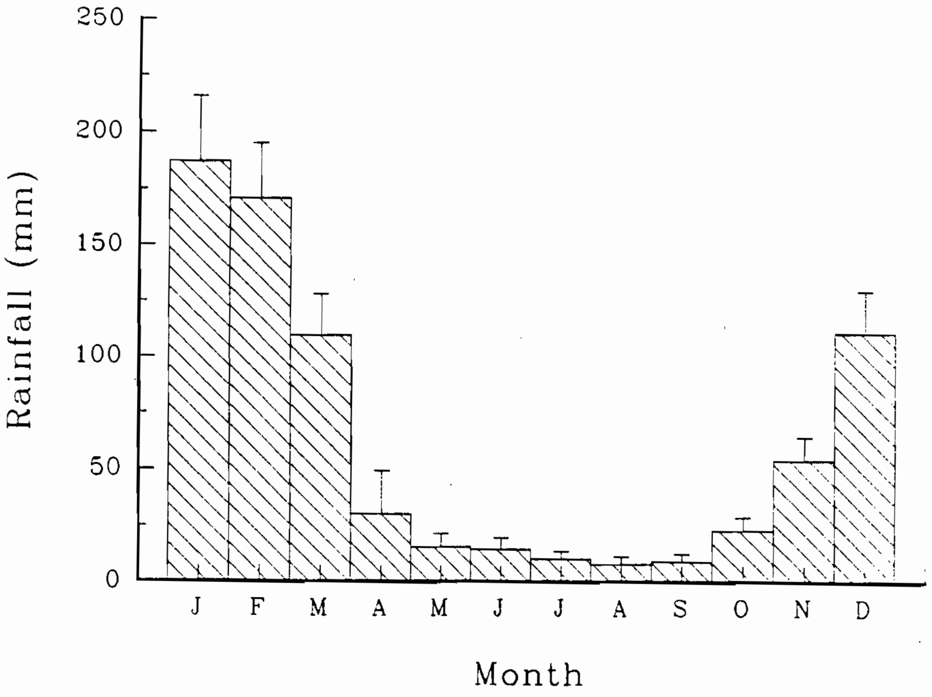
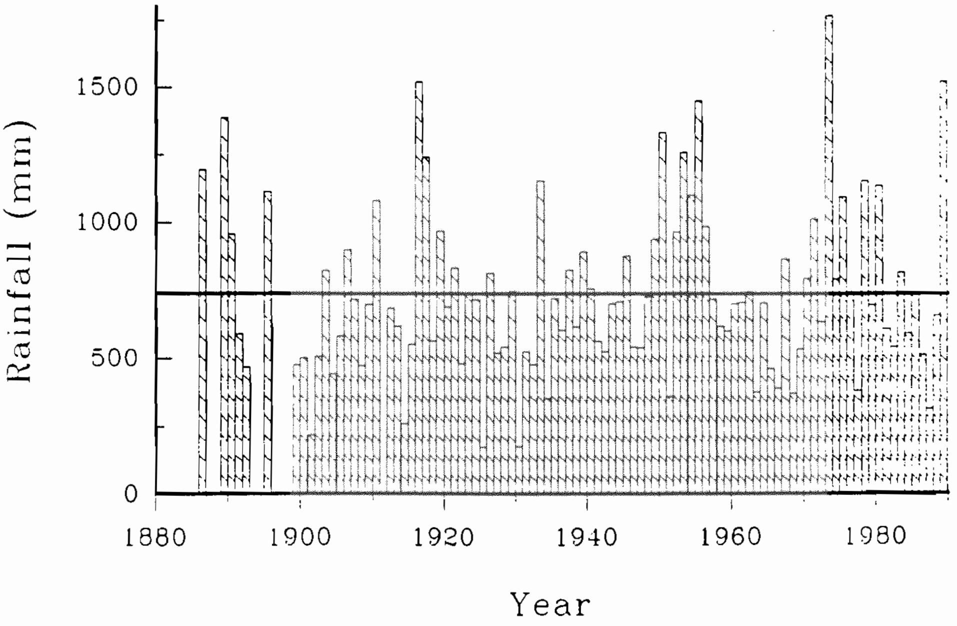


Figure 2.2 Assistant setting a trap on the main rock platform at Black Rock.

Figure 2.3a Average monthly rainfall (+95% confidence intervals) measured at 'Lyndhurst' (n=99 years).

Figure 2.3b Annual rainfall measured at 'Lyndhurst' since records began (n=99). Horizontal bar denotes the average annual rainfall (calculated for each year from July of the previous calendar year to June of that calendar year). No records are available for 1887, 1893-4 and 1896-8. Note the below average rainfall years in much of the late 1980's.


250
200
150
100
50
0
Rainfall (mm)
J
F
M
A
M
J
J
A
S
O
N
D
Month


1500
1000
500
0
Rainfall (mm)
1880
1900
1920
1940
1960
1980
Year

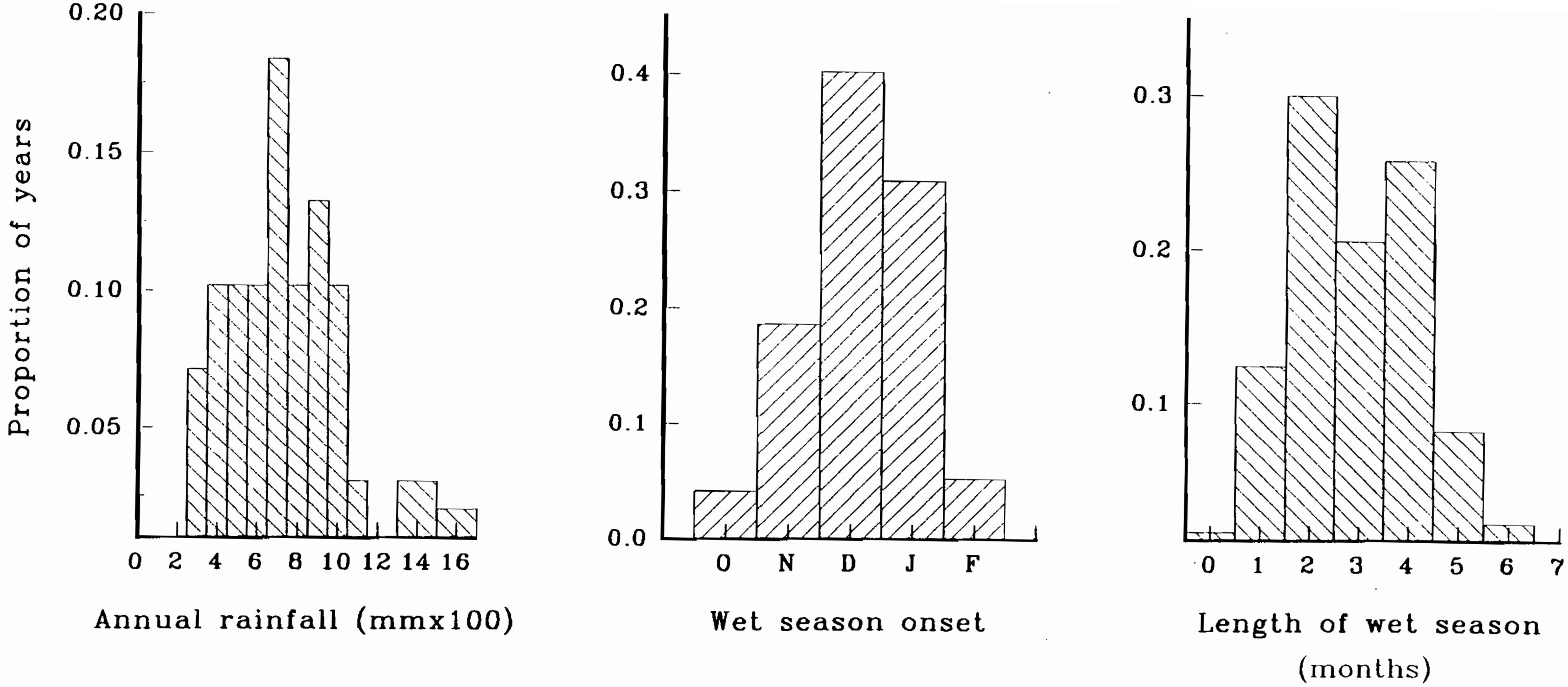


Figure 2.4 Variation in total annual rainfall and in the timing and length of the wet season at 'Lyndhurst', based on 99 years of records. The wet season is defined as starting in the first month to receive 75 mm rain and to average 75 mm per month over two successive months, and to continue as long as rainfall averages 75 mm per month over a two month period.

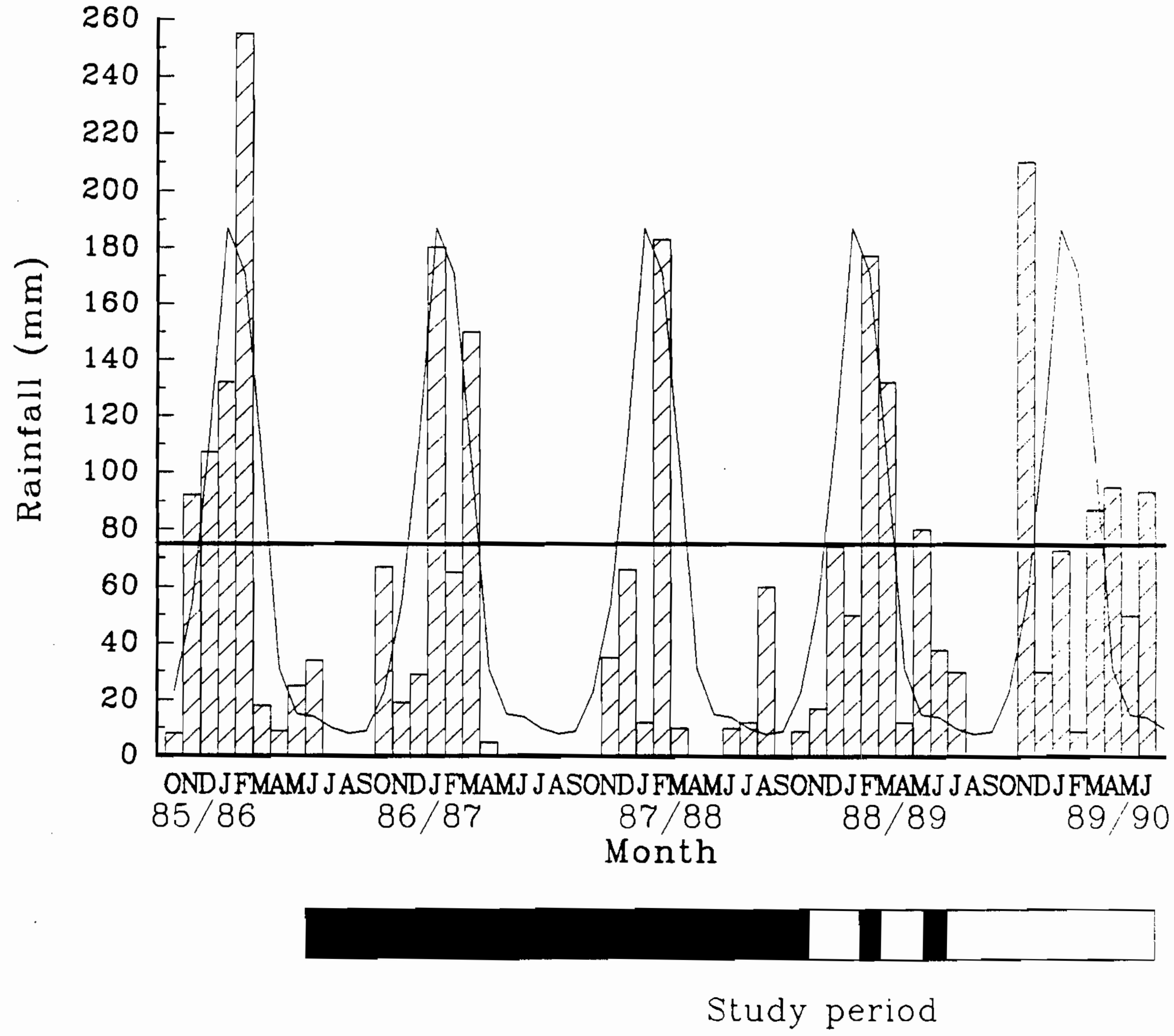


Figure 2.5 Monthly rainfall at Lyndhurst from just prior to, to just after, the trapping period. The solid curve represents the average monthly rainfall and the horizontal bar represents the mimimum amount of rainfall used to define the wet season. The bar below the graph represents the entire study period with the main study period in solid fill (see Section 2.2.1).

Figure 2.6 Monthly rainfall at Lyndhurst for the past 20 years. The solid curve represents the average monthly rainfall and, as for Figure 2.3b, the study period is represented by the bar below the graph. Note the generally greater rainfall during the 1970's *c.f.* the 1980's. Year relates to that of January of the corresponding wet season.

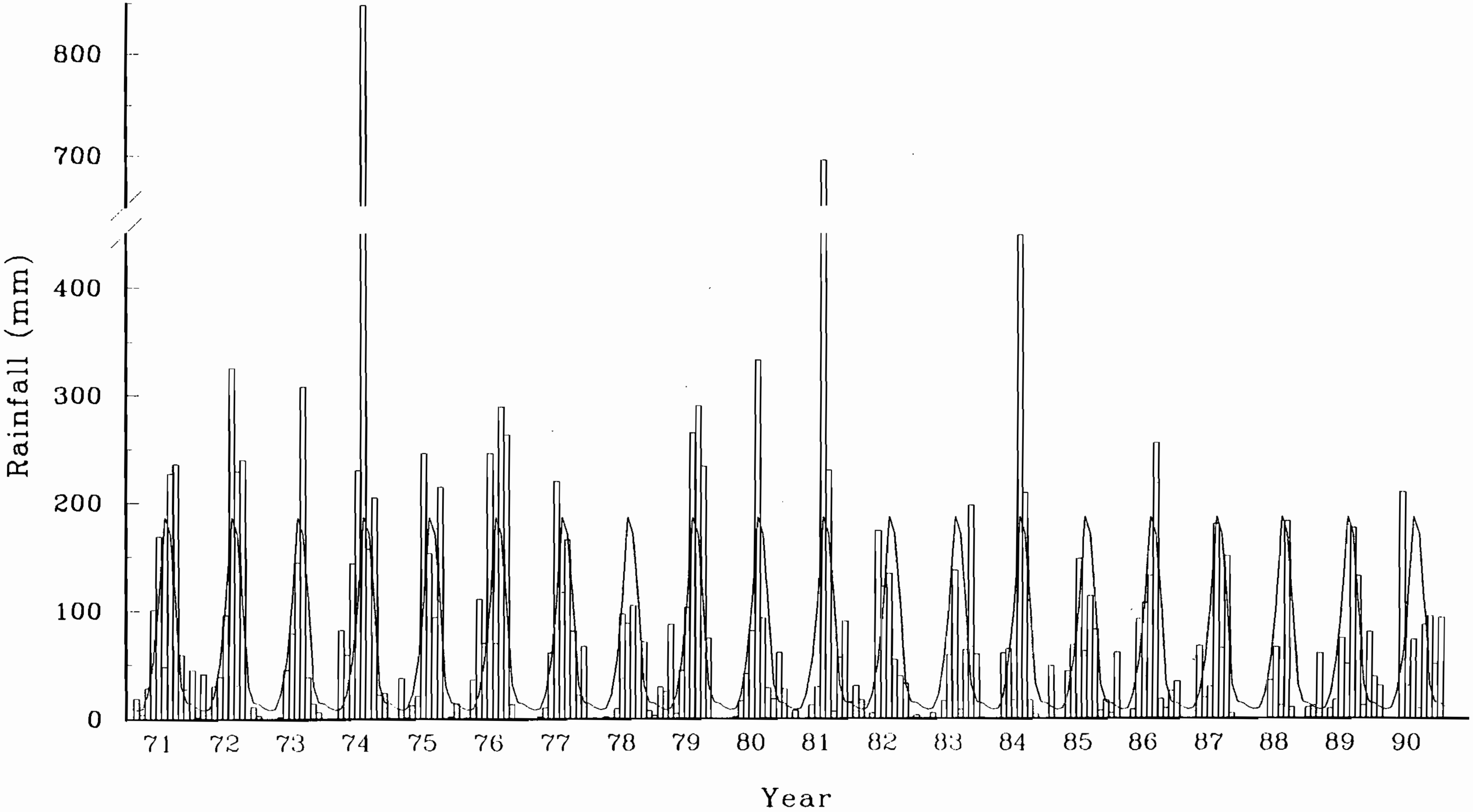

Rainfall (mm)
0
100
200
300
400
700
800
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
Year

Figure 2.7 Vegetation at the base of the main rock wallaby colony at 'Black Rock' (a) at the end of the early dry season (August 1987) and (b) at the end of the wet season (March 1986).

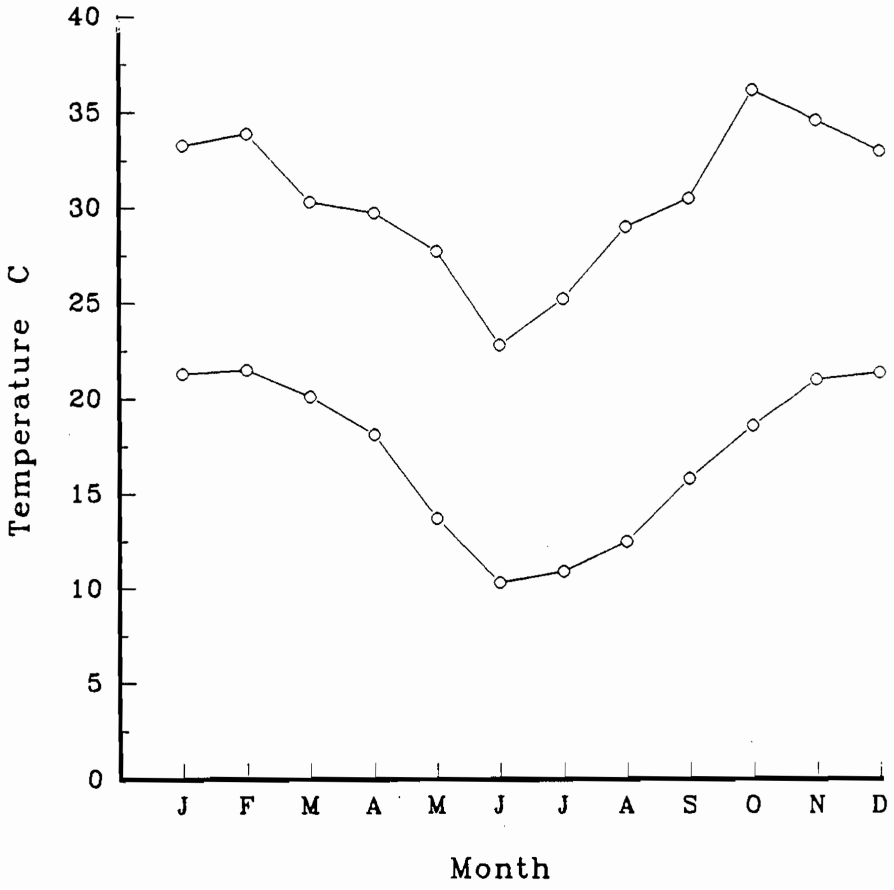


Figure 2.8 Minimum and maximum mean monthly temperatures recorded at 'Black Rock' when field workers were present between January 1986 and December 1989.

Chapter 3

Development and growth of pouch young

3.1 Introduction

Growth, including the rate of growth and development of morphological characters, is a fundamental life history trait and is included in most major theoretical treatments of life history. For example, theories invoking finite resource allocation, sexual selection, sexual and reproductive strategies, and maternal investment, all use growth in their models (see Stearns 1992 for review). Growth rates are also an important component of comparative studies.

With the exception of peramelids, the growth rates of marsupials are now considered slow compared with those of eutherians (Lee and Cockburn 1985, Cockburn and Johnson 1988). It is currently argued that this difference in growth rates reflects different strategies of reproduction in the two groups, with eutherians investing relatively more energy in gestation than lactation (gestation-specialists) and marsupials more energy in lactation than gestation (lactation specialists) (e.g. Rose 1987, Cockburn and Johnson 1988). Growth rates can also be used to compare other ecological processes such as maternal investment between individuals and between taxa (e.g. Russell 1982, Lee and Cockburn 1985).

While growth *per se* is a continuous phenomenon, most studies of age estimation and growth in macropodids can be divided into two categories: those of (1) pouch young (PY), and (2) adults (or less commonly, post-pouch young). This dichotomy is largely due to the underlying reasons for the study (e.g. use in the management of commercially culled populations) and the limitations of the techniques and time involved (e.g. studies of age determination of captive PY are more common than those on adults of the same species, due in part to the length of time involved, and different techniques are usually employed to determine the age of these two different age classes). The very few studies which have examined whole-of-life growth in macropodids have usually been based on captive colonies (e.g. Maynes 1976; Poole, Carpenter and Wood 1982a,b; Rose 1989).

This study was originally conceived to develop methods to determine the age of individual animals and (hopefully) to model whole-of-life growth. However, the lack of young surviving and entering the adult population (see Chapters 4 and 8) made a thorough study of whole-of-life growth impossible. Hence the age determination and growth of PY and adults have been treated separately (this chapter and Chapter 5 respectively). The limited data on post-PY and whole-of-life growth has been considered in the context of the data on sexual maturity and sexual dimorphism in Chapter 4.

Most knowledge of PY growth in macropodoids has been obtained from captive populations in which births could be observed, young measured at known age intervals and growth curves constructed (e.g. Shield and Woolley 1961; Sharman and Pilton 1964; Kirkpatrick 1965a; Kirkpatrick and Johnson 1969; Murphy and Smith 1970; Johnson 1979; Rose and McCartney 1982; Poole, Merchant, Carpenter and Calaby 1985). Lengths of head, pes and tail are the commonest measurements used in these studies; lengths of leg, arm, ear and body weight have also been included in some studies. These measurements vary in the accuracy with which they can be used to estimate absolute age. Head lengths are the best estimators, and lengths of pes, arm, tail and ear, and body weight are increasingly inaccurate estimators of PY age (Poole *et al.* 1982a). Weight is also a difficult measurement for smaller PY due to their permanent attachment to the mother's teat. Despite this, weight is useful for taxonomic purposes as comparisons can be made between animals of different form (Russell 1982).

Early researchers cite a number of common problems in modelling the growth curves of PY of macropodids. Individual variation in PY growth led Shield and Woolley (1961) to suggest that a large number of PY should be measured to allow any model to be representative of the population. This individual variation in PY growth is evidenced not only by such studies (e.g. Sadleir 1963, Sharman and Pilton 1964), but also in the variable length of time to permanent exit from the pouch (PEP) of different PY from the same species. Earlier researchers (e.g. Ealey 1967, Murphy and Smith 1970) also lacked access to the statistical techniques which deal with repeated measurements of the same individual and were therefore concerned about the statistical independence of their analysis of the data.

A further problem has been the inability to characterise the growth and development of PY from free-living populations as most models need the growth of individuals of known-age to be monitored at short and regular intervals (e.g. weekly). Sharman, Frith and Calaby (1964) were amongst the first to recognise this problem in macropodids. They assumed that the growth curves of wild and captive PY should be similar because the macropodid pouch provides a stable and constant environment so that growth in dependent PY should not be affected by outside factors. While this is the simplest scenario, there is little to substantiate this assumption. Wood, Poole and Carpenter (1983) reported differences in body proportions between wild *M. giganteus* and captive animals of mixed origins. Furthermore, growth rates of wild macropodoids are considered to be less than those of captives, perhaps because of poorer nutritional conditions in the wild (Ealey 1967). Taylor and Rose (1987) demonstrated that wild PY of *Bettongia gaimardi* had a lower body weight in relation to skeletal size than PY from captive populations. Despite these results, most workers have aged wild PY on the basis of growth data obtained from PY bred in captivity (e.g. Sharman and Pilton 1964, Shield 1968, Inns 1982a).

The problems discussed above occur within each study to a greater or lesser extent and have been acknowledged by individual researchers as such. A review of the literature reveals a much more fundamental problem - the inability to compare between studies. This problem largely stems from the use of empirical models. The models used have mostly been linear (or quadratic) regression models which have no theoretical basis and cannot be generalised between taxa. This difficulty was noted by Lee and Cockburn (1985) who called for a greater use of theoretical growth curves to allow comparisons between studies.

While organisms are not constrained to grow according to theoretical curves developed by scientists, five theoretical growth curves have been commonly used to describe the growth of plants and animals. These are the exponential, power, Bertalanffy, Gompertz, and logistic curves (Kaufmann 1981). The parameters of such theoretical functions lend themselves to a natural interpretation and therefore may provide insight into the underlying processes governing growth. For example, the general form of the logistic function, which is often suitable for modelling sigmoid growth, can be modelled in such a way that single parameters represent initial size, relative growth rate and maximum size.

The particular theoretical curve used is dependent on the shape of the plotted data and the underlying assumptions of each curve. The exponential and power curves are basically concave (either up or down) in shape and both assume that size increases with time, and growth is indeterminate (Kaufmann 1981). However, the rate of which size increases also increases with time in the exponential curve. This rate is more variable in the power curve and hence it is used to describe more gradual patterns of growth than the exponential curve. Gompertz and logistic curves are sigmoid in shape and assume growth is asymptotic. While the logistic curve is symmetrical about an inflection point, the Gompertz curve is not and the asymptote is approached more gradually than it would be in a similar logistic curve (Kaufmann 1981). The pattern of growth (as evidenced by body weight) for macropodids appear most nearly described by the Gompertz models. The Bertalanffy curve is also asymptotic but varies from the logistic in that there is no inflection point and the rate of increase is *inversely* related to size (Kaufmann 1981). The early phase of this model does not often accurately describe growth in organisms as the highest rates of increase occur at the smallest sizes.

The advantage of using curves of the same functional form to model the growth of an organism is the ability to compare growth between taxa and to provide a pattern against which departures from the typical condition can be assessed (Cockburn and Johnson 1988). While noting how much more could be done in this area, Lee and Cockburn (1985) used published data on birth weights to demonstrate the usefulness of such general curves in comparing the growth rates of marsupials with those of eutherians and birds. This ability is also basic to the comparison of the growth rates of wild and captive PY.

The aim of this study was to model the growth of PY of *P. assimilis* from birth until weaning so that the resultant model could be used for age estimation of such young. Furthermore, it seemed crucial that some of the problems and methodological confusion outlined above, be addressed, for this species at least. For these reasons head and pes length (as two of the commonest and most accurate measurements for age estimation) and theoretical growth curves were used. I also tested the assumption of similarity of wild and captive PY growth rates by comparing the growth of PY in wild rock wallabies from Black Rock with that from animals born and reared at Macquarie University, Sydney monitored by Robert Close and Jane Bell. The timing of developmental stages of PY at Black Rock was also documented.

3.2 Methods

3.2.1 *Wild rock wallabies*

PY were measured and weighed as described in Chapter 2.3.3. In the description of the first appearance of morphological characteristics, all PY (n=73) which were caught on or before June 1989 were included. Additional data collected up to June 1990 from the 15 core females (see Chapters 2.2.1 and 8.2.1) were used to calculate time to permanent exit from the pouch and to weaning. In the analysis of growth rates, it was necessary to use only those PY which had been caught regularly up to or before June 1989. It was decided (for statistical reasons) to use only those PY which had been caught on at least four occasions. In practice, this subset of the data included only six PY who were caught on at least five trips and these were used in the calculation of growth curves for wild animals (Appendix 4). There were equal numbers of females and males in this subset. More critically, these PY were from only four mothers (Tattoo #s: 001, 008, 010, and 107) with two PY measured from each of two females (008 and 010).

3.2.2 *Captive animals*

The captive PY used to describe PY growth in this chapter were reared in a captive colony which was established at Macquarie University (over 1600km south of Black Rock) and maintained by Dr. Robert Close and Ms Jane Bell. This colony was started using animals trapped within 100km of each other (Close and Bell 1990) and within 150km of the Black Rock study site. The animals which were studied were from the three chromosomal races that Calaby and Richardson (1988) include in *P. assimilis* and their hybrids (and that Eldridge and Close (1992) have since proposed for specific status, see Chapter 1.3). Measurements were taken at 2-weekly intervals as per Sharman *et al.* (1964).

3.2.3 *Growth curves*

Appropriate theoretical growth curves were fitted to the measurements of head and pes lengths by non-linear estimation routines (NLIN, SAS Institute Inc. 1987) which allowed for repeated measures data. A modified exponential curve was most suitable for head length. This curve initially has the most rapid growth phase followed by a deceleration of growth to a final asymptote. For pes length the growth models took the form of Gompertz curves, which are sigmoidal in nature, with a slow initial growth phase followed by accelerated growth in the mid-phase and finally slowing to an asymptote.

Approximate standard errors were then calculated on the basis of maximum likelihood theory (Cox and Hinkley 1979). Both composite and individual growth curves were fitted, leading to identification of individual differences in terms of the model parameters. Comparisons between individual curves within a group and between composite curves were based on asymptotic *F*-tests in a manner analogous to *F*-tests for nested linear regression models. Curves generated from Close and Bell's (1990) raw data from captive animals were compared with the corresponding curves from the wild population as Close and Bell (1990) had fitted linear regressions to the PY head and pes measurements. The mathematically most correct curves were fitted in all cases to aid comparisons. Thus the asymptotes are those calculated by extrapolating the data and as if PY growth continued at the same rate until adulthood.

Assistance in the statistical analysis presented in this chapter was given by Glenn D'eath of the School of Tropical Veterinary Science, James Cook University.

3.3 Results

3.3.1 *Growth*

3.3.1.1 Data from captive animals at Macquarie University

Data were available from each of five PY for which there was an extensive series of observations (n=7-22) for head and pes length and whose birth dates were known. Shorter sets of observations were available from another 20 animals. Data from these latter animals were used to assess the accuracy of age predictions from the composite models developed from the more extensive set of measures.

(i) *Head size*

A modified exponential equation was used to describe head growth, and takes the form:

$$h_{ij} = \alpha_i \left(1 - \exp -(\delta_i + \beta_i t_{ij})\right) + \epsilon_{ij} \qquad (3.1)$$

where :

the subscripts i and j denote the ith animal and the jth observation on that animal;

h_{ij} denotes head length in millimetres at age t_{ij} (days);

α_i is the upper asymptote in millimetres;

δ_i reflects the head length at birth;

β_i represents growth rate as a proportion of asymptotic size; and

$\epsilon_{ij} \sim N(0, \sigma^2)$ represents random variation about the growth curve.

Table 3.1. The parameter estimates of the individual and composite growth curves for head length (mm) of PY of captive *P. assimilis* (from Close and Bell 1990, see Methods).

Animal		Asymptote		Birth size		Growth rate		MSE^B
#	$(n)^A$	α	(se)	δ	(se)	β	(se)	
1	(22)	233.7	(47.6)	0.0257	(0.0032)	0.00197	(0.00053)	1.516
2	(20)	151.2	(20.5)	0.0429	(0.0047)	0.00302	(0.00059)	1.470
4	(7)	215.3	(58.7)	0.0332	(0.0079)	0.00199	(0.00064)	0.488
10	(14)	133.0	(10.9)	0.0566	(0.0038)	0.00347	(0.00043)	0.887
11	(10)	315.5	(62.1)	0.0242	(0.0465)	0.00122	(0.00260)	0.592
All	(73)	175.0	(16.7)	0.0396	(0.0028)	0.00252	(0.00032)	2.380

^{A} number of observations
^{B} Mean Square Error

An individual growth curve was fitted for each animal. The fits assessed by residual plots were satisfactory. A single curve of the same functional form was fitted to the pooled data for the five animals (Table 3.1, Figure 3.1*a*).

The individual curves were significantly different (F=9.52; df=12,58; P<0.001) from the composite curve, indicating individual growth differences. The asymptotes of the individual curves were significantly different (F=3.70; df=4,58; P=0.01). There were also significant differences between the individual growth rate parameters (F=2.68; df=4,58; P=0.04), and between the individual birth size parameters (F=11.55; df=4,58; P<0.001).

Given the absence of data from older (i.e. post-PY) animals, the asymptotes are estimated with a low degree of precision (i.e. S.D. of predicted - actual age is high) (see Chapter 3.3.1.1 iii). Tests for differences in asymptotes are based on the assumption that the functional form of the model is appropriate for the whole life-span of the animal. This assumption and the absence of data on older animals mean that estimates of, and conclusions about, asymptotes are considered tentative.

(ii) *Pes size*

The asymmetrical sigmoid nature of the curve suggests a Gompertz model (Gilchrist 1984), and takes the form:

$$p_{ij} = \alpha_i \exp (- \exp (\delta_i - \beta_i t_{ij})) + \epsilon_{ij} \qquad (3.2)$$

where :

the subscripts i and j denote the ith animal and the jth observation on the animal;

p_{ij} denotes pes length in millimetres at age t_{ij} (days);

α_i is the upper asymptote in millimetres;

δ_i reflects pes length at birth;

β_i represents growth rate as a proportion of asymptotic size;

ϵ_{ij} $\sim N(0,\sigma^2)$ represents random variation about the growth curve.

As for head length, the individual curves differed significantly from the composite curve (F=6.35; df=16,43; P<0.001) (Table 3.2). There were no significant differences among birth size parameters (F=0.77; df=4,43;

Table 3.2. The parameter estimates of the individual and composite growth curves for pes length (mm) of PY of captive *P. assimilis* (from Close and Bell 1990, see Methods).

Animal		Asymptote		Birth size		Growth rate		MSE^B
#	$(n)^A$	α	(se)	δ	(se)	β	(se)	
1	(22)	161.8	(14.0)	1.3583	(0.0387)	0.01118	(0.00104)	5.403
2	(20)	138.4	(8.95)	1.3356	(0.0450)	0.01209	(0.00100)	5.037
4	(7)	241.9	(68.4)	1.3699	(0.0459)	0.00818	(0.00136)	1.507
10	(14)	121.6	(5.40)	1.2998	(0.0397)	0.01356	(0.00095)	3.977
11	(10)	55.94	(6.90)	1.1026	(0.0219)	0.01957	(0.00224)	0.174
All	(73)	137.7	(5.15)	1.3410	(0.0242)	0.01239	(0.00057)	7.344

[A] number of observations
[B] Mean Square Error

P=0.551), or among growth rate parameters (*F*=1.40; df=8,43; *P*=0.224). There were significant differences among asymptote parameters (*F*=5.73; df=4,43; *P*=0.001).

(iii) *Age prediction*

By means of the composite curves for head size and for pes size, the ages of the animals of known age were predicted separately from single measurements of head (n=39) and pes (n=26). This was done by rearranging the equations (3.1) and (3.2) to express age (t_{ij}) as a function of head size (and pes size). The accuracy of prediction decreased with increasing age in both head length and pes length (Figure 3.2).

The assumption in the modelling has been that appropriate theoretical curves are more suitable than standard regression models, although Rose (1989) suggested that linear (or perhaps quadratic) regression models are adequate for

Table 3.3. Comparison of age estimates based on head and pes lengths of PY of captive *P. assimilis* (from Close and Bell 1990, see Methods) using non-linear and simple linear regression models on the composite data.

	Predicted age minus actual age (days)		
	Bias	s.d.	Root MSE[A]
Head length			
Non-linear Model	0.647	3.093	3.160
Simple Linear Regression Model	-1.246	5.224	5.371
Pes length			
Non-linear Model	3.471	6.706	7.551
Simple Linear Regression Model	7.981	6.541	10.32

[A] Mean Square Error

age prediction. To test this, a simple linear regression model was compared to the above non-linear model (Equation 3.1). For each model, the mean of the differences between each estimated and known age, is a measure of the bias in the age estimates (Hines and Montgomery 1980). The standard deviation of these differences is an index of the repeatability of the age estimates, and the square root of the mean square error (M.S.E.) is an index of the accuracy (average closeness of the estimates to the true value) (Figure 3.3). The results of the comparisons between the linear and the non-linear growth curves (Table 3.3, Figure 3.2) indicate that:

(1) age predictions based on head size are less biased, more repeatable and more accurate than those based on pes size for both linear and non-linear models;

(2) with either head or pes size, the non-linear model gives age predictions which are less biased, more repeatable and more accurate than the linear model;

(3) the accuracy of predictions based on non-linear models depends on age, the most accurate predictions corresponding to young animals;

(4) the accuracy of predictions using the linear models depends weakly on age for head size but not for pes size [due to the considerable biases in prediction of the linear model for young ages (Figure 3.2)].

If the whole series of head measurements for each individual was used to predict its age, then the bias decreased and the accuracy improved, provided that the measures corresponding to younger ages had an increased weighting. The improvement by comparison with use of the earliest head observation of the series was small and variable. The combined use of head and pes age estimates failed to improve on the age estimates based on head size alone.

3.3.1.2 *Comparison between growth curves for captive and wild animals.*

Head and pes lengths for six wild animals with a series of at least five measurements for both head size and pes, were compared with the corresponding data for captive animals.

(i) *Head growth*

The model given by Equation 3.1 was used to model head growth where t_{ij} now indicates the time since first capture and δ_i reflects the size at first capture.

Table 3.4. The parameter estimates of composite growth curves for head and pes lengths (mm) of PY of captive *P. assimilis* (data from Close and Bell 1990, see Methods) and wild *P. assimilis*.

Group	Asymptote		Growth rate		Birth size[A]		MSE[B]
	α	(se)	β	(se)	δ	(se)	
<u>Head</u>							
Captive	175.0	(16.7)	0.00252	(0.00032)	-0.0396	(0.0028)	2.380
Wild	151.7	(22.8)	0.00286	(0.00060)	na[A]		1.327
<u>Pes</u>							
Captive	137.7	(5.15)	0.01239	(0.00057)	1.341	(0.024)	7.344
Wild	152.9	(15.5)	0.01074	(0.00104)	na[A]		5.995

[A] na = not applicable due to unknown ages

[B] MSE = Mean Square Error

The composite growth curves for captive and wild animals were compared for differences in the asymptote and growth parameters. The parameter estimates for the composite curves for captive and wild animals are presented in Table 3.4. There were no significant differences between asymptotes (t=0.82, df=93, P=0.410) or between growth parameters (t=-0.529, df=93, P=0.598) (Figure 3.4).

(ii) *Pes growth*

A satisfactory fit for the growth data from the wild animals was obtained using the Gompertz curve:

$$p_{ij} \;=\; \alpha_i \;\exp\left(- \exp\left(\delta_i \; - \beta_i \, t_{ij} \right)\right) \;+\; \epsilon_{ij},$$

where the parameters are as in Equation 3.2 except that (as for head length) t_{ij} indicates time since first capture and δ_i reflects the size at first capture. There were no significant differences between the composite curves for captive and wild *P. assimilis* for either asymptotes (t=-0.93, df=83, P=0.352) or growth rate parameters (t=-1.39, df=83, P=0.164) (Table 3.4, Figure 3.5).

The composite curves for captive and wild animals, together with the individual data, are shown in Figures 3.1*a-c* and 3.4 for head growth and Figures 3.1*d-f* and 3.5 for pes growth. The ages for the wild animals at first measurement were estimated from the composite curves, assuming a birth size equal to that of the average birth size of captive animals.

3.3.1.3 Estimating the age of wild animals

The ages of the wild animals were estimated from both head and pes measurements by means of Equations 3.1 and 3.2, by assuming the head and pes sizes at birth to be the same as those for captive animals. Given that the exact ages of the wild animals were unknown, there is no direct check on the accuracy of these age estimates. However, many animals were captured and remeasured on several occasions, allowing the comparison of a series of age estimates from single animals. If the series of age estimates for a single animal is repeatable, then the difference between the estimated age and the number of days since the first observation should be constant. The standard deviation of such differences can be taken as an index of the repeatability of age estimates (Hines and Montgomery 1980). For age estimates based on head size the standard deviation was 4.10 days (df=81); for those based on pes size the standard deviation was 4.84 days (df=156). The age estimates based on head and pes size for each individual were highly correlated (r^2=0.991, df=77, P<0.001) with no evidence of systematic deviations from linearity. The average of age estimates based on both head and pes measures and weighted inversely on their standard deviations marginally improved the repeatability (sd=3.98 days, df=77).

3.3.2 *Developmental stages of pouch life*

Observations made on the various developmental characteristics of the PY from Black Rock were hindered by the time between repeated measurements of the same PY (≥ one month). The pattern of development is presented diagrammatically using age determination techniques as outlined above (Figure 3.6). The eyes opened at 124 days (range 96-140 days, n=23). PY were no longer permanently attached to the teat by 110-143 days (n=11). PEP occurred at a mean age of 201 days (range 180-231 days, n=25). For those five wild young which I know survived past weaning, weaning occurred at approximately 267 (♀), 291 (♂), 300 (♂), 385 (♂) and 387 (♂) days. These young-at-foot (YAF) had suckled for 92-179 days after PEP. The two animals which suckled the longest were siblings (Female #076, Chapter 8).

The timing of the eruption of the first incisor was chosen to test for sexual dimorphism in growth as it is a strongly definable characteristic occurring late in pouch life. There was no difference between the sexes in the timing of the eruption of this tooth (t=-0.69, df=7, P=0.514) suggesting a lack of sexual dimorphism in at least the development of this dental characteristic during pouch life.

3.4 Discussion

3.4.1 *Developmental stages*

The pattern of development of PY of *P. assimilis* follows that of other macropods with the timing of the developmental stages confirming the close phylogenetic relationship between *P. assimilis* and *P. inornata* (these species are also morphologically indistinguishable (Sharman and Maynes 1983b)). The pouches of the captive *P. inornata* studied by Johnson (1979) were inspected daily and so his estimates of the duration of the various stages are more precise than mine. PY of *P. inornata* become detached from the teat at a mean age of 127 days (range: 119-138, n=7) and emerge permanently from the pouch (PEP) at an average of 204 days (range: 189-227 days, n=6). Despite my relatively infrequent measurements, the ages observed in this study are similar to those observed by Johnson (1979) for captive *P. inornata*. However, the evicted wild young of *P. assimilis* apparently suckle for longer than captive *P. inornata* (92-179 *cf* 75-90 days). This may reflect better conditions in captivity such that young are ready for independence earlier. However, I restricted my data to young for which I had lactational data and which I knew survived at least one month after weaning. This meant I was sure that I was only sampling young which were definitely weaned and did not disappear for other reasons such as premature death. This approach almost certainly biases the data towards young which had longer rather than shorter lengths of time between PEP and weaning. Differential investment by mothers is also possible, however, data are too limited and qualified to substantiate such speculation. For example, the monthly field trips meant that ages individual young at weaning and PEP were calculated by back-dating from the birth of the subsequent young or when lactation ceased (see Chapter 8.2.2). This meant that I could not compare measurements (e.g. weight) of young at PEP or weaning to test if there was differential investment in young.

3.4.2 *Growth*

3.4.2.1 Evaluation of Methodology

For both head and pes, the growth models developed here are an improvement over the corresponding linear models proposed by most previous workers (e.g. Rose and McCartney 1982, Rose 1989) (Figure 3.2, Table 3.3). These methods can provide general models for parameterisation of other macropodoid growth curves. This approach would help interspecific comparisons as suggested by Lee and Cockburn (1985).

Once a general curve is fitted for PY of a species, one measurement of the head size of a PY is sufficient to estimate its age. This simplifies data collection as the use of later head size measures or the use of measures of several body parts does not substantially improve the accuracy of age estimates. The accuracy of this estimation decreases as the PY gets larger (Figure 3.2). As other workers have observed for other macropodoids, these data suggest that, for *P. assimilis*, head length is a better estimator of PY age than pes length. For example, Poole *et al.* (1985) also found head length to be a more reliable estimator of the age of *P. xanthopus* than pes length.

Given that the data span only the first 250 days of development (Figure 3.1), the asymptotic (i.e. adult) head size is estimated very imprecisely and extrapolation of the model beyond pouch life could give erroneous results. The following examples highlight the danger of using these curves to estimate the age of post-PY animals: the upper asymptote for head length from Equation 3.1 is 151.7 ± 22.8 mm for wild animals and 175.0 ± 16.7 mm for captive animals, whereas the head lengths of adult *P. assimilis* measured at this colony range from 95.3 mm to 116.0 mm (Chapter 4). Additionally, the 2.5 fold difference between captive individuals in the estimates of asymptotic head length (Table 3.1), is orders of magnitude greater than actually occurs in adult animals (Chapter 4). These examples strongly suggest that the specific growth models developed here are indeed inappropriate for later development. Interestingly, as the actual whole-of-life asymptotic measurements are much smaller than those predicted from growth during pouch life, growth must also slow substantially after pouch exit. This is the marsupial pattern (Cockburn and Johnson 1988).

Sexual dimorphism is common in adult macropodids (Jarman 1989). I did not test for it in the PY growth curves for either the head or pes of wild or captive animals. The five captive animals used to develop the composite curve included only one female, and the six wild animals which were extensively measured included three females. These two samples are too small to comment with any conviction on sexual dimorphism in PY although I found no sexual dimorphism in the age of eruption of the first upper incisor, which occurs during late pouch life. Poole *et al.* (1982a) found no sexual dimorphism in the PY of *M. giganteus* (which exhibits marked adult sexual dimorphism in size). As sexual dimorphism in adults of *P. assimilis* is much less than in *M. giganteus* (Chapter 4), and both sexes of the young of *P. xanthopus* maintain similar growth rates whilst in the pouch (Poole *et al.* 1985), it seems unlikely that PY of *P. assimilis* would exhibit sexual dimorphism.

3.4.2.2 Differences between growth curves

There were significant differences between individual growth curves for both wild and captive *P. assimilis* (Figure 3.1). As these differences were present in both groups of PY, it is unlikely that they are due solely to an effect of the different chromosomal races present in the captive colony or to nutritional deprivation. A similar result was obtained for captive *M. giganteus* by Poole *et al.* (1982a). Although Sharman *et al.* (1964) did not calculate individual growth curves, examination of their graphs shows clear differences among individual PY in the growth rates of head and pes. It remains to be seen whether this variation in individual growth is intrinsic or can be explained by other factors such as the timing of birth or maternal characteristics. The sample discussed here is biased towards PY which survived but not towards mothers who were more successful in rearing PY (Chapter 8). The data are too limited to show whether there is any relationship between reproductive success of mother and growth rates of their PY.

The differences between the composite curves for wild and captive animals were non-significant for both head and pes measurements (Figures 3.4, 3.5), even though the measurements at Black Rock were taken during a prolonged drought which was expected to exacerbate any differences. This result supports the use of growth curves from captive animals as a means for estimating the age of wild PY. My comparisons are based on relatively small numbers of animals, so that the power of the associated tests is relatively low. Larger samples (both in the number and age span of the animals) are needed before definitive conclusions can be drawn. Close and Bell (1990) found that PY from both captive and wild-bred adult *P. assimilis* had similar growth rates for both head and pes. Similarly, Shield and Woolley (1961) found no differences between the relative growth rates of different body parts of wild and captive quokkas.

The inflection point in the model of pes growth occurs at about 120 days (Figure 3.1*d*). This age also approximately corresponds to the time when the PY is no longer permanently attached to the teat (110-143 days, n=11) and as such, a time of major change in lactation phases (Tyndale-Biscoe and Janssens 1988). *P. inornata*, a closely related species (Briscoe *et al.* 1982), changes its suckling pattern at a mean age of 127 days (Johnson 1979).

3.4.2.3 Comparison of growth rates with those of other mammals

The only published data for macropodoids using fitted growth models is summarised in Lee and Cockburn (1985), Cockburn and Johnson (1988) and Lee and Ward (1989). Weight was the only parameter fitted (which allows for comparisons between different body forms and hence higher taxonomic levels) and I did not have sufficient weight data to fit such a curve. However, these graphs show that, when corrected for asymptotic body mass, marsupials generally have a slower rate of growth (β) than eutherians. Furthermore the relationship for macropodoids is strongly linear and generally lies just below the regression line for all marsupials indicating that macropodoids grow even slower than marsupials as a whole (Lee and Cockburn 1985, Lee and Ward 1989). One rock wallaby, *Petrogale* (*Peradorcas*) *concinna*, was included in these analyses and followed the general macropodoid pattern, having a slower growth rate than other similar sized marsupials such as *Perameles nasuta* and *Trichosurus vulpecula*.

Since there is generally a strong relationship between length and mass, it seems likely that there will also be a strong relationship between the growth rates of head and pes measurements and of body mass. If as described above, the growth in body weight for rock wallabies is slow relative to other marsupials of similar size, we might expect growth in linear measurements to also be relatively slow. Hence the growth rates for head and pes length calculated in this study (0.002 and 0.012 respectively) are expected to be typical of a macropodoid of its size and relatively slow in comparison with other marsupials. However, no more direct comparisons can be made with other macropodoids or indeed other marsupials until the growth of head and pes of the PY of other species is described using these growth models.

3.4.3 *Summary*

In this chapter I have described models for the growth of head and pes of captive and wild PY of *P. assimilis*. The models fitted allow the age of PY of this species to be calculated from measurements of head or pes. In describing models for growth of this species I have attempted, with varying degrees of success, to address the common problems noted by other workers.

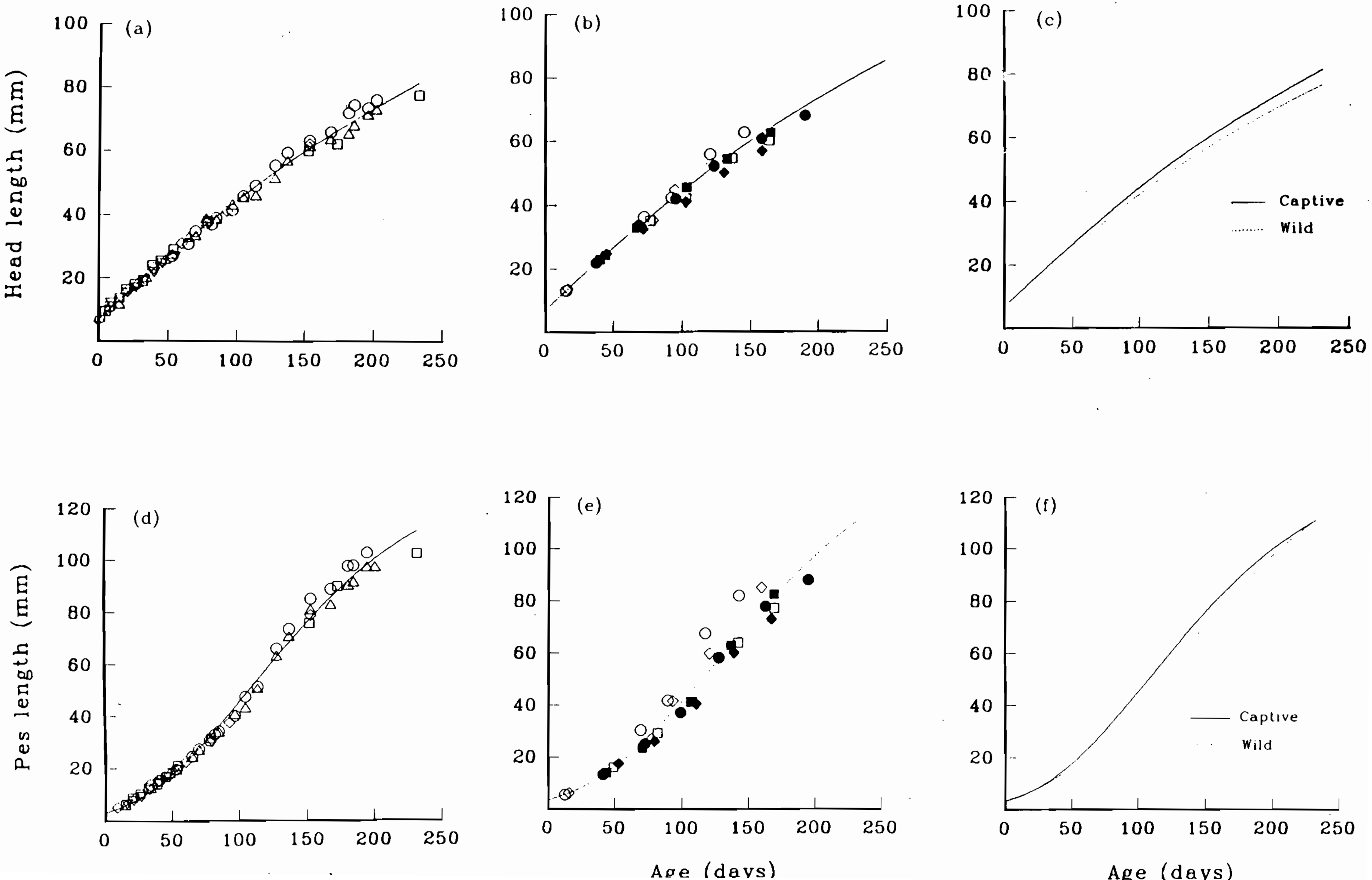
As earlier workers noted, the growth of PY varies between individuals. There is a need for generalised growth curves for a species to be based on larger sample sizes to make allowances for this variation. The observed variation also suggests that the pouch may not be the constant environment that Sharman *et al.* (1964) envisaged it to be or that variation in growth of PY is genetically inherited. Larger sample sizes, judicious use of siblings and more sophisticated statistical techniques now make it possible to test specific hypotheses relating to the cause of this variation. Such individual variation is useful, however, in that it may be used as one of the parameters in studies of maternal investment and of individual variation in reproductive success.

Questions arising from the comparison of captive and wild growth rates have not been fully resolved here. However, by assuming that head and pes size at birth was the same for both captive and wild reared PY, comparisons of the growth rate and asymptotic size were made. The results suggest that over and above individual variation, there was no major differences between the two groups in their growth (Figures 3.4, 3.5).

Our statistical knowledge of how to describe growth has vastly improved since the first studies measured the growth of PY of macropodids. As illustrated here, repeated measurements of individuals no longer cause the same limitations as they have in the past (e.g. Ealey 1967, Murphy and Smith 1970). Additionally, theoretical curves, such as the logistic and Gompertz curves which have been used to great effect in describing growth in other organisms, have been less well used for marsupials. Both Lee and Cockburn (1985) and Cockburn and Johnson (1988) pointed out this lapse, and used data on weight of marsupials gleaned from the literature to illustrate the usefulness of such curves for comparative purposes. While the Gompertz growth constants (β) calculated by Lee and Cockburn (1985) used body weight as the growth parameter, they are similar to the growth constants calculated here for head and pes of *P. assimilis* (Table 3.4) when compared with other marsupials of a similar asymptotic body weight. This suggests that the growth rates predicted here are in keeping with those expected for a macropodoid of this size. While weight is useful in other ways (e.g. comparisons of higher taxonomic groups and of metabolic rate), it is subject to much greater individual variation than other body measurements such as head length (Poole *et al.* 1982a,b) and is difficult to obtain in the early attachment phase of pouch life without increasing risk of PY mortality, an outcome which was inconsistent with the primary aims of this study.

As illustrated here with captive and wild reared PY of *P. assimilis*, the use of theoretical curves facilitates comparative studies. Such comparisons are not limited to those between animals living under different environmental regimes, but can also be used between different taxonomic groups. For example, growth data exist for many macropodid and other marsupial species. Fitting such common curves would allow intra- and inter-specific comparisons to be made as illustrated here and as envisaged by Lee and Cockburn (1985). It is to be hoped that as whole-of-life data become available for this and other species, similar curves should be fitted to add to our understanding of growth in these groups.

Figure 3.1 Growth curves for the head length and pes length of pouch young (PY) of *P. assimilis*. Individual values and composite curve for head and pes respectively of captive (*a*, *d*) and wild (*b*, *e*) animals; (*c*, *f*) Composite curves for head and pes respectively. Measurements of the same individual are represented by the same symbol. Captive data are from Close and Bell 1990.


(a)
(b)
(c)
(d)
(e)
(f)
Head length (mm)
Pes length (mm)
Age (days)
Age (days)
Captive
Wild
Captive
Wild
0
20
40
60
80
100
120
50
150
200
250

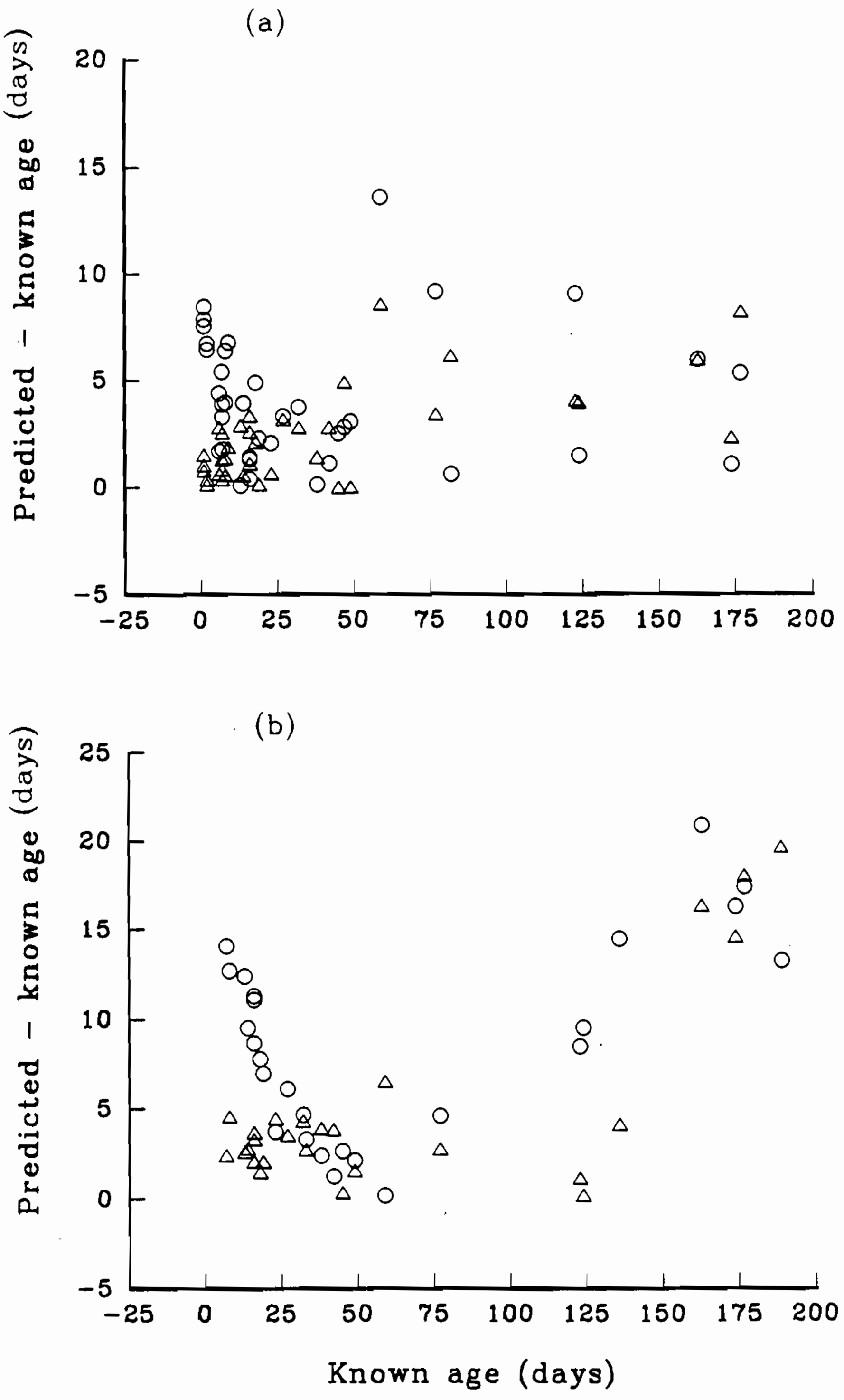


Figure 3.2 Comparison of age estimates based on linear (○) and non-linear (△) models. The absolute differences between the corresponding predicted and known ages have been plotted against age for estimates based on head (a) and pes (b) lengths. Captive data are from Close and Bell 1990.

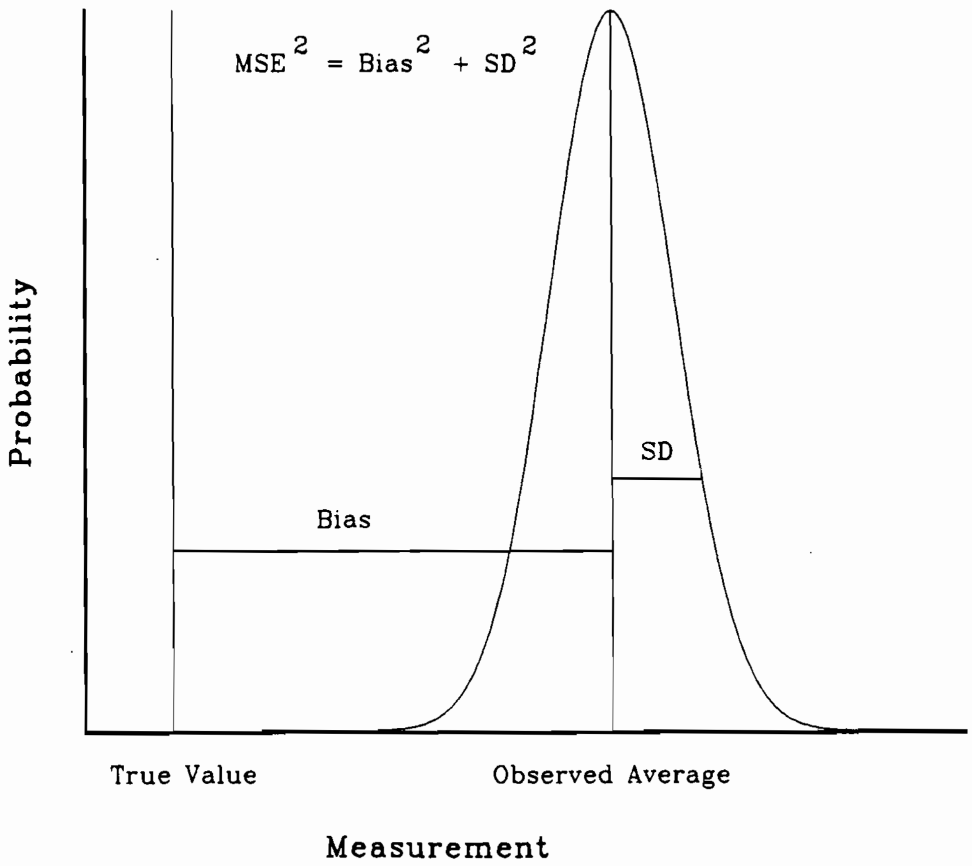


Figure 3.3 Diagrammatic representation of indices of bias, repeatability (SD) and accuracy (√Mean Square Error).

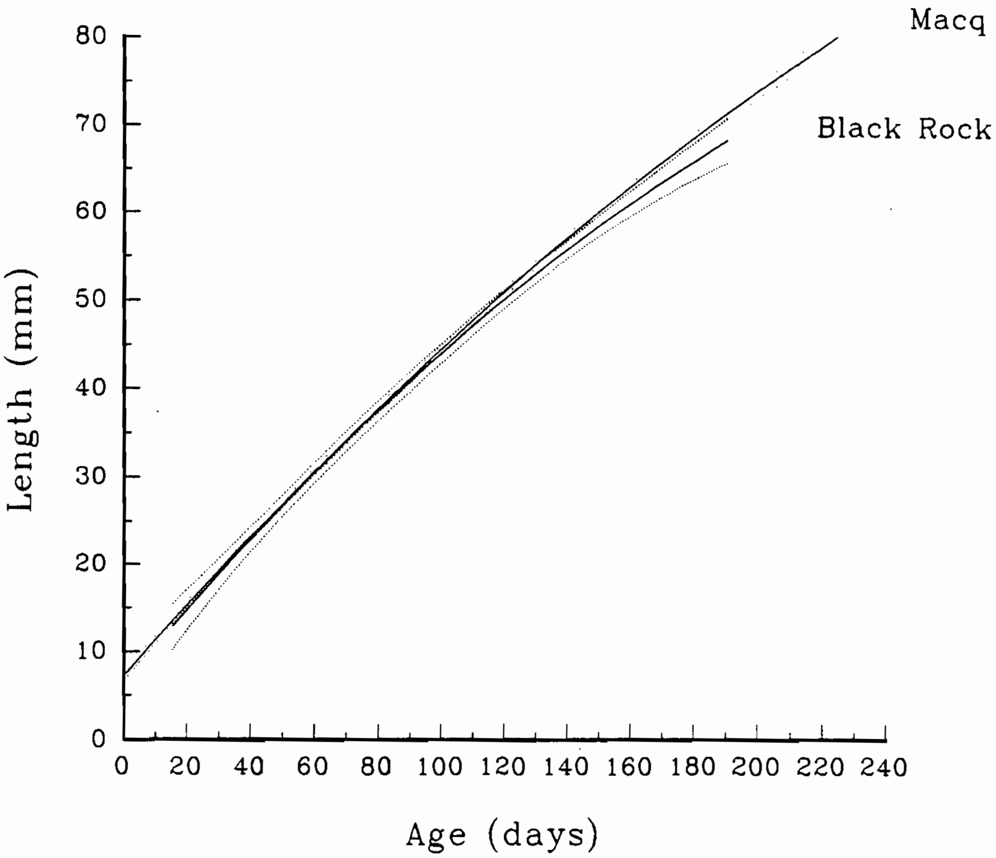


Figure 3.4 Comparison of the growth curve for the head length of captive pouch young (Macquarie University) with the corresponding growth curve and 95% confidence intervals for wild pouch young (Black Rock). Note: 95% confidence intervals are approximate only and are an under-estimation of the true intervals.

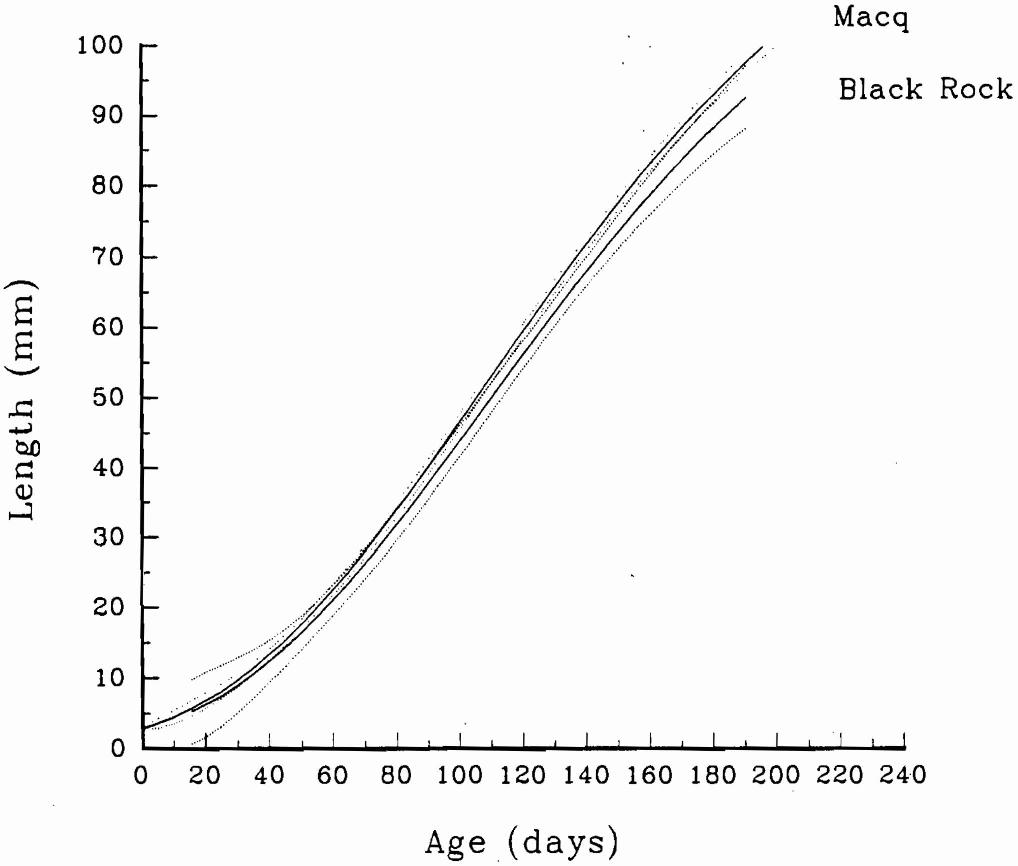


Figure 3.5 Comparison of the growth curve for the pes length of captive pouch young (Macquarie University) with the corresponding growth curve and 95% confidence intervals for wild pouch young (Black Rock). Note: 95% confidence intervals are approximate only and are an under-estimation of the true intervals.

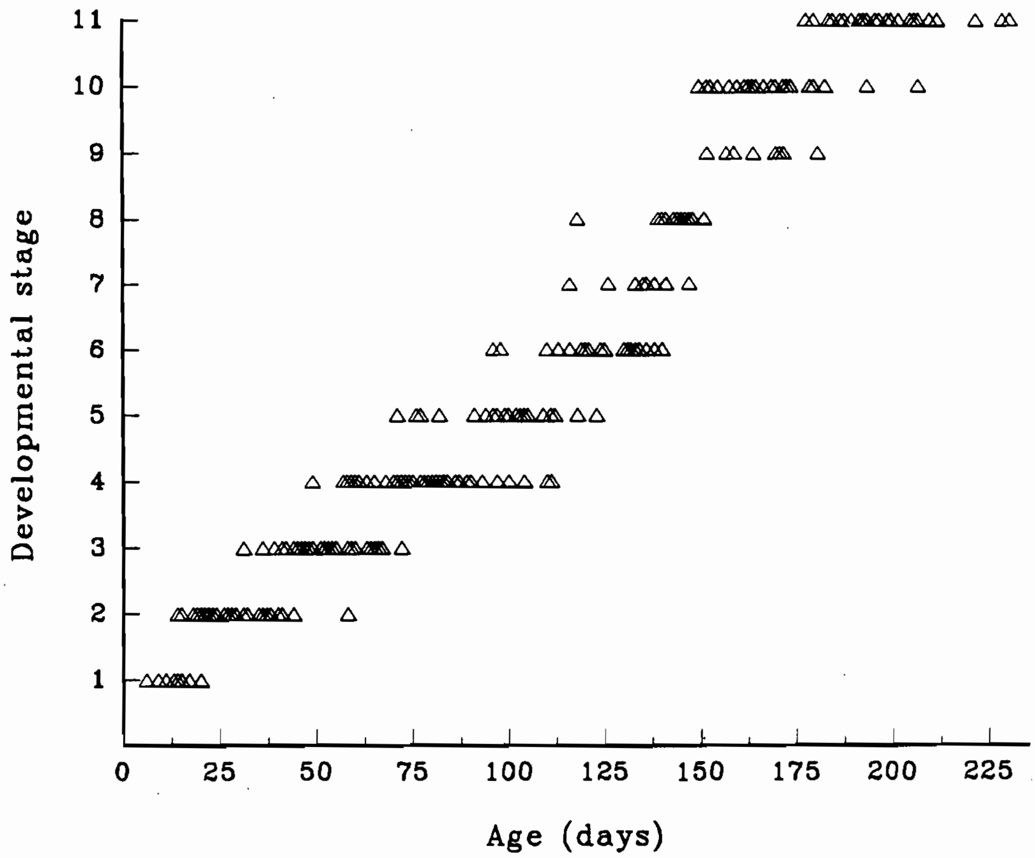


Figure 3.6 Timing of the first observations of the presence of various morphological features in PY of *P. assimilis*. Key to developmental stages: 1. Sex distinguishable to unassisted eye, 2. Tips of ears free, 3. Papillae of facial vibrissae evident, 4. Vibrissae visable to unassisted eye, 5. Eyelashes visible to unassisted eye, 6. Eyes open, 7. Fur visible on head to unassisted eye, 8. Fur visible all over body to unassisted eye, 9. Colour of fur definite, 10. Tips of first incisors through gum and, 11. Permanently out of pouch (stages defined as per Kirkpatrick 1985). N.B. due to the monthly sampling regime, the first observation of a particular developmental stage may be up to one month after its actual appearance.

Chapter 4

Post-pouch young growth, sexual maturity and sexual dimorphism

4.1 Introduction

In all species of potoroids and the smallest macropodids, there is little difference in size between adult males and females of the same species. In contrast, males of the larger species of macropodoids are up to 2.5 times as heavy as females (Jarman 1989). Between these two extremes there are many macropodid species in which males are 10-40% larger than females (Jarman 1989). This pattern is paralleled by differences in the pattern of growth (Jarman 1983, 1989). The smaller monomorphic species reach a growth plateau (asymptote) soon after sexual maturity, while at least one and usually both sexes of the medium to large dimorphic species continue to grow for the remainder of their lives. Additionally, different body parts reach adult size at different ages. For example, in the grey kangaroo, this occurs in the following order (first to last): ear, pes, head, leg, tail, arm and weight (Poole, Carpenter and Wood 1982a).

Determining how the pattern of growth and sexual dimorphism of wild *P. assimilis* (2.5-5 kg) fits into the general macropodid pattern is of interest because of some apparent interspecific differences among rock wallabies in this regard. Despite a fairly low level of dimorphism, females of the smallest rock wallaby, *Petrogale* (*Peradorcas*) *concinna* (1-1.5 kg, Sanson 1983), apparently cease growing in early adulthood while those in one of the larger species, *P. penicillata* (6-7.5 kg, Maynes and Sharman 1983), appear to show strongly persistent growth (data from Sanson and Joblin in Jarman 1989).

The body size and sexual dimorphism of taxa are commonly linked to social organisation (e.g., Kleiman 1977, Ralls 1977, Jarman 1983). The smaller monomorphic species of macropod tend to be solitary except for reproductive associations and aggregation on favoured resource patches. Most of the large heteromorphic species are gregarious and high ranked males centre their home range on the densest segment of the female population (reviewed in Croft 1989). While most behaviours of *P. assimilis* are in the repertoire of most other macropodids, their social organisation has some unusual features (Barker 1990). In contrast to the pattern outlined above, *P. assimilis* forms long-term pair bonds and has a larger repertoire of agonistic behaviours than most other species. Alan Horsup's behavioural study which was conducted in parallel to mine indicates that within the Black Rock colony, females form a stable linear dominance hierarchy. Young males progressively pair with increasingly dominant females until they form stable pair bonds with one or more of these females. These bonds may persist for at least several years (Horsup, *personal communication*). Males also scent-mark and otherwise defend their females (Horsup 1986, Barker 1990). It is not known whether these behaviours are characteristic of most rock wallabies as the social organisation of few species of *Petrogale* has been described (reviewed in Croft 1989).

This chapter considers post-pouch growth, sexual maturity and sexual dimorphism in *P. assimilis* based on longitudinal data from: (1) a small number of known-age, wild individuals from Black Rock which were repeatedly measured from birth up to a maximum of 1126 days, and (2) wild animals from Black Rock whose relative ages have been estimated on the basis of their molar eruption status (Chapter 5). Data on growth for 'known-age' animals from post-PY to adulthood were disappointingly limited. This was due to the length of the study period relative to the age of physical maturity, and was exacerbated by high PY mortality (Chapter 8) and low recruitment into the breeding colony (Chapter 5).

4.2 Methods

'Known-age' animals include PY whose age (and hence date of birth), were calculated as described in Chapter 3. Molar eruption stage (MES) was used as a measure of the relative ages of sub-adult and adult animals (Chapter 5). Most of the data for 'known age' animals older than 400 days came from only four wild animals (♀ #159, ♂ #161, ♂ #179, ♂ #U/316) (Appendix 5). Consequently, I did not attempt to model growth after *P. assimilis* leaves the pouch.

On the assumption that different body parts of *P. assimilis* would reach asymptotic size at different ages, I examined the relationship between age and three linear measurements (pes, head and arm) and weight for known age animals. Additionally, I studied whether growth persists in adult *P. assimilis* by comparing these linear measurements with those from adults of different age classes. As an individual's weight fluctuates markedly in different seasons (Chapter 6), I did not consider it appropriate to use this parameter as an index of persistence of growth in adult wallabies.

The average size of various morphological characters was calculated for adult animals of both sexes using the initial measurements taken for each individual. Sexual dimorphism was calculated using both average and maximum measurements (in case *P. assimilis* continued to grow throughout life) and to allow direct comparisons with other macropodoids, as presented in Jarman (1989).

Females were considered sexually mature when the pouch had enlarged and all nipples had fully everted (Merchant and Calaby 1981). For males the total length (including epididymis), width (both testes together) and depth (±0.5mm) of the testes were measured using vernier calipers. A testes index was calculated as the cube root of the product of the testes dimensions (as outlined in Chapter 2) and the relationship between the testes index and the presence of spermatozoa in the urine investigated.

4.3 Results and Discussion

4.3.1 *Age of sexual maturity*

A wild (#159) and two captive (#079, #W; see Table 2.2) 'known-age' females were sexually mature by 17.5, 20 and 23 months respectively (i.e. by approximately 534, 630 and 700 days of age). There were no males available to the captive females, but the wild female gave birth one month after she was classified as sexually mature. The onset of puberty occurred slightly earlier than this in captive colonies of *P. inornata* (17 months) and *P. xanthopus* (16-21 months) (Johnson 1979, Poole *et al.* 1985).

In the months prior to sexual maturity, the size of the hitherto small testes of male macropodids increases as the diameters of the seminiferous tubules grow rapidly. This change in testes size occurs in conjunction with full spermatogenesis at the onset of sexual maturity and has been described, for example, for the red kangaroo (Frith and Sharman 1964) and captive *P. assimilis* (Bell, Close and Johnson 1989). This pattern also appears to occur in *P. assimilis* at Black Rock judging from the increase in testes size and the incidence of spermatozoa in the urine (Figure 4.1a). At Black Rock, all mature males (i.e. those which had spermatozoa in their urine) had a testes index of greater than 20, and, with one exception for one animal (#007; 2800g) for one month, all had a body weight of more than three kilograms (Figure 4.1a). Two 'known-age' males (#161 and #U/316) had adult-sized testes (i.e. testes index >20) at 23 and 25 months respectively (Figure 4.1b). In the first animal, the testes began to increase in size at 20 months and spermatozoa were found in the urine at 27 months. Testes enlargement commenced earlier in captive *P. assimilis* (16-18 months) (Bell *et al.* 1989) than in the wild animals discussed here (23-27 months). The earliest occurrence of sexual maturity for captive *P. inornata* was at 19.5 months (Johnson 1979) and at 30 months for *P. xanthopus* (Poole *et al.* 1985).

4.3.2 *Growth of 'known-age' wild animals*

Growth data for the four wild rock wallabies (#159, #161, #179, #316) for the period for which measurements were available (1126 days maximum) are presented in Figure 4.2. The growth curves obtained for these individuals fit the general form of those presented for other macropods such as *P. xanthopus*, *M. fuliginosus* and *M. giganteus* (Poole *et al.* 1982a,b, 1985). Visual examination of the curves for *P. assimilis* shows a slowing of the growth rate of the pes, head and arm, several months before puberty (approximately >530 days) while weight continued to increase after puberty (Figure 4.2). A similar pattern was found for *P. xanthopus*, *M. fuliginosus* and *M. giganteus* (Poole *et al.* 1982a,b, 1985).

The relationship between age and arm length indicates that some sexual dimorphism may develop as these rock wallabies approach adulthood with males having an apparently faster growth rate than females (Figure 4.2b). This is not obvious for the other measurements reported here (Figure 4.2a,c,d). However, because the sample of 'known-age' animals contained only one female, it was inappropriate to consider sexual dimorphism of these animals. Sexual dimorphism of older animals is considered below.

4.3.3 *Persistence of growth in P. assimilis*

Two rock wallabies became adults at a molar eruption stage (MES) of 2.0 and 2.6 [See Chapter 5 for an explanation of this method of ageing adults using their teeth]. Long-term data were available for 16 females and eight males from Black Rock with a MES of at least 2.8. These animals were measured repeatedly over periods of 435-1117 days. For most individuals, changes were very slight and fluctuations were probably due to measurement error. However, if the animals are split into young (MES<4) and old (MES=4) when first captured, some trends emerge. Growth ceased earliest for pes and continued longest for arm measurements in males (Table 4.1). Males continued to grow at an older relative age (MES) than females, particularly in their arm length. This pattern is also apparent in the slightly larger *Thylogale thetis*, in which the arms of males grow relatively faster than other parts of the body, compared with those of females

(Johnson in Jarman 1989). This dimorphism in the pattern of growth in these smaller macropodids is much less pronounced than in the larger, more heteromorphic macropodids (Jarman 1989) and the significance of the low level of growth after sexual maturity in *P. assimilis* is unclear.

Table 4.1 Proportions of adult rock wallabies showing persistent growth for different age-sex classes at first capture. Adult age was defined by molar eruption stage (MES; see Chapter 5).

Sex	Adult age	MES	n	Arm	Head	Pes
Female	Young	<4.0	4	0.75	0.5	0.5
	Old	4.0	10	0.0	0.1	0.0
Male	Young	<4.0	2	1.0	0.5	0.5
	Old	4.0	6	0.83	0.5	0.0

4.3.4 *Sexual dimorphism*

Female *P. assimilis* are consistently and significantly smaller than males in all body measurements: head ($t=-6.49$, $df=81$, $p<0.001$), pes ($t=-5.73$, $df=79$, $p<0.001$), arm ($t=13.40$, $df=75$, $p<0.001$), tail ($t=-5.97$, $df=80$, $p<0.001$), and ear ($t=2.48$, $df=81$, $p=0.015$) (Figure 4.3). With the exception of those for weight, the indices based on average values indicated similar levels of sexual dimorphism to those based on maximum values (Table 4.2). In contrast, the weight index based on maximum values was 1.06 and that based on average values 1.14 (Table 4.2). Males are consistently 2-6% larger than females in most morphological characters measured and well outside the standard error intervals for females (Figure 4.3). In particular, the forearms of adult males are much longer (an average of 12%) than those of females (Table 4.2, Figure 4.3b). An indication of the differences in growth of the arms relative to the rest of the body can be given by the ratio of maximum forearm length to pes length (Jarman 1989). For males, this ratio was 0.659 and for females, 0.618, which are between the values given by Jarman (1989) for the larger *P. xanthopus* and the smaller *P. burbidgei*.

Jarman (1983) suggests that when the difference in dimorphism in macropodoid species is less than 10%, the species could be considered homomorphic. Under this definition, *P. assimilis* is a homomorph. However, the arm length of *P. assimilis* is mildly heteromorphic, with the arms of males 12% longer than those of females. The forelimbs and upper body musculature of macropodoids are used as weapons in intra-sexual competition and are considered equivalent to the cranial weaponry of the Bovidae and Cervidae (Jarman 1983). Forelimb development is displayed in aggressive interactions between males. As a result of sexual selection, dimorphism is most pronounced in this character, particularly in the medium and larger macropodoids (Jarman 1989).

The arms of male *P. assimilis* are used in threat behaviour and as weapons in aggressive interactions (Horsup 1986, Barker 1990). Although fighting behaviour between males involving use of the arms is relatively infrequent (Horsup 1986, Barker 1990), the relatively longer arms and presumably, the associated body musculature of males, suggests that the outcome of fights is an important factor in obtaining access to females.

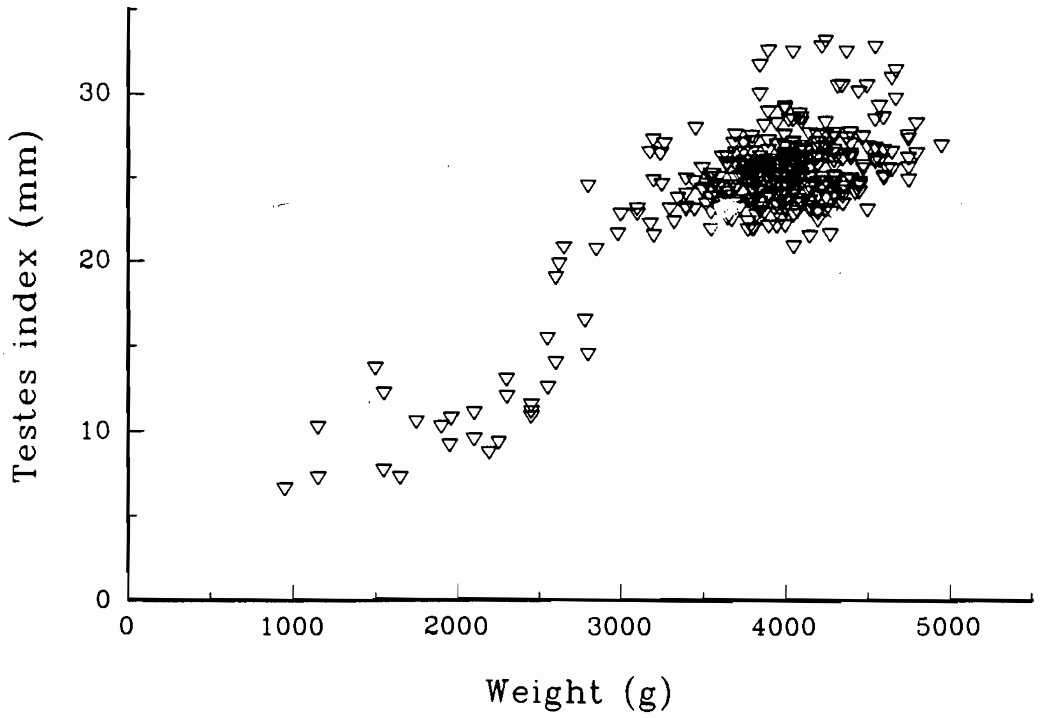
The pattern of growth and sexual dimorphism in *P. assimilis* can also be related to its social organisation. Like many other mammals exhibiting long-term pair bonds (Horsup 1989, Barker 1990), *P. assimilis* is homomorphic (Kleiman 1977, Ralls 1977). Male *P. assimilis* actively defend their females and territories on the rock outcrops, scent-mark their females and engage in frequent allogrooming to reinforce the pair-bond (Barker 1990). The relative importance of female choice and male fighting in mate selection in unknown.

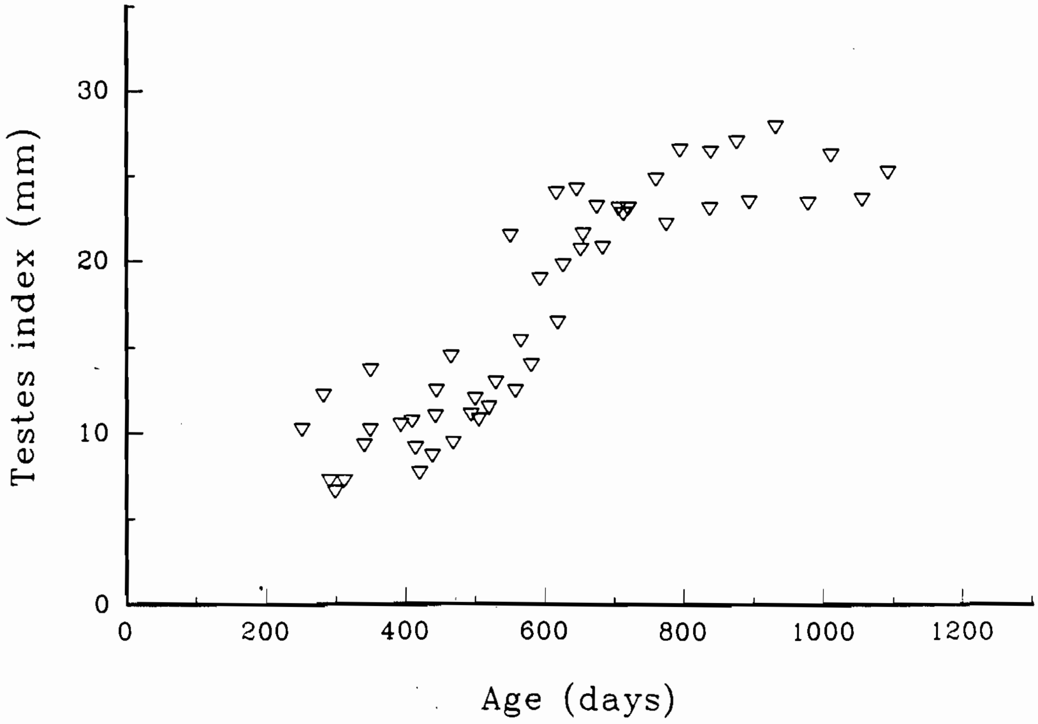
Table 4.2 Body measurements and degree of sexual dimorphism for adult *P. assimilis*.

Measurement	Females (n) S.E. Range	Males (n) S.E. Range	M:F ratio average	M:F ratio maximum
Head length (mm)	103.8	108.3	1.043	1.022
	(43)	(40)		
	0.484	0.500		
	96.8-111.8	100.0-114.2		
Pes length (mm)	131.1	135.9	1.037	1.053
	(42)	(39)		
	0.555	0.630		
	124.0-138.8	126.7-146.2		
Arm length (mm)	80.2	89.2	1.112	1.122
	(42)	(40)		
	0.544	0.404		
	72.2-85.8	84.8-96.2		
Tail length (mm)	465	500	1.075	1.063
	(43)	(39)		
	4.00	4.21		
	400-522	445-555		
Ear length (mm)	58.5	60.0	1.026	1.015
	(43)	(40)		
	0.42	0.45		
	53.5-65.4	55.5-66.3		
Weight[A] (g)	3542	4065	1.148	1.063
	(14)	(14)		
	88.5	88.5		
	2450-4750	2800-4950		

[A] mean weight and S.E. calculated as per the repeated measures ANOVA (Chapter 6), i.e. weights in this table were obtained for each animal in the months listed in Table 6.1.

Figure 4.1 Changes in testes index ($\sqrt[3]{(\text{length} * \text{width} * \text{depth})}$) with (a) body weight and (b) age.


Testes index (mm)
0
10
20
30
0
1000
2000
3000
4000
5000
Weight (g)


Testes index (mm)
0
10
20
30
0
200
400
600
800
1000
1200
Age (days)

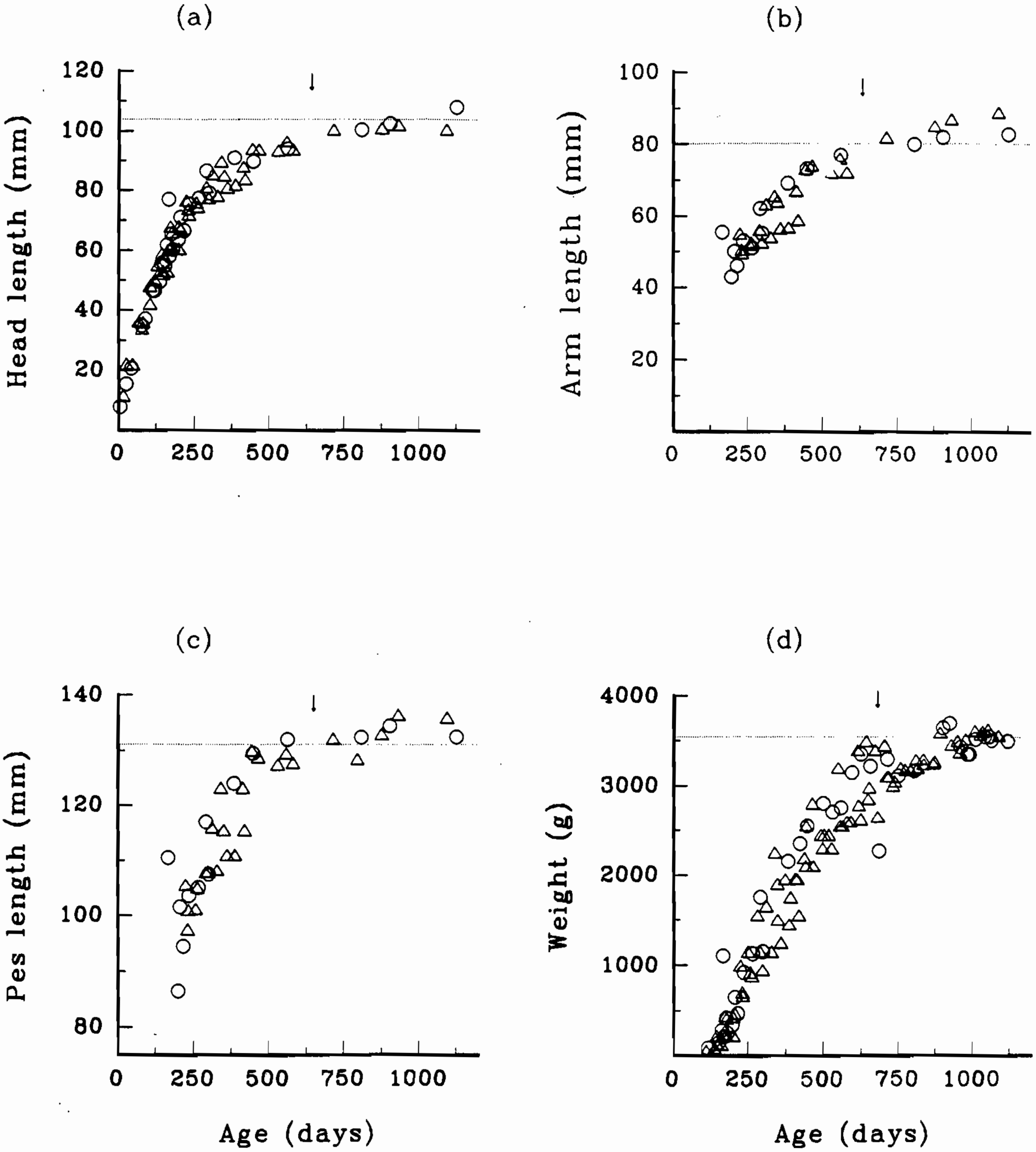
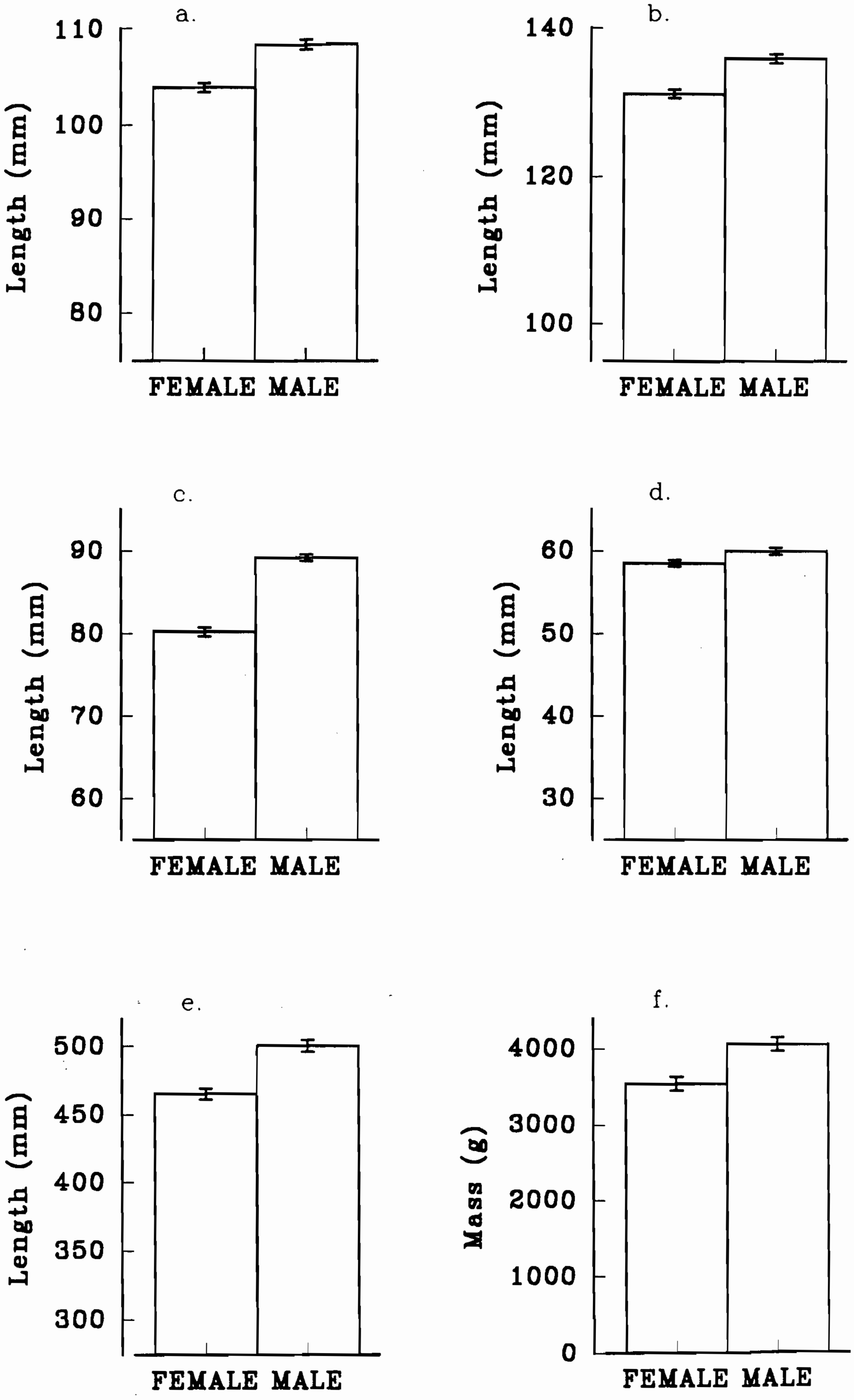


Figure 4.2 Increase in (a) head (b) arm (c) pes and (d) weight with age in 'known-age' rock wallabies; ○ females and ▵ males, with ↓ minimum age to sexual maturity and ... average adult female measurement for comparison.


a.
110
100
90
80
Length (mm)
FEMALE MALE
b.
140
120
100
Length (mm)
FEMALE MALE
c.
90
80
70
60
Length (mm)
FEMALE MALE
d.
60
50
40
30
Length (mm)
FEMALE MALE
e.
500
450
400
350
300
Length (mm)
FEMALE MALE
f.
4000
3000
2000
1000
0
Mass (g)
FEMALE MALE

Chapter 5

Tooth eruption and movement: a basis for understanding age structure and adult mortality

5.1 Introduction

Earlier chapters described how bodily measurements such as head and foot length can be used to measure growth and determine the age of young macropodoids. However, few researchers have used the changes in these measurements for determining the age of independent young and older animals [but see studies of Parma wallabies (Maynes 1976), captive grey kangaroos (Poole, Carpenter and Wood 1982a,b), yellow-footed rock wallabies (Poole *et al.* 1985) and Tasmanian bettongs (Rose 1989)]. This is because this method is more difficult to use and less precise for older animals as: (1) growth usually slows and the error of estimation is larger than for younger individuals; (2) logistic problems, such as keeping animals for the longer time period required to complete the study, may become excessive; and (3) in some species, growth is determinate and hence cannot be used for age determination after it ceases. *P. assimilis* falls into this latter category of asymptotic growth, as most body measurements cease growing not long after maturity (Chapter 4). Additionally, as mentioned in Chapter 3, insufficient data were available for *P. assimilis* at Black Rock to use post-PY growth to determine the age of most of the population.

However, there are two alternative and inter-related techniques which are commonly used for determining the age of older macropodoids. These are the rates of molar eruption and movement. Both methods use dental characteristics which, in common with most other mammals, must rank among the most studied features of macropodids. Teeth are ideal for age determination. They are enduring structures, their morphology tends to be relatively constant within a species but varies at higher taxonomic levels and the eruption and loss of individual teeth are discrete events. Furthermore, the study of macropodid dentition is well developed and has been of great interest to students of phylogeny (e.g. Raven and Gregory 1946, Tate 1948, Sanson 1978, 1982, and Flannery 1989), development (Kirkpatrick 1965a, 1978, and Bartolomai 1971), and diet (Raven and Gregory 1946, Ride 1959, Sanson 1978, 1989, and McArthur and Sanson 1988).

Kreft (1875, in Tate 1948) first described the functional difference between the larger kangaroos and the smaller wallabies that was later to become so important in age determination studies. He noted that the longer faced kangaroos have a longer diastema and a smaller permanent premolar (P4) than the smaller faced wallabies. The kangaroos tend to shed these premolars, and the other molars sequentially in later life. Conversely, the larger premolar of wallabies persists throughout life despite wear and, unlike the kangaroos, little or no forward movement of the tooth row occurs.

However, it was not until three-quarters of a century later that the rate of tooth eruption and the forward movement of teeth in the jaws of macropodid species was used to classify the ages of individuals (e.g., Ride 1957, Shield 1968, Ealey 1967, Sharman, Frith and Calaby 1964 and Kirkpatrick 1964, 1965a). As with many other aspects of life history studies of macropodids, early research on age determination of post-PY animals using molar eruption and migration has concentrated on species of *Macropus* and in particular, the larger, commercial species of this genus, such as *M. giganteus*, *M. rufus* and *M. robustus*. At least seven species of *Macropus* have been studied in this way: *M. rufus* (*Megaleia rufa*) (Sharman *et al.* 1964, Kirkpatrick 1965a), *M. robustus* (Kirkpatrick 1965a, Ealey 1967), *M. giganteus* (Kirkpatrick 1964, 1965a), *M. agilis* (Kirkpatrick and Johnson 1969, Newsome *et al.* 1977), *M. parma* (Ride 1957, Maynes 1972), *M. eugenii* (Inns 1982a), and *M. rufogriseus* (Kirkpatrick 1964, Catt 1977). There have been very few such age-determination studies of other macropodids [with the exceptions of *S. brachyurus* (Shield 1968), *P. xanthopus* (Poole *et al.* 1985), *P. lateralis* (Kinnear, Onus and Bromilow 1988) and *P. assimilis* (Bell, Close and Johnson 1989)].

In all the macropodids studied, the molar teeth erupt sufficiently slowly for the ages of individuals to be estimated well into adulthood (reviewed in Kirkpatrick 1985). Thus molar eruption stages (MES) can be used to age all species for at least a proportion of their adult life.

However, only a limited number of species show sufficient molar movement for this to be a useful ageing tool. Relative to reference points in the skull, the the premolars and molars of all species show some, usually small, movement forward with age (mesial drift). This is a result of the interaction of transeptal fibres which link the teeth together and the forces of occlusion which push teeth forward (Sanson 1982). In some species (generally browsing wallabies), the tooth rows have little curvature and the large and persistent premolar apparently acts as a buttress and limits forward movement of molariform teeth to mesial drift (Sanson 1982). Less than the full complement of cheek teeth is maintained in the tooth row as anterior teeth are worn out of occlusion and unworn posterior molars erupt (Sanson 1978, 1982, 1989). In other species (generally grazing kangaroos), however, the tooth row is curved, and the premolar is smaller than the first molar and is usually lost. Molar progression occurs and continues throughout life as old teeth are worn forward out of occlusion and eventually lost, and unworn molars are pulled forward into occlusion by the transeptal fibres. In these macropodids, the extent of molar progression has been used as the basis for estimating the age of individuals, especially those in which all the teeth have fully erupted (e.g., Sharman *et al.* 1964, Kirkpatrick 1964, Kirkpatrick and Johnson 1969, Newsome *et al.* 1977). Poole, Carpenter and Simms (1980) found that molar progression was a slightly more reliable method of age estimation for *M. giganteus* than molar eruption.

Several approaches can be used to measure molar eruption and movement depending on the type of specimens available. For dead animals, skulls can be measured (e.g. Kirkpatrick 1964). For live animals, a visual examination using an ophthalmoscope (or equivalent) (e.g. Sharman *et al.* 1964) is possible, or alternatively, radiographs can be taken of the head (e.g. Kirkpatrick 1965a). Radiographs have previously only been used on captive animals (e.g. Kirkpatrick 1965a) or on those wild animals captured close to, and transported to radiographic facilities (Barker 1982). Radiography is preferable to visual examination since it provides a permanent record of both molar eruption and progression that can easily be compared with later measurements.

The dental morphology of a species is related to its diet and methods of feeding. Macropods range from grazers such as the red and grey kangaroos to browsers such as the swamp wallaby. Rates of molar progression useful for age determination are usually manifest only in grazing species. In his review, Sanson (1978) considered *Petrogale* to be intermediate on the browser-grazer dichotomy first described for the Macropodoidea by Raven and Gregory (1946). However, the diet of *P. assimilis* was unknown at the start of this study. It was therefore decided to investigate the suitability of both the rate of molar progression and the pattern of molar eruption in this species in case the large-scale forward movement of teeth occurred.

This chapter documents the pattern of eruption and movement of the cheek teeth of individuals of *P. assimilis*, primarily as an index of their developmental stage and age. Some information on the age structure and adult mortality of the population at Black Rock during my study is also provided.

5.2 Materials and Methods

5.2.1 *Field techniques*

Alan Horsup's independent visual observations during a parallel behavioural study at Black Rock suggested that only one non-PY animal (an adult), in his observation area remained untagged by the end of my study period. Since this area incorporated the major part of the colony, it seems likely that I tagged and classified on the basis of age virtually all the adults in the colony.

5.2.1.2 Radiography

Radiographs provide a reliable and non-destructive technique for measuring the molar eruption and position of teeth. This method was chosen over technologically less demanding methods such as determining molar eruption and progression by eye, because the study was to continue after my work was completed, and x-rays would reduce the confounding effects of observer error and provide a permanent record of the teeth.

During each field trip from June 1987, a portable radiography machine (Atomscope 903-A Mikasa, Japan) was installed in an open-walled, dirt-floored shed and powered by a portable 240v generator (Honda ES3600). The x-ray machine was mounted on a steel frame erected over a table of adjustable height and standard lead safety aprons and gloves, and radiation safety badges were worn by the two operators (Figure 5.1). The exposed radiation levels were checked regularly by the Queensland Department of Health.

In contrast to most other stationary machines, the kilo-voltage (kV) and milli-Amp (mA) settings were locked together on this machine. High kV and intensifying rare earth screens and cassettes (Kodak Min-R) were necessary when radiographing the skulls to enable the x-rays to penetrate the thicknesses of bone and teeth and give the required tooth definition. Film was transferred between a light excluding box and the cassettes via a standard darkroom bag.

Initially, the kV/mA and film focal distance (FFD) of the x-ray machine were kept constant, and only the exposure time was varied. These settings were then modified by trial and error until the best possible exposures were obtained.

The exposure times used for juvenile, sub-adult and adult rock wallabies are given in Table 5.1.

Initially, only dorso-ventral radiographs for molar progression were taken under anaesthesia for each animal (Chapter 5.2.1.2). Later, a lateral radiograph for molar eruption was also taken. The lateral view was also useful as an aid to interpreting the individual teeth in dorso-ventral radiographs. A dorso-ventral radiograph was taken by placing the lower jaw of the rock wallaby on the x-ray plate and pushing down firmly on the vertebrae at the base of its skull. This forced the occlusal plane of the teeth to be parallel to the x-ray film. A perfect lateral radiograph was more difficult to obtain as both tooth rows had to be superimposed so that only one image appears on the radiograph. By applying appropriate support to the rock wallaby's head, it could be adjusted so that its sagittal plane was parallel to the radiographic plate.

Table 5.1 The exposure times for radiographs taken of animals of given head length, at 80 kV / 20 mA and a film focal distance of 900 mm.

Age class (approx.)	Head length (mm)	Exposures times (sec)	
		Lateral	Dorso-ventral
juvenile	60 - 75	0.20	0.30
sub-adult	75 - 95	0.35	0.40
adult	95 - 115	0.45	0.50

Adults were typically x-rayed every six months. Younger wallabies were radiographed more frequently. 'Known-age' animals (n=17) were first caught as pouch young; their ages at first capture were estimated from head and pes measurements (Chapter 3, Appendix 6). They include four animals (#079, #W, #M, #R) orphaned as PY and reared in captivity (Chapter 2.3; Table 2.2).

5.2.1.2 Anaesthesia

To reduce stress, it was necessary to anaesthetise the rock wallabies before they were radiographed. After initial trials outlined in Appendix 7, the barbiturate thiopentone sodium (Abbot: Pentothal) was routinely administered. This was given to effect by injection into the lateral tail vein at a maximum dosage of 12.5 mg/kg (although this amount was rarely used). Induction was rapid, the depth of anaesthesia was controlled and recovery times were always less than one hour.

After each animal had been x-rayed, it was placed in a cage lined with hessian bags and monitored as it recovered (from the drug-induced stupor). The animal was left in a comfortable position and regularly checked and moved as it recovered. On cold days, two animals would be put together in a cage and a domestic heater used for additional warmth. There were no known fatalities attributable to anaesthesia or radiography during my study.

5.2.2 *Laboratory techniques*

The exposed x-ray film was processed at a commercial radiographic laboratory in Townsville, North Queensland.

5.2.2.1 *Measurement of molar eruption*

My cheek tooth nomenclature follows Thomas (1888, cited in Sanson 1980). Molar eruption stages (MES) were scored from 366 lateral radiographs of the upper jaw of 111 rock-wallabies using the method of Newsome *et al.* (1977). Each fully erupted molar was scored as 1. A partially erupted molar was categorised as either 0.2, 0.4, 0.6, or 0.8 as an index of its eruption status. Thus an animal with the first and second molars fully erupted and the anterior loph of the third molar just through the gum had a MES of 2.4.

5.2.2.2 *Measurement of molar movement*

Before the molar index could be scored the average length of each molariform tooth had to be calculated. To this end, skulls and molar teeth of *P. assimilis* from Black Rock (n=11) and from museum collections [Australian National Wildlife Collection, CSIRO, Canberra (n=80); Queensland Museum, Brisbane (n=16); and the Australian Museum, Sydney (n=4)] were measured correct to 0.1 mm using vernier calipers.

The molar index was scored as the proportion of molar teeth that were forward of the reference line drawn across the anterior rim of the orbits (Kirkpatrick 1964). For example, a molar index of 3.3 indicated that the first three molars and 0.3 of the fourth molar were anterior to the reference line. If M4 was forward of the reference line, a molar index of >4 was calculated by assuming the presence of a fifth molar of length equal to that of the fourth (Kirkpatrick 1964). To aid calculation of the proportion of the last molar, a perspex plate etched with lines spaced at intervals corresponding to 20% of the average length of each molar (calculated on the basis of the measurements of teeth in the skulls) was placed over the required skull (n=21) or dorso-ventral radiograph (n=452). In practice, the mesial edges of individual teeth were obscured by the superimposition of bone and teeth, and it was easier to score the position of the distal edge of the teeth spanning the reference line and to subtract each of these scores from one. There was good agreement between independent estimates of molar movement and molar eruption stages obtained directly from skulls and from the corresponding radiographs.

5.2.3 *Methodological limitations*

The data from known-age animals from Black Rock are limited both in numbers and in time and sometimes could not be treated independently. Despite some sexual dimorphism in size in adult *P. assimilis* (Chapter 4), I considered the sample size was too small to draw conclusions about gender differences in the analysis with any degree of confidence. Sexual dimorphism does occur in the pattern of molar progression and in the rate of molar movement in *Macropus agilis* (Newsome *et al.* 1977), a more dimorphic species than *P. assimilis* (see Jarman 1989 and Chapter 4). Only three years (a small proportion of the life-span of a rock-wallaby) (see Chapter 2), could be reported, due to time constraints imposed on this study.

5.2.4 *Data analysis*

The rate of adult mortality in each season was calculated as the ratio of adults which died during that season to those adults known to be trapped regularly prior to or during that season. The first season of trapping was omitted from the analysis as no animals could be classified as "regularly trapped" during this initial period. Adults whose death was known to be caused by human interference were also omitted. The variables influencing adult mortality were investigated using a series of logistic regression models and analysis of deviance (Tabachnick and Fidell 1989). The models were developed using backward elimination. As the data were non-orthogonal, each variable was adjusted for the effects of the other variables in the model. The variables tested were sex of adult, and season and year of death.

5.3 Results

5.3.1 *General Pattern of Dentition*

The dentition of *P. assimilis* corresponds to the normal macropodid pattern as described by Kirkpatrick (1978). Young animals have two deciduous molariform teeth, P3 and dp4, which are replaced by the sectorial permanent premolar, P4, in the adult wallaby. The adult dental formula is: $I^1_1 P^1_1 M^4_4$. No canine teeth were observed in either the skulls or radiographs.

The average length of each cheek tooth is summarised in Figure 5.2a. P4 was always longer than M1 in individual animals. Neither sex (F=2.72; df=1,703; P=0.100) nor position (left or right side) (F=0.01; df=1,703; P=0.909) had a significant effect on the length of individual cheek teeth (3-way ANOVA). The interactions, [sex by position (F=0.07; df=1,703; P=0.792), sex by tooth (F=0.14; df=4,703; P=0.965), and tooth by position (F=0.10; df=4,703; P=0.983)] were not significant.

The length of M1 did not decrease significantly with age (based on MES) (1-way ANOVA, F=1.48, df=9,57, P=0.176). However, the size of M1 was much more variable in older wallabies (Figure 5.2b). This may be an artefact of the small sample of wallabies with less than a full complement of teeth (Figure 5.2b). Particularly in older animals, some M1 showed obvious wear and tended to be (1) worn to the roots (2) displaced labially or (3) markedly reduced in length (Figure 5.3b,c,d). Such extreme changes were not observed in any other cheek teeth.

Few molariform teeth were lost. To be sure that only those teeth that were lost during life and not after collection for museums were included, all museum specimens were excluded from my estimates of tooth loss. The upper and lower jaws of 78 adult animals (MES ≥ 2.2, see below) from Black Rock were examined from radiographs. This revealed that eight (2.56%) P4 teeth from seven animals, 14 M1 (4.49%) from 14 animals and three M2 (0.75%) from two animals were missing. Most animals (70.5%) had a full complement of teeth. No animal had lost more than two teeth.

The cheek teeth of most *P. assimilis* apparently remain in occlusion throughout life (Figure 5.3a,b,d). However, in some of the study animals, the fully erupted posterior molars were not occluded, while the worn anterior teeth were not occluded in others (Figure 5.3c). Imaginary lines through the crests of both upper and lower cheek teeth were only slightly curved, and the ventral margin of the mandibular ramus was parallel to the dorsal margin (Figure 5.3a-d). The roots of teeth in some animals with full MES were deflected slightly backwards (Figure 5.3d).

5.3.2 *Molar eruption*

Extensive sets of observations were available from five 'known-age' animals (2 captive reared ♀'s and 3 wild ♂'s) . Shorter sets of observations were available from another 12 animals (1 captive ♀ and 1 captive ♂, and 3 wild ♀'s and 7 wild ♂'s) (Appendix 6).

Two of the three pairs of upper incisors were fully erupted and the third was erupting by permanent pouch emergence. The first molar was fully erupted at 226-268 days ($n=2$). P4 erupted between the time of full eruption of M2 and M3 ($n=8$). Two captive females reached reproductive maturity (eversion of the teats, Chapter 4.3.1) at MES of 2.0 (20 months) and 2.6 (23 months). Full molar eruption has not yet occurred in any of the known-age animals. The oldest known-age animal (31 months) was a captive animal (#079) with a MES of 2.6. Two wild animals did not have a full complement of cheek teeth when at least 4.5 years old.

A logarithmic equation was used to describe molar eruption. Individual curves were constructed from the five animals measured extensively. The fits assessed by residual plots were satisfactory. A single curve of the same functional form was fitted to the pooled data for these animals. The individual curves were significantly different from the pooled curve ($F=9.740$, df=6,17, $P<0.001$) indicating individual differences in the timing of eruption. However, in view of the small sample of animals which were extensively measured, a pooled curve was fitted to all 'known-age' animals and its form was:

$$\text{MES} = 1.2784 * \text{Ln (Age in days)} - 6.0512 \qquad (5.1)$$

(r^2=0.90, range: 175 - 948 days).

The inverse of Equation 5.1 should not be used to predict age from MES as the error structures of the inverse equation and that of the curve independently derived for predicting age from MES are different. Since age is predicted from MES for most of the wild populations, the data from the 13 known-age wild animals (listed in Appendix 6) were used to generate a second pooled curve to describe the relationship between age and MES:

$$\text{Ln (Age in days)} = 0.8587 * \text{MES} + 4.9629 \qquad (5.2)$$

(r^2=0.90, range: 175 - 581 days).

Molar eruption stages potentially estimate age very well until full molar eruption (Figure 5.4a). The asymptotic age predicted by Equation 5.2 is 9 years 2 months (95% C.I.: 8 years 2 months - 10 years 1 month). My estimates of rock-wallaby age were converted to months so that I could derive a curve of the same functional form as that used by Bell *et al.* (1989) for captive *P. assimilis*. The values of the parameters of my curve were within the 95% confidence limits of those of Bell *et al.* (J. Bell *personal communication*) and hence are not significantly different. As the curve generated by Bell *et al.* (1989) was based on more complete data for older animals, I used this curve for age prediction (Equation 5.3) [I have used logarithms to base *e* rather than to base 10 as in Bell *et al.* (1989) as the former is more appropriate for mathematical modelling (G. De'ath *personal communication*)].

$$\text{Ln Age} = 0.670 * \text{MES} + 1.727 \qquad (r^2=0.97) \qquad (5.3)$$

where age is measured in months (range: 6 - 80 months)

5.3.3 *Molar movement*

Insufficient data were available from 'known-age' animals to compare individual curves describing the change in the molar index with age. Accordingly, the data from all 17 'known-age' animals from Black Rock (6 females and 11 males; see Appendix 6) were pooled and a logarithmic curve fitted (Figure 5.4b). This was of the form:

$$\text{MI} = -4.2992 + 0.91463 * \text{Ln (Age)} \qquad (r^2=0.92) \qquad (5.4)$$

where age is measured in days and MI is the molar index.

There was no significant gender difference in the estimated annual rate of molar movement for 'known-age' animals from Black Rock (F=0.148; df=2,39; P=0.863).

There were 23 animals from Black Rock with fully erupted molars for which there are good sequences of radiographs over at least one year. These include 14 animals whose molar index increased by 0.2-0.3, seven animals with an increase of 0.1 and two with no change in molar position over the study period. This indicates that the forward movement of teeth in this species is variable and slight after full molar eruption has occurred. There was a strong correlation between molar index and MES (r^2=0.97, n=66).

5.3.4 *Age Structure*

The year of birth of the 48 radiographed animals at Black Rock which were caught as adults was estimated using Equation 5.3. A minimum age of seven years at first capture was assigned to animals whose teeth were fully erupted when they were first caught on the assumption that tooth wear, movement and eruption are constant between individuals and over time at this site. Most animals had full MES although this occurs at least five years after reproductive maturity. Their MES (Figure 5.5) indicated that most of the adults examined (33/48) were born prior to early 1980's. This indicates an age structure biased towards older adults and suggests that recruitment into the adult population of the colony was very low throughout the 1980's coincident with years of mostly less than average rainfall (Chapter 2).

5.3.5 *Maximum lifespan*

Data on the maximum lifespan of *P. assimilis* are sparse. An unknown number of rock-wallabies were tagged at Black Rock in 1973-6 (W. Davies *personal communication*). When I commenced my study ten years later, only one of these tagged individuals (#413) was confirmed alive. As it was tagged as an adult, it lived for at least 12 years (W. Davies *personal communication*). The teeth of this animal were like those of no other animal examined as they were extremely worn and 'peg-like'. An individual reared in captivity, lived to almost 8 years (J. Bell and R. Close *personal communication*) and a second, semi-captive *P. assimilis* is reported to have lived to 11 years 2 months, but this age remains unconfirmed (P. Johnson *personal communication*).

5.3.6 *Adult mortality*

The remains of 15 marked adults (4 ♀'s and 11 ♂'s) were found during the study period. While emigration cannot be discounted, a further 12 animals probably died judging by either (1) the state of their empty radio collars (n=2) (A. Horsup *personal communication*), or (2) their poor health just prior to disappearance (trapping records) (n=3), or (3) their abrupt disappearance after a long period of regular observations (A. Horsup *personal communication*) or trapping (see Appendix 8) (n=7). Adult mortality in the colony was probably under-estimated as it is doubtful that all dead animals were found. I estimate that at least 27 adult rock wallabies (9 ♀'s and 18 ♂'s) [excluding the three that died in traps (see below)] died throughout the study period (Figure 5.6). These animals represent a known loss of 28.7% of the tagged adult population during the three year period.

The pattern of mortality was not affected by year (Δ Deviance = 0.03, df=2, P=0.985), season (Δ Deviance = 0.88, df=2, P=0.644) or sex (Δ Deviance = 0.18, df=1, P=0.671). Most of the dead adults (19 of 23 animals) were relatively old (MES=4.0). The other four adults for which data were known, had an MES ≥3.2. There was no significant difference between the age composition (as determined from MES) of the adults dying and those of the entire population (χ^2=2.75, df=4, P=0.600).

The full extent of capture stress is unknown although trapping directly caused the death of three females (from heat stress, cold stress and as a result of fighting with an adult male caught in the same trap) (Figure 5.6). However, 12 of the 27 animals which died were trapped regularly (and often more than once during a single trip) and died at least one year after initial trapping.

For most animals, post-mortems were necessarily conducted too long after death for the cause of mortality to be identified, and in some cases only a skull was found. However, a proximate cause of death could be inferred for several animals. The oldest known animal (#413) (≥12 years), was caught only once and her deterioration may have been exacerbated by capture stress. Her teeth were peg-like and extremely worn, and her body condition was poor. Her body was never found. The health of another female (#008) as measured by blood parameters (P. Spencer *personal communication*), declined over several months, with the suspected contraction of the bacterial disease *Toxoplasma* and blindness in one eye. A complete fracture of each premaxilla of an adult male (#071) was detected on successive field trips, before he disappeared from the colony. Radiographs indicated that the fractures had occurred between field trips (K. Barry, R. Waterhouse *personal communication*).

5.4 Discussion

5.4.1 *Estimating the age of P. assimilis*

Molar eruption has proved to be a valuable basis for estimating the age of *P. assimilis* well into adulthood, despite significant individual differences in the timing of eruption of specific teeth. Full molar eruption is not attained until at least 4.5 years (Bell *et al.* 1989) and possibly not until 10 years (upper 95% confidence limit). On the basis of a trapping study, Kinnear *et al.* (1988) reported that *P. lateralis* with four erupted molars were 6+ years old and that some animals lived for at least 12 years.

Although there were no significant differences between the data from captive animals (Bell *et al.* 1989) and wild animals from Black Rock in the ages of molar eruption, this conclusion should be treated with caution as the curve generated for the Black Rock animals had to be extrapolated.

After all teeth have erupted, the forward movement of teeth is slight in *P. assimilis* and is probably more consistent with mesial drift than molar progression. This result suggests that measurements of molar movement have limited application for age determination in this species, despite their use for age estimation in *P. xanthopus* (Poole *et al.* 1985). However, in his review, Sanson (1989) considered that *P. xanthopus* tends slightly more towards the grazer grade than other *Petrogale* spp. This conclusion is consistent with faecal analyses which suggest that *P. xanthopus* (in the Flinders Ranges of South Australia), consumes more grass than *P. assimilis* at Black Rock (Copley and Robinson 1983, Horsup and Marsh 1992).

5.4.2 *Population age structure*

Assuming that the age distribution of the trapped animals was representative of the adult population (which seems likely in view of the high proportion of tagged animals), the age structure of the rock wallaby colony at Black Rock was skewed in favour of older animals. I trapped surprisingly few young adults

(Figure 5.5), a result which is consistent with Horsup's behavioural observations during the same time period (unpublished data), and which indicates that there was little recruitment into the adult population in the 1980's. The age distribution indicates that this low recruitment pre-dates the start of my study in 1986 and thus is not solely attributable to handling stress as suggested for a captive colony of *P. xanthopus* (Poole *et al.* 1985). It is, of course, possible that handling stress exacerbated the already extreme environmental stress on these animals. Low recruitment occurred despite the continuous breeding pattern of *P. assimilis* and the high proportion of females with pouch young (87%) (Chapter 8). There is little evidence of movement of wallabies between the Black Rock colony and the nearest, small colony 2 km away, although this has not been studied explicitly. Low recruitment is thus unlikely to be the result of emigration.

Several factors have probably combined to cause the low rate of adult recruitment at Black Rock. Local landowners consider the last decade to be one of almost continuous drought and certainly below average rain has fallen for seven of the ten years (Chapter 2). Drought has been recorded as seriously affecting the recruitment patterns of other macropodids in seasonal environments, in particular *M. rufus* (Newsome 1977) and *M. giganteus* (Kirkpatrick and McEvoy 1966). These studies reported a severe or total reduction in survival of pouch young leading to low recruitment into the breeding population coincident with long drought periods. The climate at Black Rock is notably unpredictable (Chapter 2, Ridpath 1985, Jones 1987), and while there is no evidence of the population entering anoestrus, there is evidence of individuals entering anoestrus (Chapter 7).

Pouch young survivorship in *P. assimilis* is also seriously affected by seasonal droughts (Chapter 8).

The effects of drought on rock wallabies are probably exacerbated by predation. Rock wallabies are dependent on rocky crevices for shelter sites and exhibit strong site fidelity [Animal #413 was found occupying the same shelter site as it was first observed ten years previously (W. Davies *personal communication*)]. Young animals may be forced to occupy sub-optimal shelter sites particularly on the periphery of the colony. These animals would then be more susceptible to greater environmental extremes and predation. At least eight rock wallabies including five juveniles were eaten by a feral cat at Black Rock after my main study period had finished (Spencer 1991). Kinnear *et al.* (1988) present convincing evidence that fox predation caused a population decline in colonies of *P. lateralis* in Western Australia.

The cause of most adult mortality could not be determined, although more than 25% of tagged adults died during the three year study period. There was no differential mortality of either sex or age class when compared with that found in the Black Rock population. Nor were rock wallabies dying in proportionally greater numbers during different seasons or years, which is surprising in view of the poor environmental conditions in late 1987 relative to other years (Horsup and Marsh 1992, Chapter 6).

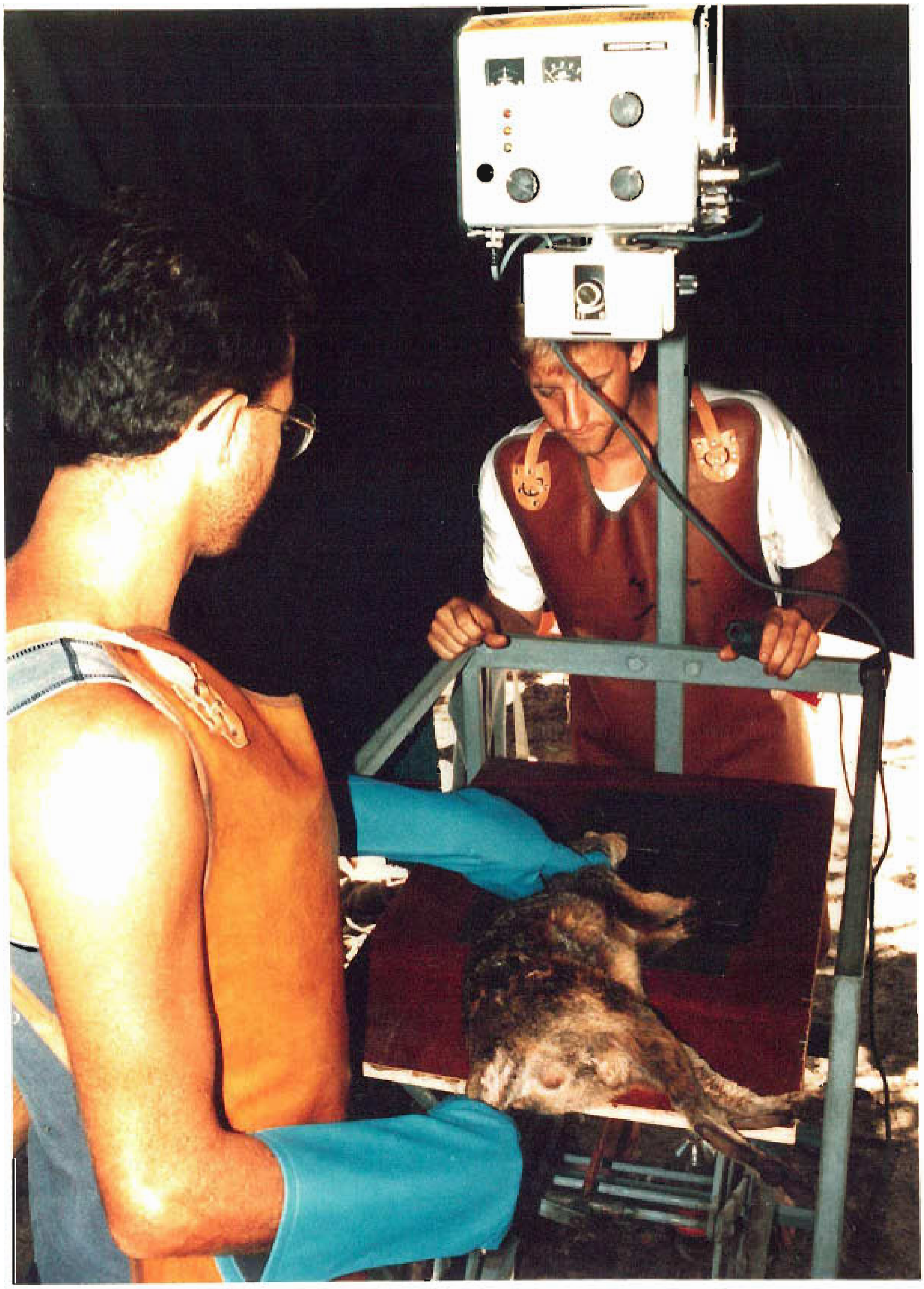


Figure 5.1 Radiography machine in use at 'Black Rock' with operators positioning the head of an adult rock wallaby for a lateral radiograph. Note the use of safety gloves and aprons.

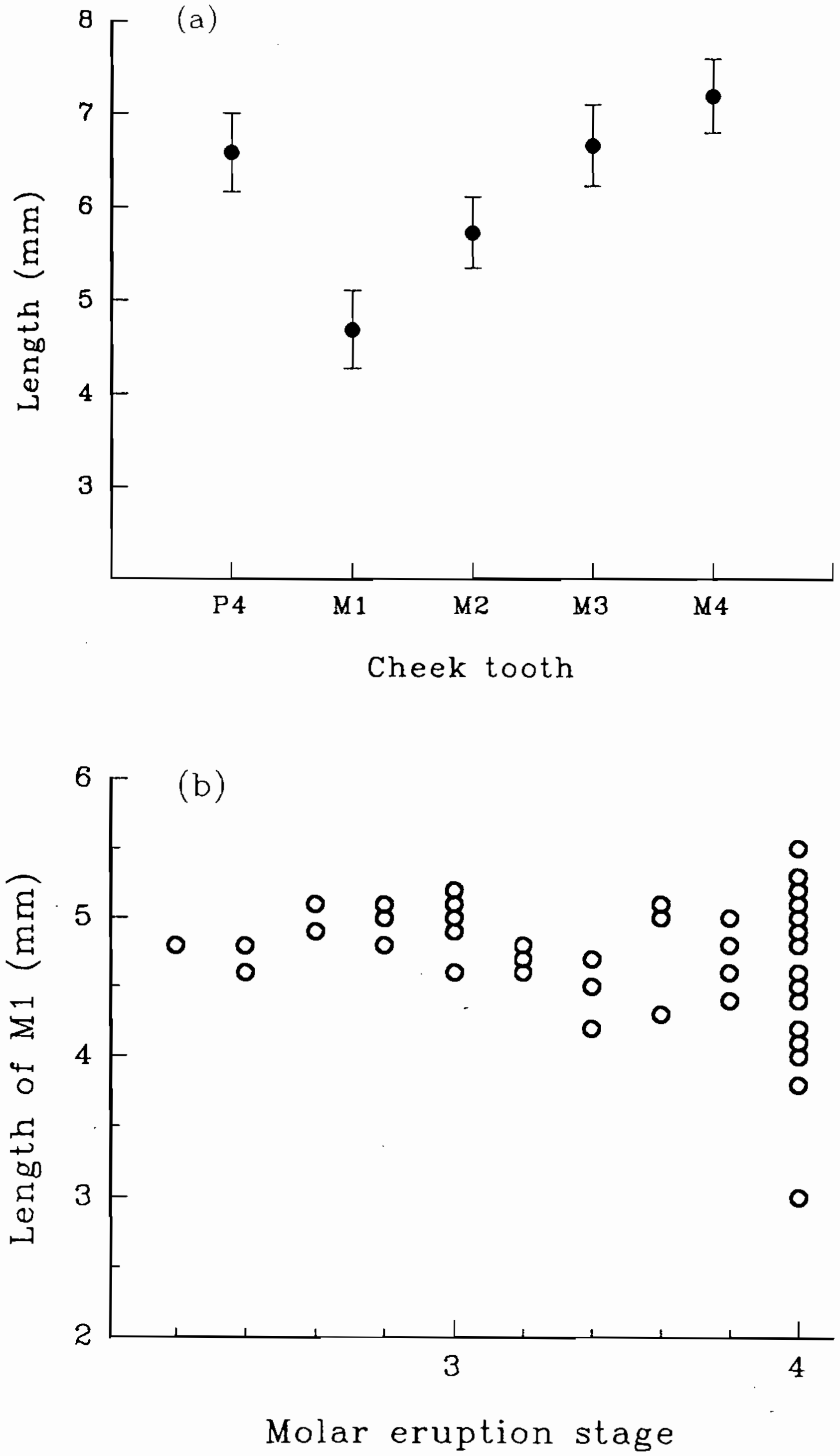
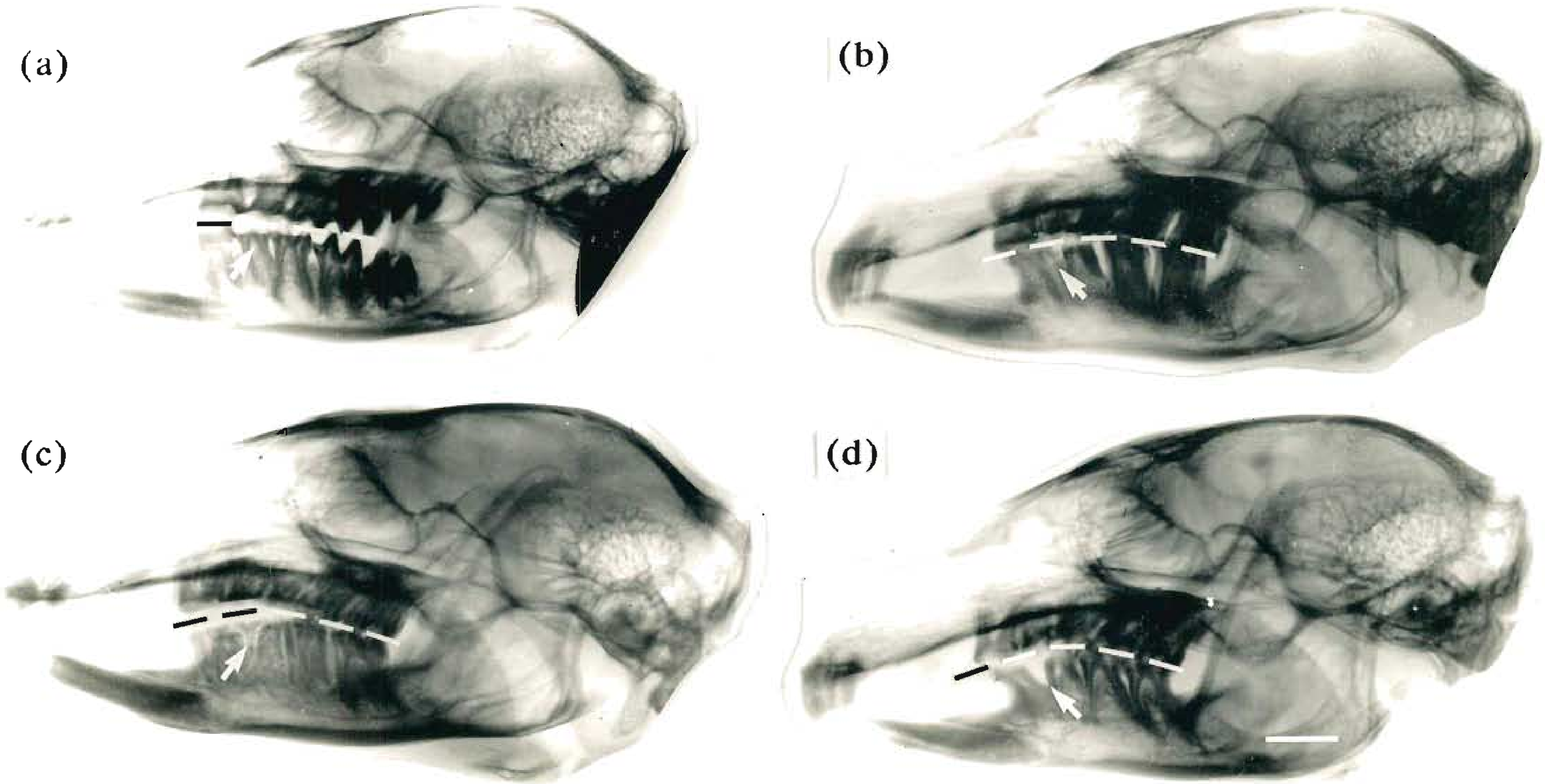


Figure 5.2 Length of cheek teeth measured from skulls of *P. assimilis*. (a) for each cheek tooth (mean ± 1 s.e.) and (b) the length of M1 measured in skulls of different Molar eruption stage (MES).

Figure 5.3 Comparison of lateral radiographs of four P. assimilis from 'Black Rock' (a) ♀ Molar Eruption Stage 3.2; (b) ♀ MES 4.0; (c) ♂ MES 4.0; (d) ♀ MES 4.0; showing variability in (1) the size and wear of M1; (2) the occlusion of cheek teeth; and (3) backward deflection of the roots of some molars (see 4.3d).


(a)
(b)
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(d)

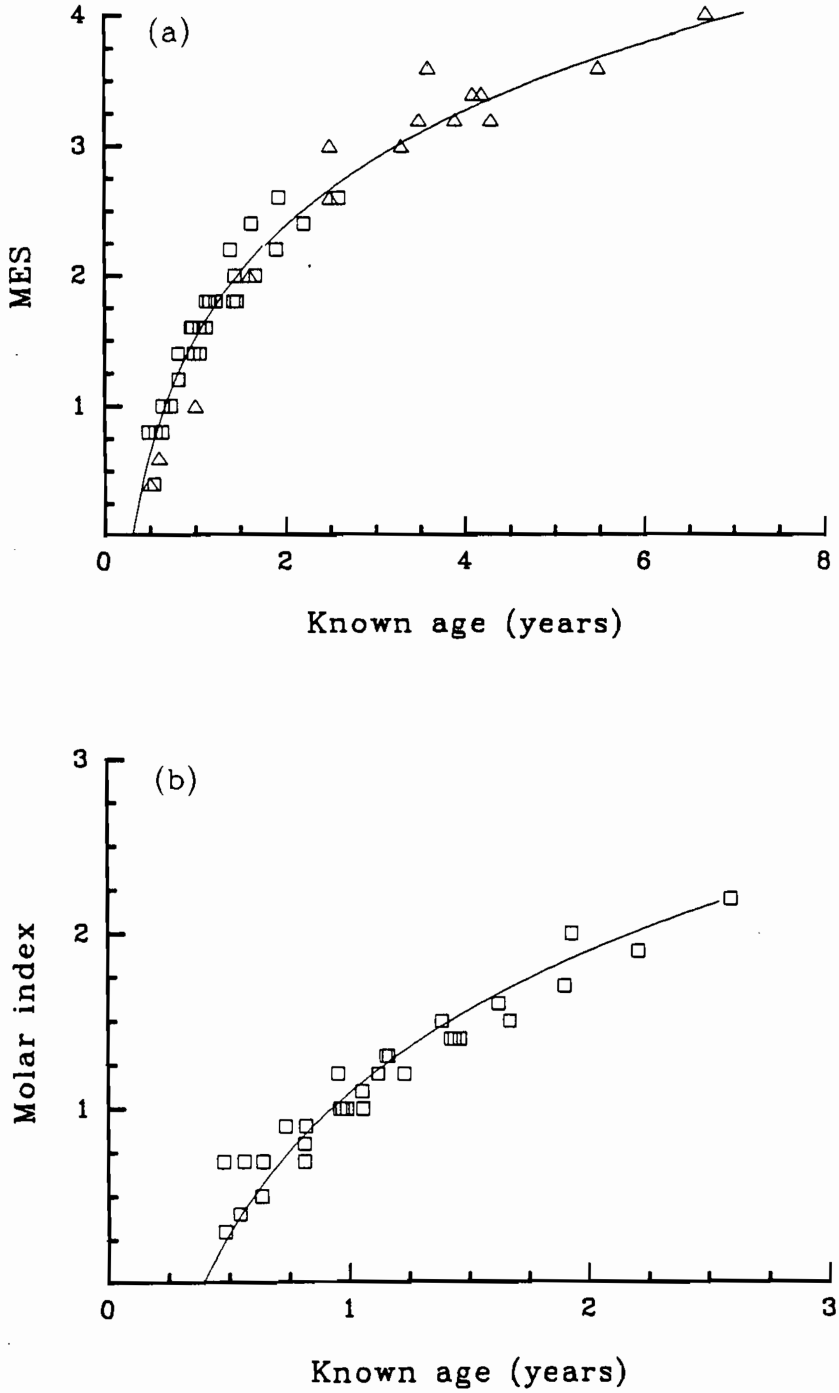


Figure 5.4 Raw data and regression curves for *P. assimilis* of known age showing (a) Molar Eruption Stage (MES) and (b) molar index. (□) 'Black Rock', (▵) data from Bell *et al.* (1989).

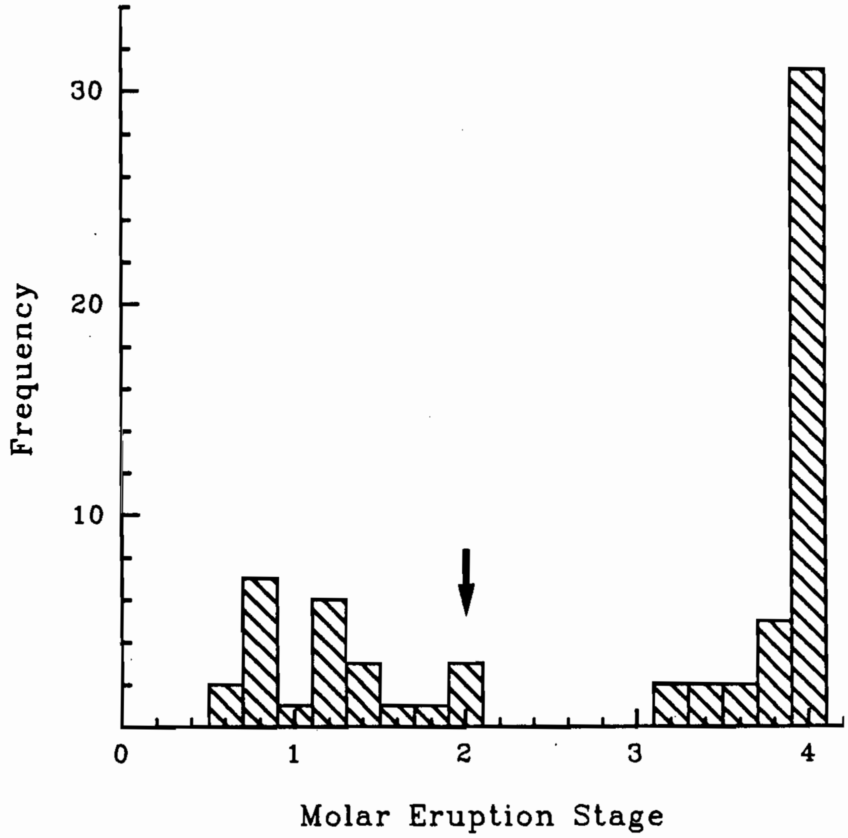


Figure 5.5 Frequency of rock wallabies of different MES (Molar Eruption Stage) sampled within the 'Black Rock' population between June 1987 - June 1989. Arrow marks MES at sexual maturity. Note the lack of young adult animals.

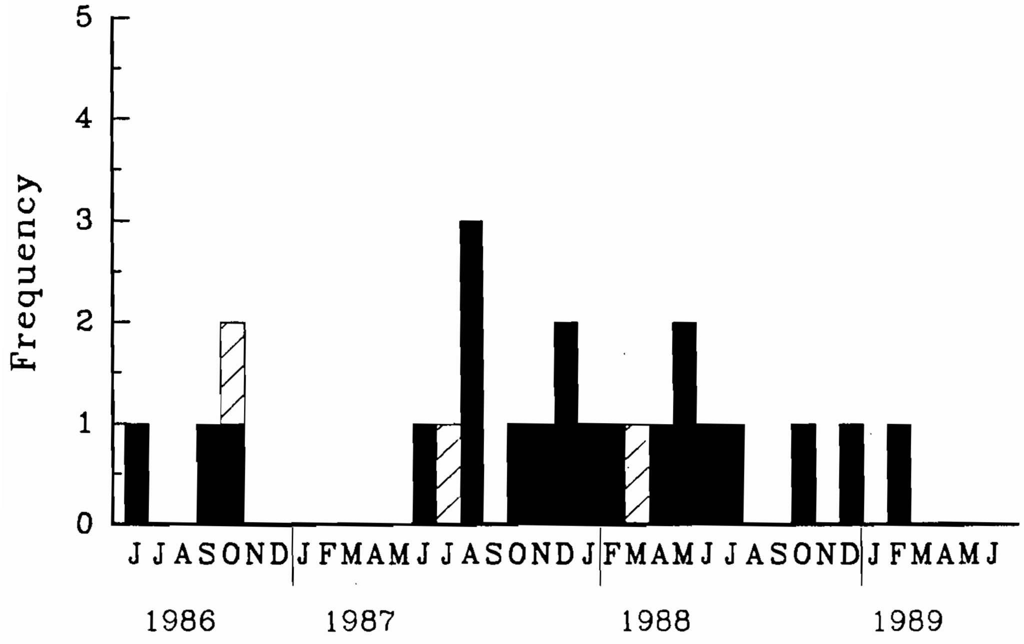


Figure 5.6 Monthly distribution of ■ natural and ▨ trapping mortality of adults during my study period. Vertical bars on the x-axis denote the change from the late dry season to the wet season of each year (see Chapter 2).

Chapter 6

Influence of seasons on body weight and packed cell volume of the blood

6.1 Introduction

The influence of the seasons on the body condition of a species is manifest through the availability of free water and the quality and quantity of forage (as energy and protein) (Main 1970). These factors are dependent on the unpredictable wet season in the wet-dry tropics of northern Australia, as pasture growth is usually restricted to a period during and just after the wet season in this region (Ridpath 1985). While unseasonal rain may prolong pasture growth and water availability, the quality and quantity of forage and free water available usually decreases during the year to its lowest point at the end of the dry season. Both the water and nutrient content of forage decrease during this time (reviewed in Hume 1982). As the quality of the diet falls below that necessary for physiological well-being, animals lose body condition (Main 1970).

While it has long been recognised that a relationship exists between the state of the environment and an animal's physiological condition, no single method has been used to measure this phenomenon. The techniques used include aspects of growth, deposited fat reserves, adrenocortical hypertrophy, blood haematology and chemistry, and urinary excretion of hydroxyproline (Hanks 1981, Humphreys *et al.* 1984). All of these methods have both advantages and disadvantages. Some, such as measurements of deposited fat reserves and adrenocortical hypertrophy, are invasive and may require killing animals, although more recently, techniques such as those using doubly labelled isotopes have circumvented this process (Nagy 1989). Other methods such as indices of blood chemistry and haematology and urinary excretion of hydroxyproline are less invasive. The most commonly used (and least invasive) methods use aspects of an animals growth and are based on the premise that reduction in weight or growth rates can be equated with poor condition. All of the above mentioned methods have met with varying success in different species in equating physiological condition with environmental parameters (Hanks 1981, Humphreys *et al.* 1984).

The physiological condition of macropodidsis usually studied by measuring some aspect of growth (usually weight) as an individual's body weight has been shown to be an indicator of its condition and may fluctuate with the seasons. For example, for four species of macropodid in Western Australia, the decrease in the weight of wild animals as the dry season progresses was correlated with the duration and intensity of the yearly drought season (Main 1970).

Some authors have also used blood haematology (notably Ealey and Main 1967 and Shield 1971) and have reported seasonal changes in constituents of the blood for at least two species of macropodids. In a tropical population of the Euro, *M. robustus*, significant changes occurred in haemoglobin levels and these were reflected by changes in haematocrit values and erythrocyte counts (Ealey and Main 1967). The lowest values occurred in summer when the level of plant protein (as measured by nitrogen content) was lowest. The highest values were observed during April when the vegetation had ceased growing and was beginning to dry. Similarly, Shield (1971) observed a decrease in haematocrit levels, red cell volume and weight in the quokka, *S. brachyurus*, during autumn, commensurate with a period of semi-starvation which occurs during late summer and autumn associated with a decline in forage quality (Shield in Shield 1971). During a very severe drought, individuals may starve, their health deteriorates and ultimately they die (Main 1968). While Algar, Arnold and Grassia (1988) did not observe any significant changes in haematocrit values with changes in dietary nitrogen in captive grey kangaroos, they did report significant seasonal changes in these blood parameters. The highest haematocrit values occurred when body weight was also highest.

I expected *P. assimilis* to show marked seasonal changes in body condition since it is an opportunistic herbivore, varying its diet according to plant availability (Horsup and Marsh 1992). Rock wallabies at Black Rock feed mostly on forbs and browse, but proportionately more grass is selected when fresh green growth is available than at other times. The preferred food species are relatively rare in the surrounding savanna woodland (Horsup and Marsh 1992), but are concentrated in areas such as the rocky outcrops where rock wallabies are found.

Freeland, Winter and Raskin (1988) observed that in Australia, specialised rock dwelling species of mammals are concentrated in the seasonal tropics. They postulated that both the fauna and flora of these rocky outcrops are able to take advantage of the associated unique environmental features. Moisture accumulation among rocks has resulted in a greater species diversity and a higher biomass of the grass-forb layer than is found in the surrounding habitat. Rock mammals may gain an energetic advantage and suffer less dehydration by sheltering in cool caves during periods of high temperature (Russell 1974). Thus for *P. assimilis*, rocky outcrops presumably act as a buffer ameliorating the harshness of the environment as detailed in Chapter 1.

In this chapter, I examine the influence of the seasons on the body weight and blood packed cell volume (PCV) (or haematocrit) of adult *P. assimilis* during the two complete weather years (i.e. including wet to late dry seasons) of my study. I could not directly examine the relationship between body condition and seasonal changes in forage quality or quantity by studying the rate of water turnover in individual rock wallabies, as funds were not available. However, this aspect of the physiological ecology of *P. assimilis* is being studied by Helene Marsh of James Cook University and Jim Merchant of C.S.I.R.O. (Merchant and Marsh 1992). Unfortunately their work has not been finalised.

6.2 Methods

The study period (June 1986 - June 1989; Chapter 2.2.1) included two complete years as defined by the onset of the wet season (see Chapter 2.1.3, Table 2.1) (January 1987 - January 1988 and February 1988 - December 1988 inclusive) which had similar amounts of rainfall (413mm and 425mm respectively). Unless otherwise stated years refer to weather years (as defined in Chapter 2.1.3) in this chapter. Most methods of measuring body condition (reviewed in Hanks 1981 and Humphreys *et al.* 1984) require either killing animals (e.g. to measure total body fat) or specialised equipment and were thus unavailable to me. However, body weight and packed cell volume of the blood (PCV) have been shown to change seasonally in other macropodids (e.g., Ealey and Main 1967, Hume 1982), and so they were chosen as measures of body condition. The PCV or haematocrit value of the blood (red cells plus white cells and the platelet layer as a proportion of the whole blood volume) used was not corrected for plasma trapped amongst the cells. Nor was any allowance made for the effects of water deprivation or diurnal variation on the values obtained for PCV. Initially, the tail condition index of each animal was also taken each time it was examined by ranking the proportion of muscle:bone at the base of the tail (1-6; lowest to highest). This index proved to be very subjective and hence was considered inappropriate and abandoned as a measure of body condition.

A variable number of observations was available for each trapping month depending on trap success. Individual wallabies were recaptured during zero to 27 trapping months during the study. Repeated measures ANOVAs were the most appropriate and powerful analyses as they allow for the influence of measurements taken in one month for an individual affecting those of other months (Tabachnick and Fidell 1989). These repeated measures ANOVAs were used to test the effect of season (wet, early dry and late dry), year (n=2) and sex on adult body weight and PCV. To overcome the problems of analysing the extremely unbalanced design caused by the variable number of observations between months, the maximum number of individuals which were caught in all the chosen months was used i.e. 14 adult individuals of each sex. Season, year and sex were treated as fixed factors and individual as a random factor nested within sex. Data from a single month each season were used to represent that season, and this month was selected separately for each year to maximise the interval between successive sampling times and the available data (Table 6.1). In order to achieve a balanced design, I used data from an adjoining month on the 22 occasions a study animal was not captured during the month selected.

Table 6.1 The month selected to represent each season and the length of each season for repeated measures ANOVAs of body weight and packed cell volume of the blood.

Weather Year	Wet	Early dry	Late dry
1987	February (Feb-Apr)	June (May-Aug)	November (Sep-Jan)
1988	March (Feb-Mar)	June (Apr-Jul)	October (Aug-Jan)

6.3 Results

6.3.1 *Body weight*

Adult males of *P. assimilis* ranged in weight from 2800 to 4950 grams and were consistently heavier than adult females (2450 to 4750g) (Figure 6.1). If the effect of repeated measures is ignored, then males had an average weight of 4030g (n=352, s.d.=319.3) and females an average weight of 3534g (n=385, s.d.=403.8). The average body weight varied for each trapping month during the study period with, in general, both sexes reflecting the same trends (Figure 6.1; Appendix 9). Generally weight declined as the dry season progressed. This was particularly noticeable in 1987/88. Conversely, there appeared to be little decrease in weight during the dry season of 1988/89. This probably reflects the pattern of rainfall during these years (Figure 2.5). The only two months which were sampled in 1989 (February and June) show a similar decline in average body weight between the wet season (February) and the dry season (June) and suggest that this decline was probably part of a general pattern.

Data used for the repeated measures ANOVAs were not significantly different from the whole sample for each month as in all cases the 95% confidence intervals for the sub-sample overlapped the mean value for the whole sample (Figure 6.2). Results from the repeated measures ANOVAs confirmed the patterns observed in Figure 6.1 for the total data set. There was a significant interaction between season and year on body weight (Table 6.2). This was due to the rock wallabies losing weight (an average of 9.7% of overall mean weight) in the late dry season of 1987 but not in 1988 (Figure 6.3). Both sexes were similarly affected as the interactions between sex and season, sex and year and sex, season and year were not significant (Table 6.2). There were also significant differences between individual wallabies (Table 6.2) indicating that some animals were consistently lighter or heavier than others.

6.3.2 *Blood Packed Cell Volume*

If the effect of repeated measures is ignored, then adult male rock wallabies had a haematocrit value ranging from 28 to 62 (mean=45.52, s.d.=6.195, n=309). This is somewhat higher than that measured for females (mean=42.48, s.d.=4.971, range: 29-60, n=338). The average PCV varied each trapping month during the study period with, in general, the same trends being reflected by both sexes (Figure 6.4).

The changes observed in weight for all animals during the entire study period (Figure 6.1) were also reflected in the PCV (Figure 6.4). Although both

Table 6.2 Repeated measures ANOVA on the effects of sex, season and year on adult body weight. Significant values are in bold type.

Source	df	MS	F	P
Sex	1	11466000	17.42	**0.0003**
Wallaby nested within Sex	26	658270	15.52	**0.0000**
Season	2	484090	11.41	**0.0000**
Year	1	934750	22.03	**0.0000**
Season*year	2	558106	13.70	**0.0000**
Sex*season	2	3712.3	0.09	0.9091
Sex*year	1	46231	1.09	0.2988
Sex*season*year	2	37010	0.87	0.4236
Error	111	42422		

sexes follow the same general trends and their 95% confidence intervals overlap, males consistently had a higher PCV than females. As was the case for weight, there was a strong decrease in blood PCV as the dry season progressed in 1987/88 but there was little such change in 1988. The relationship between trapping month and PCV was in general not as obvious, and hence probably not as strong as that for weight. This probably reflects the fact that the relationship between PCV and seasonal changes is more tenuous than the relationship between season and body weight, and suggsts that variables other than weight influence the observed values of PCV.

Data used for the repeated measures ANOVA were not significantly different from the whole sample for each month as in all cases the 95% confidence intervals for the sub-sample overlapped the mean value for the whole sample (Figure 6.5). Results from the repeated measures ANOVA confirmed the patterns observed in Figure 6.4 for the total data set (Table 6.3).

The repeated measures ANOVA indicated there was a significant interaction of season and year although the differences between the average PCV of the wet and early dry seasons of both years were not significant for either sex (Figure 6.6). However, in the late dry season of 1987 the PCV decreased significantly (mean=38.68), concomitant with the significant weight loss at this time. In contrast, there was a significant increase in PCV in the late dry of 1988 (mean=47.42) (Table 6.3, Figure 6.6). While females have a significantly lower PCV than males (41.77 *cf* 45.16), the interactions between sex and year, sex and season, and sex, season and year were not significant, indicating that both sexes

Table 6.3 Repeated measures ANOVA on the effects of sex, season and year on blood pack cell volume (PCV). Significant values are in bold type.

Source	df	MS	F	P
Sex	1	484.1	8.74	**0.0065**
Wallaby nested within Sex	26	55.4	3.51	**0.0000**
Season	2	26.72	1.69	0.1879
Year	1	615.5	38.86	**0.0000**
Season*year	2	254.0	16.03	**0.0000**
Sex*season	2	0.653	0.04	0.9485
Sex*year	1	31.74	2.00	0.1597
Sex*season*year	2	14.14	0.89	0.4152
Error	110	15.84		

were similarly affected. There was a significant difference between individual wallabies (Table 6.3).

6.4 Discussion

Both 1987 and 1988 at Black Rock were characterised by below-average rainfall (513 and 425 mm respectively *cf* 738 mm) although the rainfall pattern in the two years was quite different. In 1987, the proportion of rain falling in the wet season (77%) was similar to the average (79%). However, my unquantified observations suggest that the rainless late dry season of 1987 was the worst seasonal drought experienced during my study. In contrast, 1988 was unusual in that rainfall was more evenly distributed throughout the year with most rain falling in the dry seasons, and only 43% falling in the wet season. Most of this unseasonal rain occurred between June and August and the resulting flush of pasture growth persisted for most of the dry season of 1988.

The different pattern of rainfall between these two years is reflected in the different proportions of plant species available (Horsup and Marsh 1992). The wet season brought a flush of forb and grass seedlings and rapid regeneration of existing grass clumps. The ground cover of forbs and browse was higher nearer Black Rock than in the surrounding area. While Horsup and Marsh (1992) did not quantify the changes in ground cover in 1987, they noted that very little vegetation at ground level was alive during the dry seasons. In contrast, plant growth was almost continuous in 1988.

P. assimilis at Black Rock is flexible in its diet, selecting different proportions of the plant groups present in different seasons to maximise intake of nutritious and digestible plants (Horsup and Marsh 1992). The amount of grass eaten is generally low, but it was eaten in significantly higher proportions when fresh new growth was available during the wet season or after unseasonal rain. Such new growth is highly nutritious (Dawson 1989). Significant changes in the diet occurred during the late dry season of 1987, with a decreased intake in the dominant forbs and increase in browse. Browse species with stellate trichomes were selected against in all seasons except in the late dry season of 1987 when very little other ground cover was present (Horsup and Marsh, 1992).

This seasonal decrease in the quality and availability of food and water was reflected in the change in individual body condition. In accordance with the lack of sex difference in diet (Horsup and Marsh 1992), and the low level of sexual dimorphism in size (Chapter 4), no differences were found between the sexes in their body condition response to seasonal changes. This is similar to the findings of Spencer and Speare (1992) for blood parameters (including PCV) of rock wallabies at the same study site. Spencer and Speare (1992) also found that neither the age of pouch young nor season had any effect on the haematology of lactating females. Body condition was maintained over the wet and early dry seasons of both years as measured by body weight and PCV. Rock wallabies maintained weight during the late dry of 1988 and their PCV increased. These responses were probably a result of the continued supply of free water and succulent food (and the maintenance of nutrient levels in the forage). In contrast, many of the rock wallabies began to starve and became anaemic during the late dry season of 1987.

While the response of PCV to environmental changes can be explained in rock wallabies, it appears to be quite complex. PCV has been used as a measure of physiological condition of other mammal species and has been found to be both a good indicator (e.g. quokkas, Shield 1971; and sable antelope, *Hippotragus niger*, Wilson and Hirst in Hanks 1981) and a poor indicator (Californian deer, *Cervus elaphus*, Rosen and Bischoff in Hanks 1981) of body condition. Too little is known of the precise relationship between PCV, deposited fat reserves, and the plane of nutrition (Hanks 1981) and until this knowledge is gained, PCV cannot be considered to be a good measure of body condition.

Weight loss has been associated with poor seasons and nutrition in various macropodids by several authors (Hume 1982). While it has been argued that seasonal changes in haematology are independent of nutrition and body condition for some species (Algar *et al.* 1988), a decrease in PCV and red cell volume has been linked with weight loss and semi-starvation in the quokka, *S. brachyurus* (Shield 1971). My results indicate that body condition in *P. assimilis* also changes with the seasons and variation in environmental conditions.

Figure 6.1 Mean body weight (± 95% confidence intervals) of adult rock wallabies during the trapping period; ○ females and □ males. Sample sizes for each sex range from 3-21 (mean=13.1). Only the months which were trapped are labelled. Dotted lines join points in consecutive months.

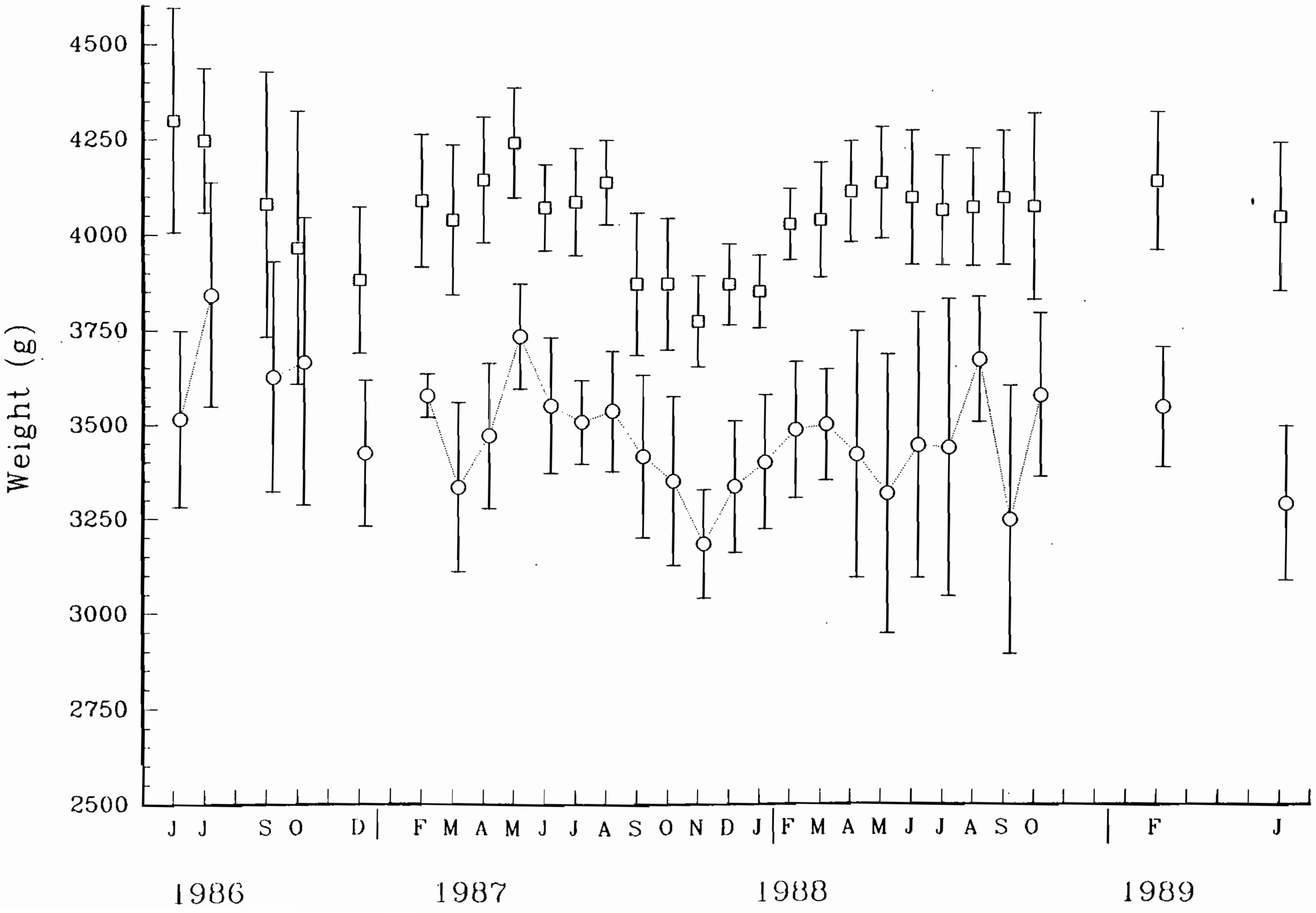
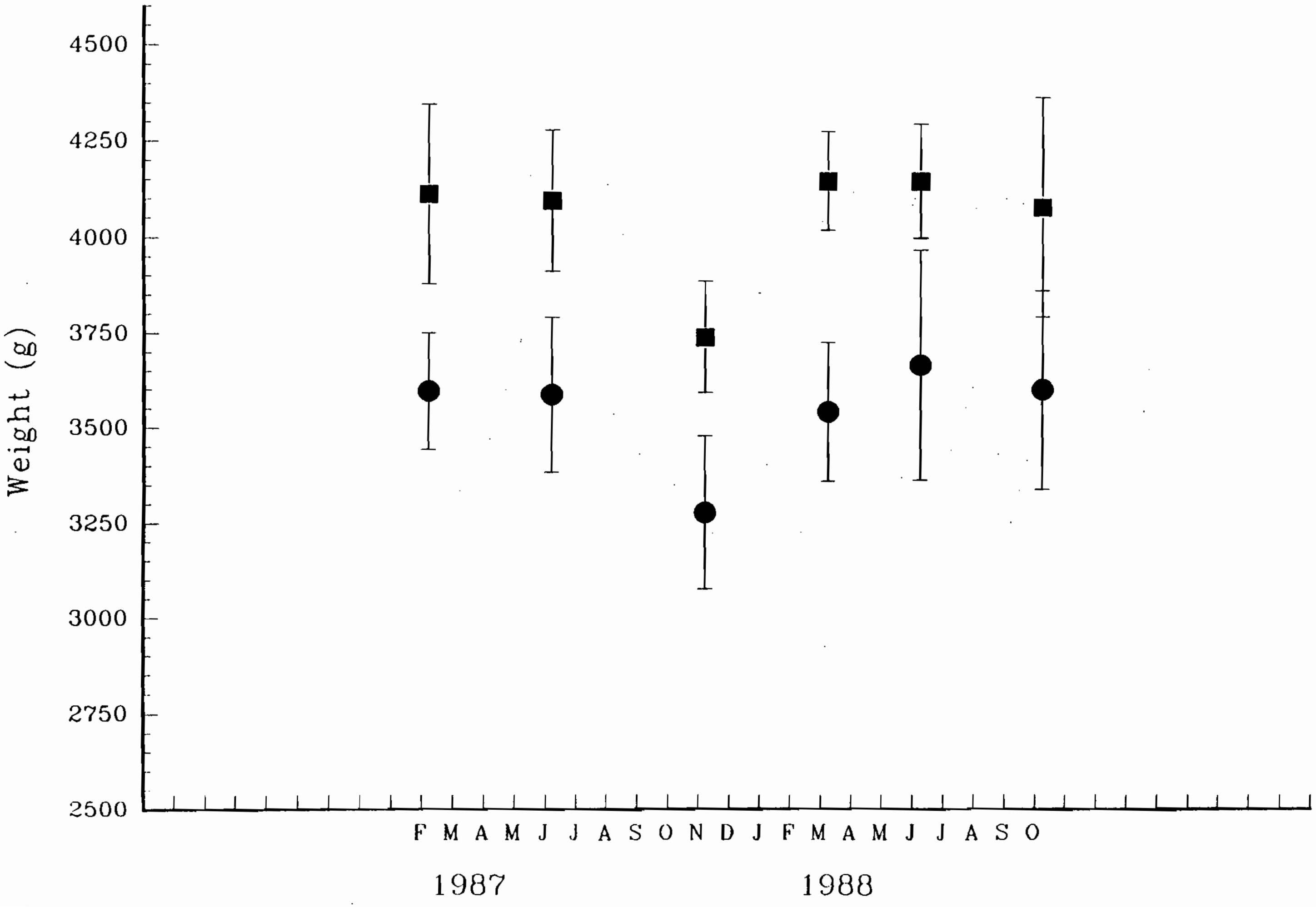

Weight (g)
4500
4250
4000
3750
3500
3250
3000
2750
2500
J J S O D F M A M J J A S O N D J F M A M J J A S O F J
1986
1987
1988
1989

Figure 6.2 Mean body weight (± 95% confidence intervals) of the subsample of adult rock wallabies used in the repeated measures ANOVAs (● females and ■ males) *c.f.* change in mean weight for the whole sample (...) (see Figure 6.1).


Weight (g)
4500
4250
4000
3750
3500
3250
3000
2750
2500
F M A M J J A S O N D J F M A M J J A S O
1987
1988

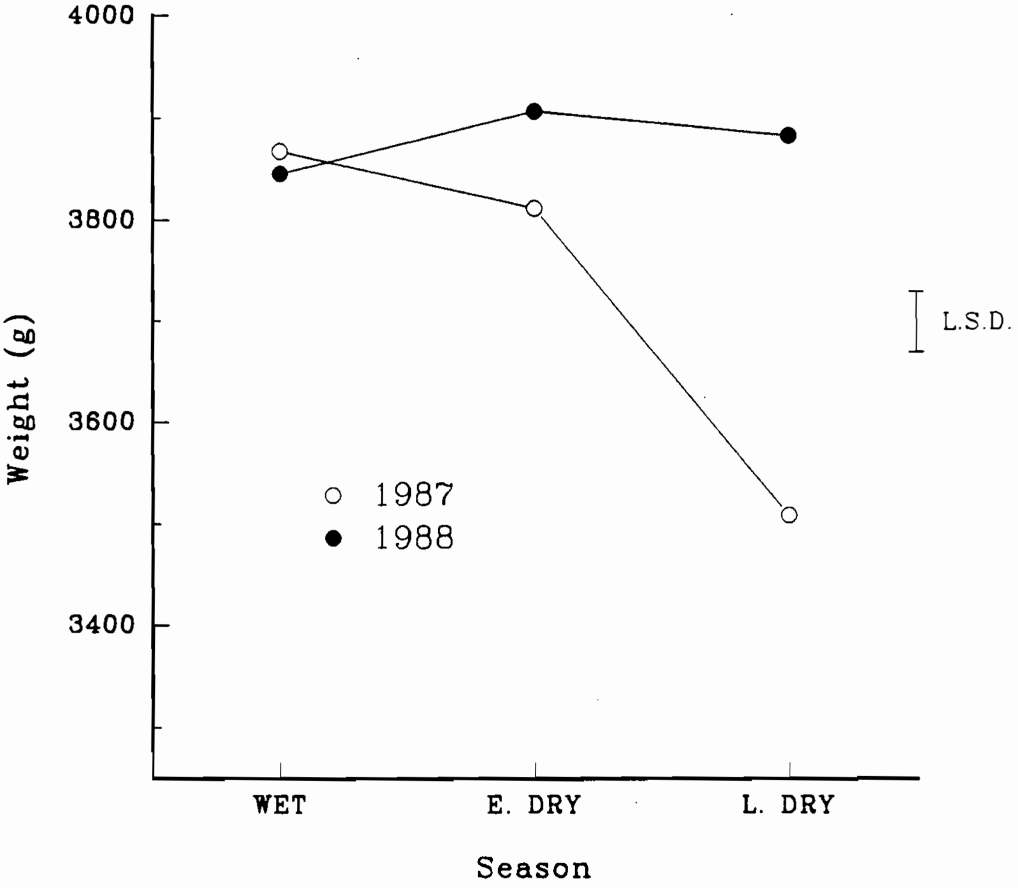


Figure 6.3 Interaction of the effects of year and season in the weight of rock wallabies of both sexes. E. DRY = early dry season; L. DRY = late dry season; L.S.D. = least significant difference (i.e. the smallest difference between any two means which is statistically significant).

Figure 6.4 Mean packed cell volume (PCV) (± 95% confidence intervals) of adult rock wallabies during the trapping period; ○ females and □ males. Sample sizes for each sex range from 3-20 (mean = 13.8). Only the months which were trapped are labelled. Dotted lines join points in consecutive months.

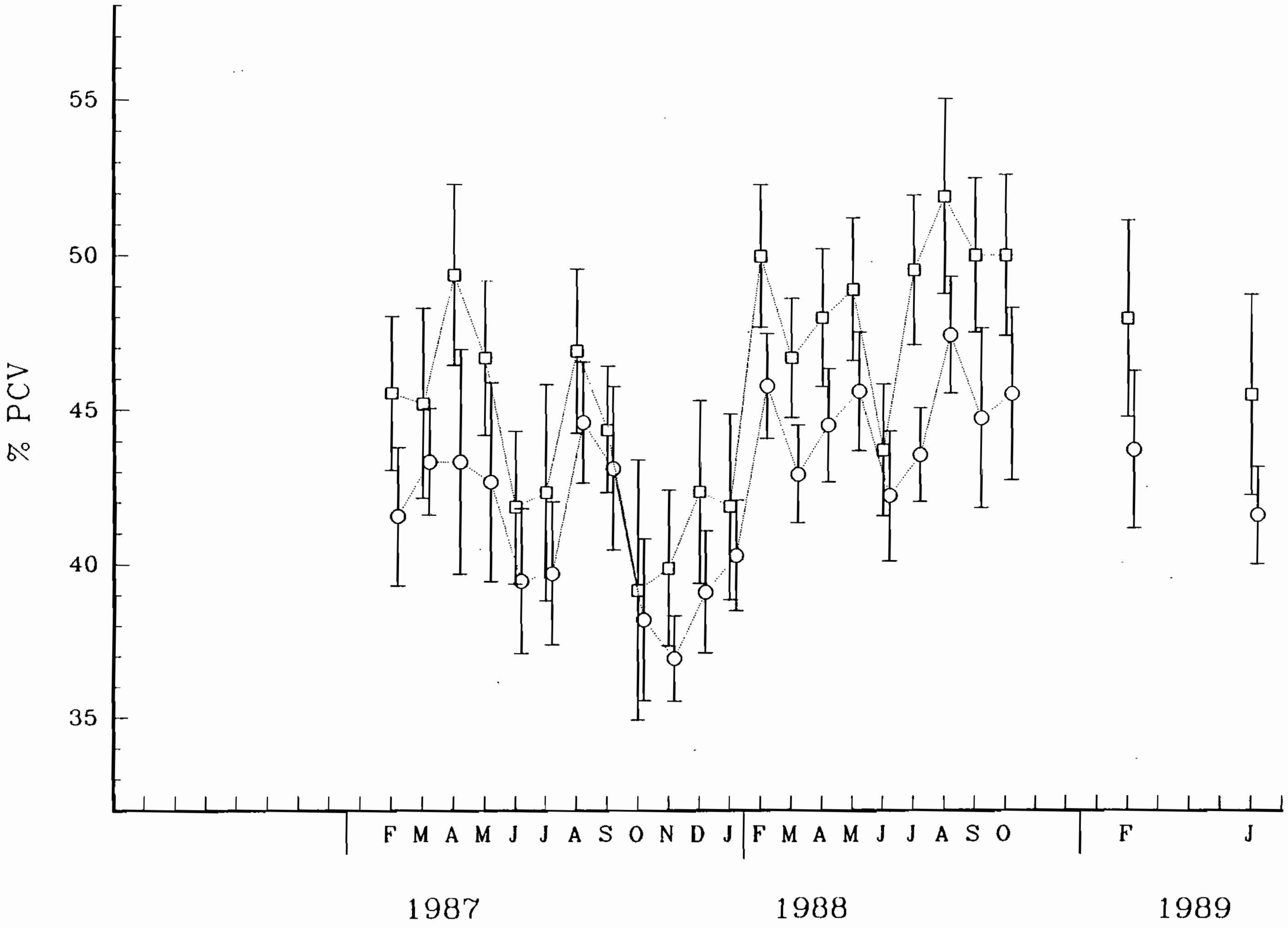
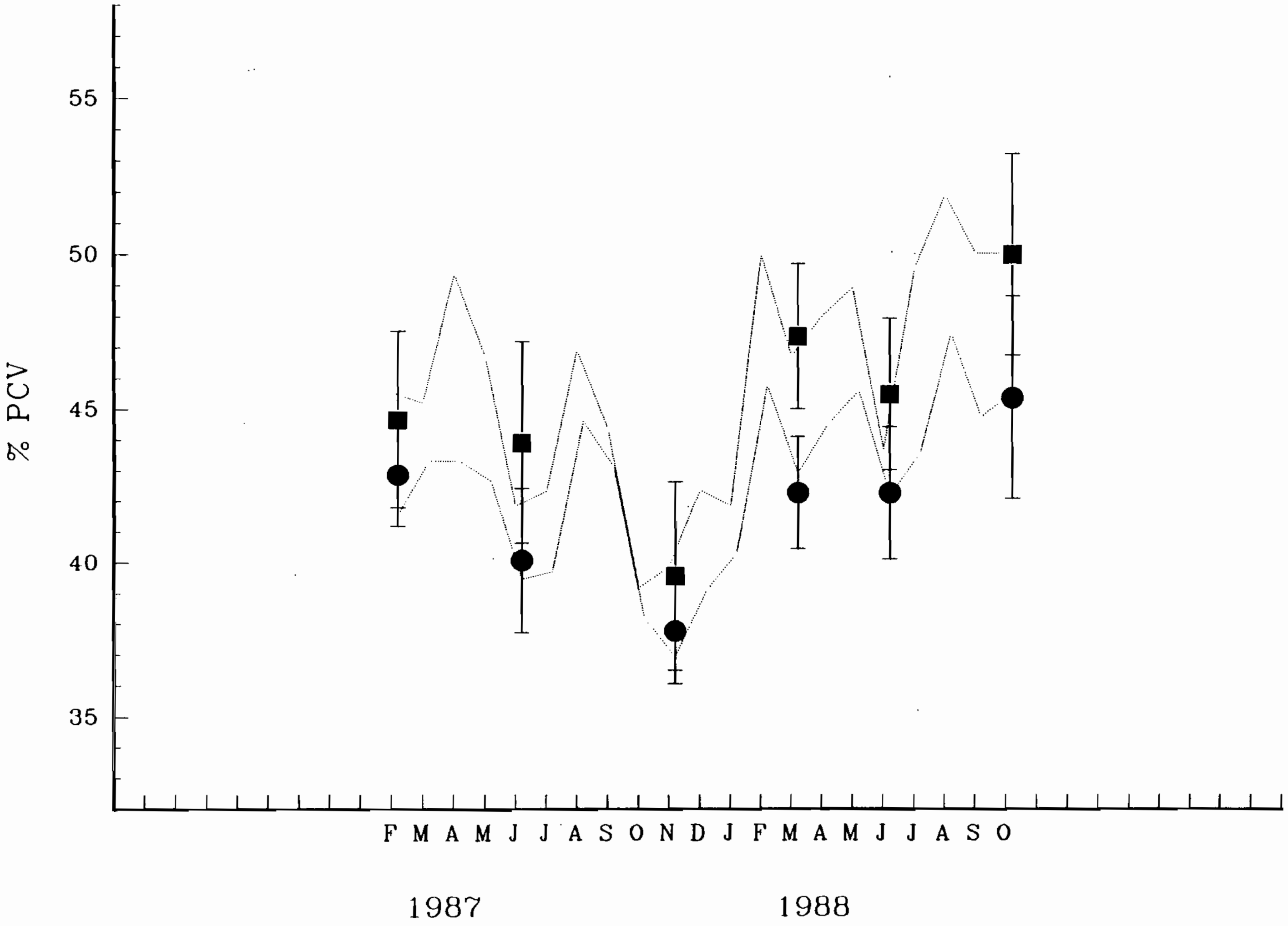

% PCV
55
50
45
40
35
F M A M J J A S O N D J F M A M J J A S O F J
1987
1988
1989

Figure 6.5 Mean packed cell volume (%PCV) (± 95% confidence intervals) of the subsample of adult rock wallabies used in the repeated measures ANOVAs (● females and ■ males) *c.f.* mean change in weight for the whole sample (...) (see Figure 6.4).


% PCV
55
50
45
40
35
F
M
A
M
J
J
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O
N
D
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F
M
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M
J
J
A
S
O
1987
1988

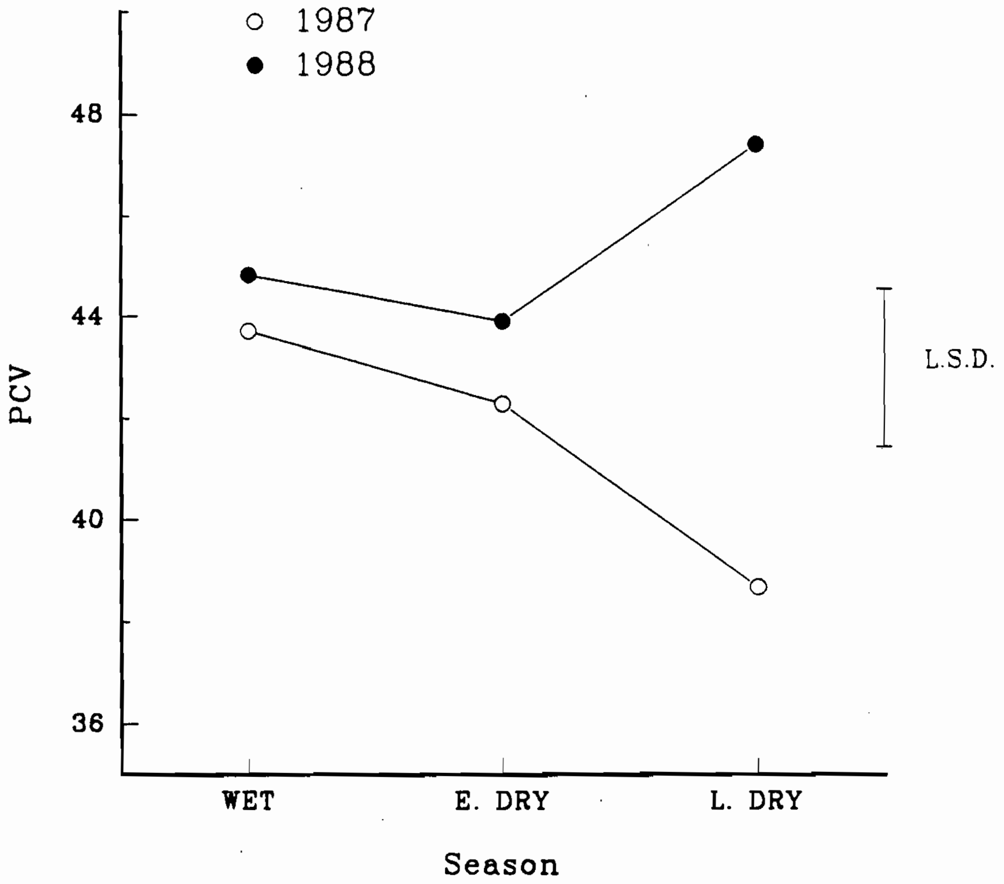

Figure 6.6 Interaction of the effects of year and season in the PCV of rock wallabies of both sexes. E. DRY = early dry season; L. DRY = late dry season; L.S.D. = least significant difference (i.e. the smallest difference between any two means which is statistically significant).

Chapter 7

Overall pattern of reproduction

7.1 Introduction

Many features of the reproduction of macropodoids are exhibited by species of both the potoroidae and the macropodidae. All species except *Hypsiprymnodon* which bears twins (Johnson and Strahan 1982), are monovular and polyoestrus (reviewed in Tyndale-Biscoe and Renfree 1987). The gestation period occupies a much larger proportion of the oestrous cycle (0.84 to 1.09) than in other marsupials. A post-partum oestrus and ovulation usually occur. Conception can occur at this time, but if lactation proceeds normally, the corpus luteum of post-partum oestrus and associated ovulation is inhibited. Lactational-controlled delayed implantation (or embryonic diapause) occurs in all known species of macropodid except some populations of the eastern grey kangaroo (where it is rare (Poole 1973, Stuart-Dick and Higginbottom 1989)) and in the western grey kangaroo (Poole 1975). Females are either continuous, opportunistic or seasonal breeders, the pattern of reproduction reflecting the pattern of seasonal change in the environment. Where seasonal changes are regular, species tend to have precise breeding seasons, but in areas of erratic rainfall macropodids tend to be opportunistic breeders. The different patterns are achieved by slight changes to the basic macropodid reproductive cycle, in particular the timing of ovulation and the time when the corpus luteum is reactivated (Tyndale-Biscoe and Renfree 1987). Anoestrus may occur regularly during lactation [e.g. *M. fuliginosus* and *M.*

giganteus (Poole and Catling 1974)] or can be drought induced [e.g. *M. rufus* (Frith and Sharman 1964)].

Once mature, male macropodids produce spermatozoa continuously unless spermatogenesis is impaired by environmental stress (Setchell 1977, Jones 1989). Males do not show seasonal changes in spermatogenesis, testes size or seminiferous tubule diameter (Inns 1982b). However, seasonal changes observed in the size of accessory reproductive organs may be a response to the breeding condition of females (Inns 1982b, Curlewis 1991).

As this was a field study of *P. assimilis*, not all features of the reproductive cycle were accessible. In particular, those which require internal examination, hormonal studies or sampling at more frequent intervals than the monthly field trips permitted were deemed inappropriate. Nonetheless, the reproductive patterns documented in this study were compared with those of other rock wallabies and macropodids, in order to assess the influence of the unpredictable climate at Black Rock on breeding in this species.

7.2 Methods

The birth dates of all pouch young were calculated using size at first capture as outlined in Chapter 3. This gave birth dates to within a few days, however, for most analytical purposes, accuracy to the nearest month only was used (Appendix 10).

7.2.1 *Data analysis*

Log-linear models were used to test the effect of season (n=3) and year (n=2) (as defined in Chapter 2.1.3), on the number of births per mother. Repeated measures ANOVAs were used to test the effect of season (n=3) and year (n=2) on the size of testes (see Chapter 2) of 11 adult males for which there were sufficient data (Tabachnick and Fidell 1989). Both season and year were treated as fixed factors.

7.3 Results and discussion

7.3.1 *Length of oestrous cycle and gestation*

P. assimilis is usually monovular with only two incidences of twins (both to female #001) recorded at Black Rock since studies commenced (P. Spencer *personal communication*). Of the first set of twins, one young died between 8 and 65 days of age while the other survived to PEP. The second set of twins both survived to at least 111 days but had both died when the mother was caught one month later (P. Spencer *personal communication*).

The teats of one 'known-age' animal (#159) were recorded as inverted (immature) when she was 16.5 months old. Thirty-two days later, the teats were everted indicating sexual maturity. A further 28 days (i.e. at 18.5 months of age) her first young was born. In seven cases for wild females, a small PY was present during one trip and a month later had been replaced by a different small PY, indicating that the first PY had died. These events provided me with the opportunity to estimate the maximum length of the second gestation. The interval between the presence of the first small PY and the calculated birth date of the next was a maximum of 27, 29, 30, 30, 32, 33 and 34 days. In these cases, it seems likely that the mother had a perinatal oestrus and mating and the second PY was the result of the re-activation of a delayed embryo. Additionally, in three cases cloacal plugs were observed within 24 hours of the birth of a young, indicating a post-partum oestrus and mating had taken place.

Captive *P. inornata* have an oestrous cycle of 30.2 to 32 days and a gestation of 30 to 32 days (Johnson 1979). The larger *P. xanthopus* has a slightly longer oestrous cycle (32-37 days) but a similar gestation period (31-33 days) (Poole *et al.* 1985). The limitations of my field data preclude precise estimates of these cycles in *P. assimilis*. However, they are consistent with the hypothesis that *P. assimilis* is similar to other *Petrogale* in the length of the oestrous cycle and gestation period.

7.3.2 *Evidence for embryonic diapause*

The timing of the birth of the second PY in the six cases mentioned above suggests embryonic diapause. Data from other *Petrogale* suggest that too little time had elapsed for these births to be a result of re-activation of the oestrous cycle, subsequent mating and gestation. Embryonic diapause has also been confirmed in captive populations of *P. inornata* and *P. xanthopus* (Johnson 1979, Poole *et al.* 1985).

7.3.3 *Temporal pattern of births*

Females breed continuously with pouch young born in all months of the year (Figure 7.1). The log-linear modelling indicated that the most parsimonious model relating season and year to the number of births per mother, contained only two seasons (wet versus early plus late dry seasons) ($\chi^2=19.6$, df=2, $P<0.001$). This result indicates that there was no difference between years and no difference between early and late dry seasons. However, the pattern of births differed significantly between wet and early and late dry seasons (Table 7.1; $\chi^2=11.29$, df=1, $P<0.001$). During the wet season, 28 of 41 (68.3%) of captured females did not give birth; the remainder gave birth once (13/41 or 31.7%). No captured female gave birth more than once. Most captured females gave birth only once during the dry seasons (49/82 or 59.8%) but some lost their first young and gave birth to at least one more PY during this period (8/82 or 9.8%). Other captured mothers (25/82 or 30.4%) did not give birth during this time. The shortness of the wet season (1-3 months) relative to the minimum inter-birth interval (approximately one month) meant that it was unlikely that a captured female could have a second birth during this season even if her first PY died. The higher survivorship of PY born during the late dry season (Chapter 8) meant that most females captured were already carrying a PY during the wet season and hence there was a lower incidence of births in this season. Despite the difference in the pattern of body weight loss observed between years (Chapter 6), there was no evidence that this difference affected the pattern of births.

Captive *P. inornata* and *P. xanthopus* also breed continuously, as does wild *P. lateralis* (Johnson 1979, Poole *et al.* 1985, Kinnear *et al.* 1988). There is limited evidence that, in northern New South Wales, *P. penicillata* has a peak breeding season although births occur all year (*personal communication* K. Joblin via P. Jarman). Sanson, Nelson and Fell (1985) suggest that another tropical rock

Table 7.1 Contingency table based on the result of the final model used to test the pattern of births against year, season and number of births per mother.

	Number of births / female / season		
Season	0 births	1 birth	>1 birth
Wet	28	13	0
Early + late dry	25	49	8

wallaby, *P. concinna* breeds seasonally (but see also Sanson in Lee and Cockburn 1985). However, it may also be that the constraints of a limited data set and differential survivorship of PY [as found in *P. assimilis* (Chapter 8)], suggest such seasonal breeding.

Continuous breeding may be a response to an environment where resources are either relatively constant or very unpredictable. For wild *P. assimilis*, it seems that continuous breeding is a response to an unpredictable environment (described in Chapter 2). This will be discussed further in Chapter 8 with respect to PY survivorship.

7.3.4 *Pattern of lactation*

Of all captures of adult females between June 1986 and June 1989 (n=476 captures), 87% were of lactating females (Figure 7.2). Most of these captures were of females (73.5%) which were supporting a PY only, a few (5.9%) captures were of females supporting a young at foot only, while others (7.6%) were supporting both a PY and a young at foot when caught (Figure 7.3). Two factors influence these proportions: (1) pouch life (mean=201 days) is much longer than the period from PEP to weaning (mean=41 days) (Chapter 3) and (2) the mortality of PY and young at foot is high (Chapter 8). However, no statistically valid means of comparing the proportion of females in different classes between years and seasons could be found due to the data's being based on repeated observations on individual females and the individual females may change lactational status within a season and hence, I could not determine the influence of climate on this pattern.

Table 7.2 Comparison between three different studies of the proportions of females captured which were supporting young of various age classes.

			Proportion of Females (%)			
Species	Seasonal conditions	N	No Young	PY only	PY + YAF	YAF only
M. rufus[1]	variable	2225[a]	12.2	61.6	16.8	9.4
M. rufus[2]	variable drought	1449[a]	28.4	68.9	1.0	1.7
P. assimilis[3]	drought	476[b]	13.0	73.5	7.6	5.9

[1] Frith and Sharman (1964) [a] Individual specimens
[2] Newsome (1965) [b] # captures of females
[3] this study

My observations are consistent with the general pattern found in macropodids with most females lactating at any time. Few studies have reported the lactation status of all the teats of individual females in sufficient detail to be able to distinguish between those females without PY, with PY only, YAF only or those with both PY and YAF. The two studies that do so, examined populations of *M. rufus* in western N.S.W. and Queensland (Frith and Sharman 1964) and in central Australia (Newsome 1965). The more extreme environmental conditions (including the prevalence of drought) in central Australia is probably reflected by the high proportion of females which were suckling a PY only (68.9%) or had no PY (28.4%) (Table 7.2). Newsome calculated that on average, only 28.7% of all young born survived to become YAF, but this rate of mortality varied from 6 to 100%, depending on the intensity of the drought. In contrast in the more benign conditions examined by Frith and Sharman (1964), proportionately more females were supporting PY and more of these females were supporting a YAF. Frith and Sharman (1964) noted that greater rates of PY mortality occurred at the drier sites. The proportion of *P. assimilis* captured with PY only was slightly higher in comparison with these two studies of populations of *M. rufus* (Table 7.2). The proportions of females with PY and YAF or YAF only was between those observed in the two populations of *M. rufus* studied by Frith and Sharman (1964) and Newsome (1965).

7.3.5 *Evidence of true anoestrus*

In true anoestrus, 'the ovaries lack corpora lutea or tertiary Graafian follicles, the endometrial glands are short and straight with closed lumina and the uteri are very small' (Tyndale-Biscoe and Renfree 1987). I could not assess this on the Black Rock animals without killing animals. However, there was no external evidence of a high proportion of adult females at Black Rock entering such anoestrus during the study period and in particular, the long seasonal drought of 1987 did not induce this phenomenon.

Four females (#013, #053, #107, #133; MES: 3.4-4.0) may have become anoestrus as they spent periods of more than three months without a suckling young (Table 7.3). These incidents were spread throughout the study. The time of entry to these 'lactation-free' phases shows no seasonal pattern; nor is there a consistent pattern in the fate of the previous or subsequent PY. The longest such period was almost ten months (#133) and in this case, the subsequent PY survived to weaning. These phases without PY may have occurred for various reasons: these animals may have not been cycling; cycling without mating; copulating but not conceiving; getting pregnant and losing the new PY in between trapping trips; or continuing quiescence beyond weaning or loss of earlier PY. The last option has never been observed in a macropodoid but could be a unique strategy of rock

Table 7.3 The relative age, PY fate and timing of 'anoestrus periods' for females which had periods without lactation greater than three months.

Female		Time			Fate of PY	
#	MES	Entered	Left	Total (mths)	Previous	Next
013	3.4	Oct 1987	Feb 1988	4.5	failure	failure
053	4.0	Oct 1989	>May 1990	>7	success	unknown
076	4.0	Jun 1990	Sep 1990	3.5	success	unknown
107	4.0	Jan 1990	Jun 1990	6.2	success	failure
133	4.0	Jun 1988	Nov 1988	4.6	failure	failure
		Dec 1988	Sep 1989	9.6	failure	success

wallabies (H. Tyndale-Biscoe, *personal communication*). I am unable to distinguish between these options with the available data. However, the high proportion of young lost within the first month of pouch life (Chapter 8) suggests that the sequence of pregnancy and almost immediately losing the newborn PY is the most likely explanation.

A fifth female (#076) showed evidence of lactational anoestrus; for five months she suckled only a young-at-foot. This was followed by a further four months without a PY. Interestingly, this female was one of the most successful mothers over the study period (Chapter 8). The oldest known animal (#413, >12 years, W. Davies, *personal communication*), had no young suckling at the single time of capture and her teats were assessed to be those of a senescent animal (R. Close, *personal communication*).

Anoestrus occurs regularly during lactation in *M. fuliginosus* and *M. giganteus* (Poole and Catling 1974) and in response to drought in *M. rufus* (Frith and Sharman 1964). No species of macropodid which is confined to the tropics has been shown to enter anoestrus at the scale seen in *M. rufus*, although this may reflect the lack of data on these species rather than a real pattern.

7.3.6 *Sex ratio of PY at birth*

I was able to sex a total of 167 PY (74 ♀'s and 93 ♂'s). There was no significant difference from parity between the sexes in this ratio ($\chi^2=1.08$, df=1, $P=0.298$). The sex ratios of PY of both captive and wild *P. xanthopus* were significantly biased towards males (Poole *et al.* 1985, Lim *et al.* 1987). Cockburn

(1990) showed that significant biases in sex ratios are common in marsupials and most often favour males.

7.3.7 *Comparison of female pattern with other macropodids*

The similarities in female reproductive pattern between *P. assimilis* and other macropods such as *M. rufus*, *M. robustus* and *M. agilis* (Newsome 1975; Bolton, Newsome and Merchant 1982) reflect both their common phylogeny and their distribution in unpredictable environments. These species share the trait of continuous breeding which is thought to be ancestral by most workers (Tyndale-Biscoe 1989). It is likely that *P. assimilis* has a post-partum oestrus and embryonic diapause similar to that observed in most other macropodids. Thus, in favourable conditions, this species is capable of suckling both a young at foot and a PY, while a diapausing blastocyst may be in the uterus. Unlike other studied species of macropodid, a high proportion (44%) of female *M. rufus* becomes anoestrus in persistent (6 months or more) drought conditions (Newsome 1964). This is thought to be a response to the extreme harshness and unpredictability of its habitat in central Australia. While *P. assimilis* lives in an unpredictable environment, the effect of the environment is ameliorated by the rocky habitats to which this species is confined (Freeland *et al.* 1988). There is limited evidence that some female *P. assimilis* may also stop cycling. However, this is not a widespread phenomenon and it is more likely that *P. assimilis* is similar to most other continuously breeding macropods in its overall pattern of reproduction.

7.3.8 *Production of spermatozoa*

The size of the testes of individual adult males remained constant throughout the study period. The mean testes measurements were: 29.5 mm total length, 33.2 mm width (across both) and 16.1 mm depth. In another study of *P. assimilis*, testes greater than 15 mm in length were considered mature (Bell, Close and Johnson 1989). I found individual differences between animals in testes size as measured by the testes index (defined in Chapter 2) (F=3.61, df=10, P=0.013). I do not consider that the significant difference between years in the testes index (F=31.29, df=1, P<0.001) is meaningful as the means differed by 1 mm in each dimension, and this was less than the error of measurement. All 17 adult males (based on size of testes) examined had spermatozoa in their urine (see Figure 4.1). Spermatozoa was present in 93.5% of the samples examined (n=170). The 11 samples in which spermatozoa were absent were from eight animals in eight different months of the two years (Figure 7.4). Hence, neither the size of testes nor urine samples suggest any seasonality in reproductive activity in males of *P. assimilis*.

No evidence of seasonal reproduction was observed in captive or wild male *P. assimilis* by Bell *et al.* (1989), although they reported two males in which spermatogenesis was defective. Hence, males of *P. assimilis* are similar to those of other macropodids in their constant physical readiness to mate, allowing them to exploit fully the continuous breeding pattern of their females.

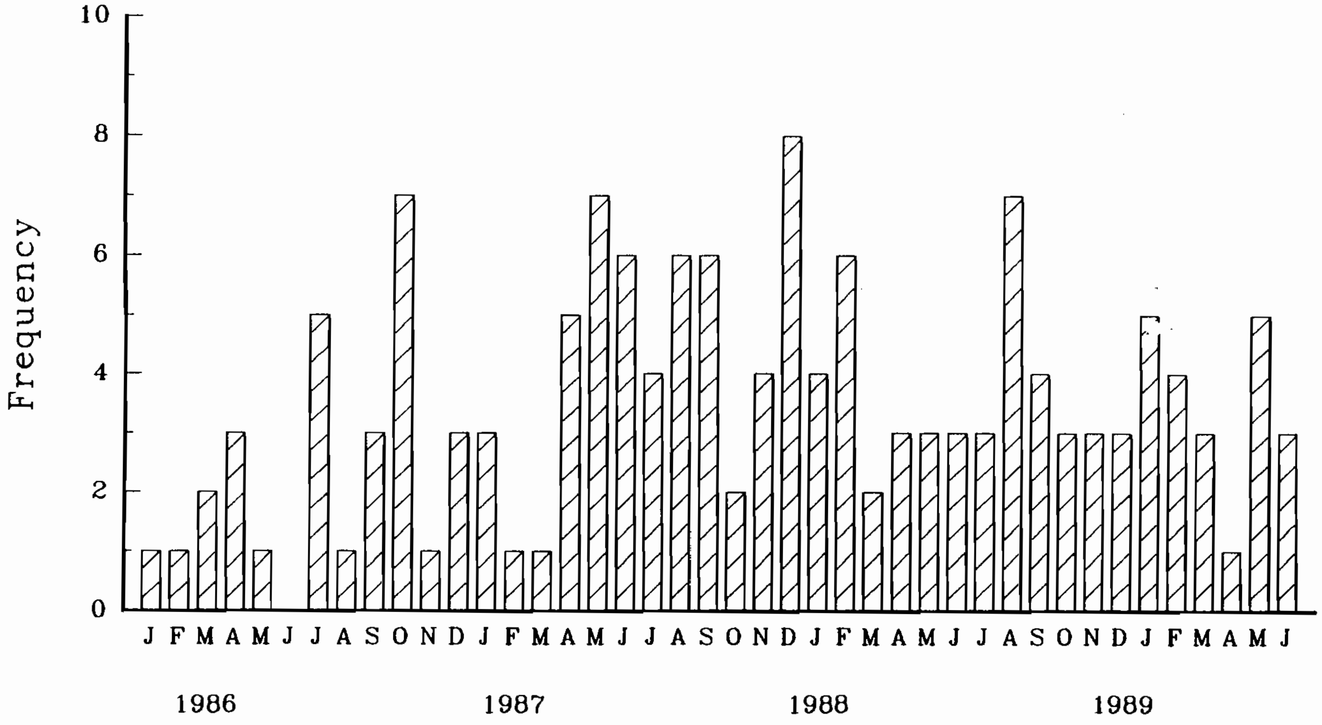

Figure 7.1 Temporal distribution of all births recorded at 'Black Rock' for all females caught during the study period (June 1986 - June 1989).

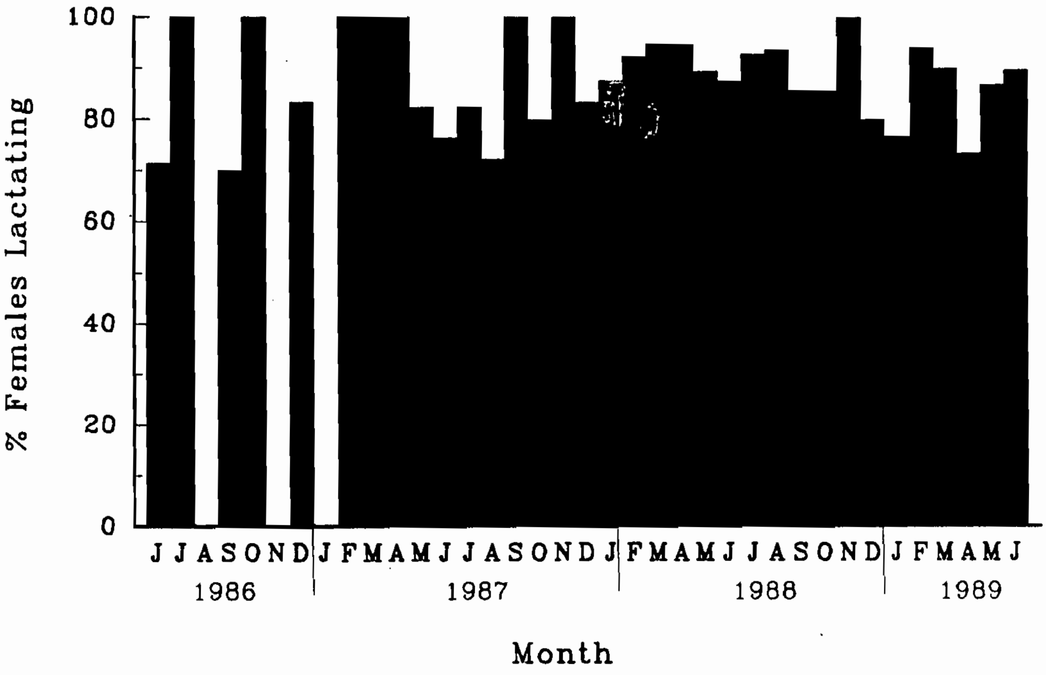

Figure 7.2 Proportion of females caught each trip which were lactating. Note that three months were not sampled.

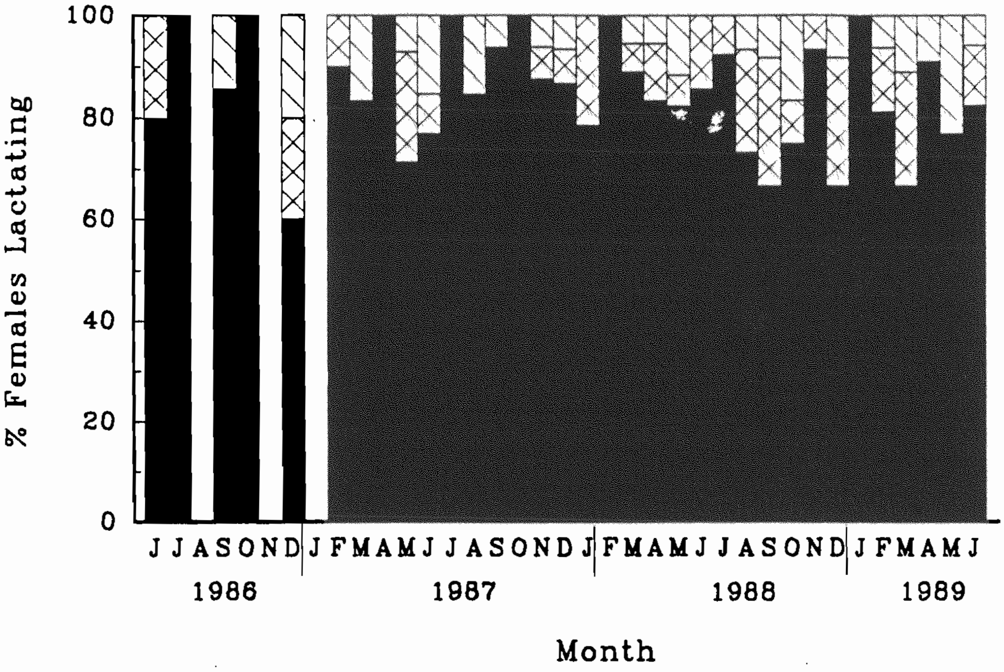

Figure 7.3 Proportion of the females caught which were lactating which were supporting (■) PY only, (☒) both PY and young at foot or (⧅) young at foot only. Note that three months were not sampled.

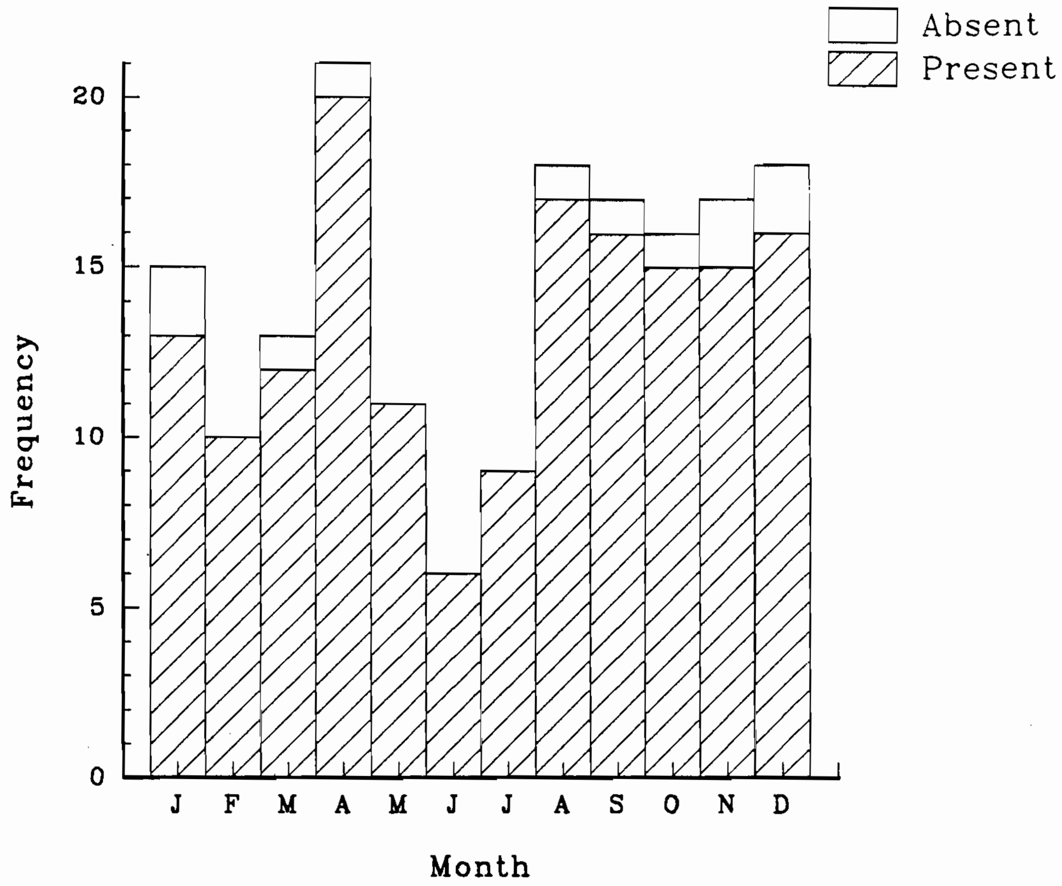

Figure 7.4 Presence and absence of spermatozoa in urine samples from 17 adult males.

Chapter 8

Factors influencing survivorship in pouch young

8.1 Introduction

Since Darwin, biologists have recognised that differential reproductive success among individuals within a single population provides the basis for both natural selection and sexual selection. Variations in the age at sexual maturity, longevity, interval between births, and infant survival all potentially contribute to differential reproductive success among female rock wallabies and my research forms part of a long-term study designed to document individual variation in each of these traits. However, the limited duration of my study precluded my obtaining much information which is pertinent to the first three traits. I was, however, able to obtain data on the survival of the PY of 15 mothers who were caught regularly. Clutton-Brock (1988b) identified individual differences in offspring survival as one of the most important components of reproductive success among breeding females in many birds and mammals.

The relationship between macropodid mothers and their pouch young has several advantages for studying variation in infant survival:

(1) The mother is unquestionably known.

(2) During the months while it is in the pouch, the status of the young can be unequivocally determined as it is inevitably caught with the mother. This means that mortality can be measured with unusual accuracy.

(3) The care of the young in the mother's pouch and the generally polygamous mating systems means that paternal care may be severely limited. Thus it is usually possible to eliminate this confounding influence on female reproductive success (Russell 1982).

(4) Only one young is usually born each time and therefore there is no confounding effect of litter size.

Different influences can be expected to be important for infant survivorship during the two distinct phases of pouch life. During lactation phase 2 [*sensu* Tyndale-Biscoe and Janssens (1988)], the PY lives totally within the pouch environment. It receives all sustenance from its mother's milk and initially, is permanently attached to a teat (Chapter 3). I have termed this early phase of pouch life 'total lactational dependence'. The end of this phase corresponds to the opening of the eyes, the development of endothermy and the first interactions with the external environment, albeit from the safety of the mother's pouch (Tyndale-Biscoe and Janssens 1988). From this time until PEP, the young is still dependent on the mother but is interacting with the external environment. This 'late pouch life' phase provides a young rock wallaby with the opportunity to gain experience of the environment while still in the protective care of its mother (Russell 1982).

In this chapter, I examine the variation in the survivorship of PY from individual mothers in relation to several environmental and maternal factors. Care must be taken in assigning causation fom the results of this analysis, however, as even in a population of phenotypically identical individuals, variation in reproductive success and survivorship will occur as a consequence of environmental variation *per se* (Clutton-Brock 1988a).

8.2 Methods

8.2.1 *Field techniques*

As outlined in Chapter 2, *P. assimilis* were trapped during 44 monthly field trips between June 1986 and June 1990. Only data from the 15 adult females which were caught on at least 17 trips over a minimum of 23 months are included in the data analysed (Appendix 3).

8.2.2 *Pouch Young*

PY were measured as outlined in Chapter 2 and their age and date of birth were estimated using the method developed in Chapter 3. A PY was considered to have survived total lactational dependence when it was 150 days old. It was then still permanently in the pouch and gaining all its nutrition from milk. However, by 180 days (i.e. one month later) PY were supplementing their diets with vegetation and some were emerging from the pouch. At this stage, PY were still suckling even though they were not always caught with their mothers. The continued survivorship of a PY was decided by its presence in the pouch or by its mother's having the appropriate teat still lactating. [Females which lose young stop lactation within one week (B. Green, *personal communication*)]. The lactational status of the mother's teat was also used to estimate the date of death of a PY. The data from Black Rock suggest that *P. assimilis* exhibits a post-partum oestrus (Chapter 7). The resultant embryo undergoes diapause but is born

29-34 days after the removal or death of the PY (Chapter 7). Thus, an independent estimate of the date of death of a PY could usually be obtained by calculating back from the calculated date of birth of the subsequent PY. This technique usually enabled me to estimate the date of death of a PY to within one week, despite my field trips being at monthly intervals. I did not attempt to model individual variation in survivorship after PEP because of the difficulty of confirming why a teat was no longer active. i.e. in most cases I could not determine whether lactation had ceased because the YAF had been weaned or died.

8.2.3 *Data analysis*

PY were included in the analysis of survivorship (1) if they were caught with their mother within ±15 days of birth and (2) if their fate was known and could not be linked to human interference. The variables influencing the survivorship of PY from birth to 150 days (total lactational dependence) and from 150-201 days (late pouch life) were investigated using a series of logistic regression models and analysis of deviance (Tabachnick and Fidell 1989). The models were developed using backward elimination. As the data were non-orthogonal, each variable tested was adjusted for the effects of the other variables in the model. The relative probability of survivorship for PY associated with a particular factor (e.g. season of birth or individual mother) could also be calculated using the linear predictors from the analysis of deviance analysis (Tabachnick and Fidell 1989). The sample size used in the analysis of survivorship during total lactational dependence was 81 young from 15 mothers.

This was reduced to 49 young from 14 mothers for the analysis involving survivorship in late pouch life, as not all young survived to enter this stage, their fate could not be determined or their death was linked to human interference (e.g. Table 2.2). One female died while carrying her only PY to survive to late pouch life.

The variables tested were sex of PY, season (wet, early dry and late dry; Table 2.1) and year (weather years: 1986 - 1990; Table 2.1) of birth, identity of the mother and the following maternal attributes: age [molar eruption stage (MES) and molar index (MI) [*sensu* Chapter 5], leg length, head length, an index of absolute body size (see below), and two indices of body condition (1) PCV (Chapter 6); and (2) an index of fatness. In order to separate maternal fatness from maternal absolute body size, natural log (weight) was regressed against natural log (leg length) for the combined data for all females caught at Black Rock during the study period. The predicted weight and the deviation from the predicted value (residual) for the leg length of each female obtained from the resultant regression represent the proportion of an individual female's weight due to absolute body size and fatness respectively. Thus the fatness index represents the difference between a female's actual weight and that predicted by her leg length, and if for example, a female weighs less than the predicted weight for her size (leg length), the fatness index will be negative. This is similar to the condition factor developed by Wake (in Hume 1982).

8.3 Results

8.3.1 *Pattern of births and lactation*

There was an equal probability of male and female offspring being born to these 15 females (χ^2=0.827, df=1, P=0.363). The sex of an offspring was not influenced by the sex of its previous sibling (χ^2=0.06, df=1, P=0.81). Young were born in all months of the year (Figure 8.1). Despite this, there was a significant difference between females in the number of trips during which they were recorded as lactating or not (χ^2=77.76, df=14, P<0.001), indicating the proportion of time spent supporting young varied between females (range: 58-100%).

8.3.2 *Mortality between conception and birth*

Information on survivorship from conception to birth is limited. Four dead foetuses at varying stages of development were discovered while collecting routine urine samples (data from all females caught; n=265 urine samples). These foetuses were flushed from the cloaca by the passage of urine. None appeared fully developed and all were still within the placental sac and showed no visible sign of life. They are therefore considered to be the result of pre-natal death. One hundred and eleven live births were recorded during this period from all females at Black Rock.

8.3.3 *Mortality from birth to weaning*

Mortality of the young was high and PY died in all months of the year (Figure 8.2). No seasonal trend was evident (although no adjustment was made for any unequal representation sampling effort across months). Of the 81 PY born: 38 (47%) died between birth (day 0) and 150 days (during total lactational dependence; 11 (14%) died between 151 days and 201 days (mean PEP) and a further 20 (25%) between 201 days and 242 days (maximum recorded PEP). Only 12 (15%) young were known to survive until 242 days. Twice as many PY (32 *cf* 16) died in the drier six months (June-Nov) of the year as in the remaining six months, although this was not significant for either age group of PY (χ^2=0.00, *d.f.*=1, *P*=0.948). The highest probabilities of pouch mortality occurred either in the first 30 days after birth (0.234) or in the 30 days before PEP (0.256) (Figure 8.3). However, even higher probabilities of dying occurred after PEP with 0.625 of the PY which survived until 201 days dying before 242 days and while still YAF. Equal proportions of male and female young died between birth and PEP (χ^2=0.0078, df=1, *P*=0.78) and there was no difference between males and females in the age (in months) at which this mortality occurred (χ^2=2.74, df=5, *P*=0.74).

8.3.4 *Factors influencing survivorship during total lactational dependence*

The initial analysis of the variables influencing survivorship to the end of total lactational dependence tested the effects of mother (n=15), season (n=3) and year of birth (n=5) (Appendix 11A). Season of birth had the strongest influence on survivorship being significant when adjusted for mother and year (χ^2=10.79, df=2, *P*=0.005) (Table 8.1).

The late dry season was the best time for a PY to be born. A PY born during this season was 2.09 (95% Confidence limits: 0.829 - 5.272) times more

Table 8.1 Significant results of logistic regression analysis (using backward elimination models) to test the effects of mother, season and year on the survivorship of PY <150 days old (see Appendix 11 (A)).

Variable	Adjusted for	Δ Deviance	*d.f.*	*P*
Mother	Season, year	25.15	14	0.0439
Season	Mother, year	10.79	2	0.0045
Season	Mother	7.62	2	0.022
Season	Year	6.1	2	0.0473

likely to survive than one born in the remainder of the year. Maternal identity also had a significant effect on the survivorship of PY when adjusted for the season and year of birth ($\chi^2=24.15$, df=14, $P=0.044$). After adjustment for the average season and year, the relative probability of a PY born to a particular mother, surviving to the end of total lactational independence could be calculated (Tabachnick and Fidell 1989) and is shown in Table 8.2. These probabilities allow females to be ranked according to their success in raising PY to the end of total lactational dependence and ranged from a mere 10% chance for PY of female 133 to a 99% chance for PY of female 054 (Table 8.2).

Variables measured for each mother within one month of the birth of the offspring were modelled in an effort to understand why some mothers were more successful in rearing young through dependent lactation than others (Appendix 11B). The only significant variable was PCV when adjusted for mother ($\chi^2=42.57$, df=27, $P=0.029$). However, this effect was not significant when adjusted for season (Chapter 6) ($\chi^2=36.91$, df=27, $P=0.097$) indicating that it was unlikely to be the major component of the observed differences between mothers.

Table 8.2 Individual variation in the probability of PY survivorship during pouch life. Probabilities have been adjusted for the effect of season and year on different mothers. Note the change in probabilities of survivorship between the two phases of pouch life for different mothers. Such probabilities effectively act as a means of ranking individual mothers (given in parentheses (separately for each stage of pouch life) from the highest (1) to the lowest (15) ranked females).

		Probability (survival)		Direction of change in *P*(survival) during pouch life
Female #	# of PY	Total lactational dependence	Late pouch life	
001	6	0.8184 (5)	0.0308 (10)	decrease
008	6	0.8187 (6)	0.0000 (12)	decrease
010	3	0.7184 (7)	0.0000 (12)	decrease
013	6	0.6270 (10)	0.0312 (9)	decrease
014	6	0.3866 (12)	0.9999 (1)	increase
032	6	0.9147 (2)	0.1431 (6)	decrease
037	8	0.3851 (13)	0.0192 (11)	decrease
046	3	0.6305 (9)	------	-------
053	3	0.6985 (8)	0.0000 (12)	decrease
054	4	0.9997 (1)	0.0379 (8)	decrease
070	7	0.9037 (3)	0.1316 (7)	decrease
076	7	0.5679 (11)	0.4959 (5)	little change
107	5	0.8905 (4)	0.9999 (1)	little change
111	7	0.1516 (14)	0.9999 (1)	increase
133	4	0.0987 (15)	0.9999 (1)	increase

I was unable to investigate the effects of maternal age on PY survivorship to 150 days as most of the mothers were too old to be aged accurately. When first measured, ten of the fifteen females had full molar eruption (MES=4.0), while another three animals had a MES of 3.8. The PY of the youngest (#111, MES 2.8) and second youngest (#013, MES 3.4) mothers had relatively low probabilities of survivorship to 150 days (mothers were ranked 14th and 10th respectively on the basis of the probability of PY survivorship (Table 8.2), where 15 was the lowest rank).

8.3.5 *Factors influencing mortality during late pouch life*

The mortality of pouch young surviving from the end of total lactational dependence (150 days) until average PEP (201 days) was examined in a similar manner. The initial model examined the influence of mother (n=14), current season (n=3) and year (n=5) on survivorship (season and year were those when the PY was aged 150 ± 15 days) (Appendix 11C). Again, individual mother had a significant effect when adjusted for other factors in the model (χ^2=33.94, df=13, P=0.012). The effects of season (χ^2=3.98, df=5, P=0.552) and year (χ^2=8.66, df=4, P=0.070) were not significant. After adjustment for the average season and year, the relative probability of a PY born to a particular mother surviving the late lactation phase could be calculated (Table 8.2). Given that a female's PY had already survived to 150 days of age, the probability that it would survive this late lactation phase ranged from almost no chance (#008, #053) to almost complete success (#014, #107, #111 and #133).

The second model tested the effects of mother (n=14), and season of birth (n=3) and year of birth (n=5) on the survivorship of PY from the end of total lactational dependence to PEP (Appendix 11C). Again only the mother had a strong influence on survivorship being significant when adjusted for season and year of birth (Table 8.3) and neither season nor year of birth significantly influenced the survival of PY during late lactation.

Table 8.3 Significant results of logistic regression analysis (using backward elimination models) to test the effects of mother, and season and year of PY birth on the survivorship of PY 150-201 days old (see Appendix 11C).

Variable	Adjusted for	▵ Deviance	*d.f.*	*P*
Mother	season, year	28.25	13	0.0084
Mother	year	30.56	13	0.0039
Mother	season	28.46	13	0.0078

Qualities of mothers that may account for the individual differences between females were analysed (Appendix 11D). There were significant effects of mother adjusted for all other factors re-affirming that the individual mother was the major contributor to the variation involved. Absolute body size has a significant effect when adjusted for fatness (as defined in Chapter 8.2.3) with smaller framed females more successful in rearing PY in late lactation than larger females ($\chi^2=6.28$, $df=1$, $P=0.012$). However, this effect disappears if absolute body size is adjusted for mother as well as for fatness ($\chi^2<0.001$, $df=1$, $P>0.75$), suggesting that the overall influence of 'mother' is much greater than the influence of an individual mother's body size *per se*.

Due to the clumped age classes (see Chapter 8.3.4), I was unable to investigate the effects of maternal age on PY survivorship during late lactation. However, of the two youngest females (#111, #013), one had the highest and the other, one of the lowest probabilities of success in rearing PY during this phase (Table 8.2).

8.3.6 *Individual variation in PY survivorship*

The survival of one PY to the end of late pouch life did not significantly influence either the fate ($\chi^2=0.68$, df=1, $P=0.408$) or the sex ($\chi^2=0.83$, df=1, $P=0.363$) of the subsequent PY.

The pattern of PY mortality varied for different mothers with two extremes evident. In the first group of three mothers with a total of 17 PY, the probability of their PY surviving greatly increased from total lactational dependency to late pouch life (Table 8.2). For the second group of nine mothers (49 PY), the probability of their PY surviving late pouch life was less than or equal to that of surviving total lactational dependence. For two other mothers (12 PY), the probabilities for each stage were similar. There was a negative correlation between the probabilities of the offspring of an individual mother surviving the two stages of pouch life ($r=-0.5925$, n=14, $P=0.025$). These results have to be interpreted with caution because of the small number of PY studied for each mother. For no individual mother would it be possible to prove that there was significant difference in survivorship from birth to the end of total lactational dependence and from then until PEP.

8.4 Discussion

8.4.1 *Nature of maternal investment*

Although marsupials have a longer developmental time than that predicted for a similar sized eutherian occupying a similar ecological niche (Lee and Cockburn 1985), the ratio of weight of offspring at weaning to adult female weight is similar for both marsupials and eutherians. While macropodid mothers invest far more reproductive energy in lactation than in gestation (Tyndale-Biscoe and Renfree 1987), they do not necessarily invest less energy in reproduction than eutherians. When the length of lactation is scaled to body weight (i.e. physiological time), the female tammar wallaby expends approximately the same amount of energy on reproduction as do cattle and sheep (Cork and Dove 1989).

The volume and composition of marsupial milk changes throughout lactation (Green 1984). Furthermore, macropodoids are the only mammals which can simultaneously produce milk of different compositions from different mammary glands to support young of different ages (Merchant 1989). Data for the tammar wallaby [a species which has a similar length of pouch life to *P. assimilis* (Tyndale-Biscoe and Renfree 1987; Chapter 3)], indicate that a macropodid mother initially invests very little energy in producing milk for a young PY which consumes about 1mL/day at Day 30. This investment increases to 9mL/day at Day 130 and substantially increases to 43mL/day at day 210, at which time the young commence weaning (Green, Merchant and Newgrain 1988). This increase in milk intake by the PY is reflected in its rapid growth and weight increase during late pouch life and prior to weaning. Shortly before the time her PY permanently emerges from the pouch, a female rock-wallaby is required to supply the energy to produce a considerable volume of milk and to carry the young (up to 10-15% of her weight). In female Bennett's wallabies, there is a steep increase in food consumption coincident with late lactation (Loudon 1987). Green (1989) suggests that for the tammar wallaby, the field metabolic rate of such a female may be double that of a non-lactating female.

A young-at-foot of *P. assimilis* can be suckled until it is almost 13 months old (387 days) (Chapter 3), a considerable proportion of its pre-reproductive life of 18-23 months. *P. inornata* also spends a considerable proportion of its pre-reproductive life suckling from its mother (Johnson 1979). However, the relative length of lactation is markedly greater in several smaller species of macropodoid where sexual maturity can occur before, or just after, weaning (Tyndale-Biscoe and Renfree 1987). In this respect, *P. assimilis* shows maturation-timing more characteristic of larger, rather than the smallest macropodoids.

Successful mothers may invest in a young to the possible detriment of subsequent offspring. A young *M. giganteus* is less likely to be reared to weaning if its previous sibling had been weaned than if it had disappeared (Stuart-Dick 1987), a pattern similar to that recorded for red deer (Clutton-Brock, Albon and Guinness 1982). I could only test this hypothesis for *P. assimilis* by studying the effect of survivorship to PEP rather than to weaning, as only eight out of 81 PY studied were known to survive to weaning, compared with 32 surviving to PEP. However, the success of rearing the previous sibling to the YAF stage (242 days) had no effect on the fate or sex of a PY of *P. assimilis*. Furthermore, there was no detectable relationship between females entering 'anoestrus' periods and the fate of their subsequent offspring (Chapter 7).

There appeared to be considerable phenotypic plasticity between females in the timing of PY mortality, with two extremes evident (Table 8.2). Thus some females successfully reared most of their PY through the total lactational dependence phase, but were unlikely to rear these young to PEP. This large decrease in the probability of PY survival towards the end of pouch life exhibited by some of these females may have been exacerbated by the otherwise probable survival of PY of several of these females (notably #008, #013, #032, #054) which were affected by human intervention just before PEP (e.g. see Table 2.2). The omission of these PY from the analysis may have falsely depressed the estimated probability of PY survivorship for their mothers. Conversely, several females had a low success rate in rearing PY during total lactational dependence, but those young which did survive usually survived until PEP (e.g. PY of #111, #133; Table 8.2).

For the same number of successfully reared PY, females which adopt this second strategy will expend less energy than females which rear most PY through total lactational dependence and relatively few through late lactation to PEP. However, using the tammar wallaby as a model, Cork and Dove (1989), calculated that the energetic difference between these two strategies is likely to be low as proportionately little of the total reproductive energy is used during total lactational dependence. Perhaps the most important factor, at least from a population perspective, is that this phenotypic plasticity may be an important strategy for coping with an unpredictable environment.

After her young leaves the pouch, the mother also invests in its learning and socialisation, an investment which may be crucial for the offspring's own survival and future reproductive success. A young at foot closely follows its mother and time is spent in mutual allo-grooming (Horsup 1986). As *P. assimilis* forms long lasting pair bonds (Horsup 1989, *personal communication*), a female's consort may also play a role in this socialisation, a behaviour which would be unusual for a macropodid. Barker (1990) reported social play between a juvenile and adult male *P. assimilis*, and Horsup (*personal communication*) also observed allogrooming between an adult male and the young of his consort female. The extent of this paternal investment is unknown, but is probably low compared with that of the female.

Female *P. assimilis* invest equally in young of both sexes from birth to PEP: the sex ratio at birth was not significantly different from 1:1, and there was no sex difference in the rate of mortality during pouch life or age at which it occurred. While Newsome (1965) found no difference in the sex ratio of most age classes of PY of *M. rufus*, there was a significant bias towards male offspring in PY aged between 151 and 180 days and when all PY were combined. No significant bias in the sex ratio has been recorded for offspring of *M. eugenii* (Inns 1980), *M. parma* (Maynes 1977) and, *M. agilis* and *M. robustus* (Cockburn 1990), although biased sex ratios (particularly those favouring males) are relatively common in macropodid (reviewed by Johnson and Jarman 1983, and Johnson 1989b) and other marsupial young (reviewed by Cockburn 1990). Explanations for this bias include variation in short-term rainfall (Johnson and Jarman 1983), sex-based dispersal and philopatry (Johnson 1989b), local resource competition, and differential investment (Cockburn 1990), although other data sets have no obvious explanation and cannot be accommodated within existing theory (Cockburn 1990). Skewed sex ratios at birth have been recorded and differential parental investment in progeny has been documented in a variety of eutherian species (e.g., *Galago crassicaudatus*, Clark 1978; *Macaca radiata*, Silk *et al.* 1981; *Neotoma floridana*, McClure 1981; *Cervus elaphus*, Clutton-Brock, Albon and Guinness 1981).

8.4.2 *Pattern of offspring mortality*

Several prenatal deaths were recorded. Similar observations have not been reported in the literature, however, Dr Rick Speare (*personal communication*) has observed such deaths occurring in captivity in agile wallabies and in an eastern grey kangaroo (which aborted twins). He suggests these prenatal deaths are a response to trauma and are underestimated due to the difficulty of obtaining such observations (Rick Speare, *personal communication*). Because at least a month elapsed between successive examinations of each female, the incidence of prenatal deaths and mortality occurring immediately post-partum is possibly underestimated, particularly in those few females which had a long period without a PY.

Mortality rates of young (pre-weaning) marsupials are variable, ranging from 0% to 100% (Russell 1982). Only 15% of PY monitored at Black Rock during my study survived pouch life. The age of death of young has not generally been reported in detail in marsupials although such data should exist, at least for captive colonies. At Black Rock, the probability of a PY dying was highest (0.234) early (<30 days of age) and late (0.256) in pouch life (150-201 days of age) (Figure 8.3). However, a major proportion (0.625) of the PY which permanently exited the pouch had died by 242 days, while still YAF (Figure 8.3). Macropodid studies usually suggest that, under non-drought conditions, offspring mortality is significant only between PEP and weaning. For example, Johnson's (1989a) data suggest that mortality is low in early pouch life in the red-necked wallaby and highest during late pouch life when the lactational load is greatest. Under drought conditions, PY mortality will increase and may result in loss of all

PY (e.g. Newsome 1975, Kirkpatrick 1965b, Kirkpatrick and McEvoy 1966, Frith and Sharman 1964). The data presented here suggest that *P. assimilis* is living in an environment which is more akin to the cycle of droughts and good seasons usually associated with arid Australia. However, in the wet-dry tropics this probably occurs on an almost annual basis rather than on the longer time frame which occurs in the arid zone (Ridpath 1985). The pattern of mortality for offspring of *P. assimilis* is consistent with findings in eutherian mammals where the highest rates of mortality occur either around birth or weaning. For example, in captive macaque monkeys, nearly all juvenile mortality occurs within one month of birth (Silk *et al.* 1981).

The loss of young close to weaning may reflect the mother's inability to produce the quantity of milk demanded by her rapidly growing young. It was impossible for me to test this due to the confounding effects of seasons and the different ages at which young were caught. Late pouch life is a period of great change for the young as it moves from living in the pouch to the outside environment and further losses could be expected from predation, misadventure and disease. The greatest probability of young dying occurred during the YAF stage (Figure 8.3).

Predation is the major cause of mortality in newly emerged young of *M. rufogriseus* (K. Higginbottom *personal communication*). Although a feral cat was occasionally observed at Black Rock from the beginning of this study, it was not seen eating a rock-wallaby until March 1990. Between September 1989 and May 1990, Spencer (1991) obtained evidence that five of 11 known YAF (45.5%), one of seven sub-adults (14.2%) and at least two of 43 (4.6%) known adult rock wallabies were eaten by this cat. However, as I saw no evidence of its eating rock wallabies, its impact on young rock wallabies during most of my study is unknown, but it is considered lower than that reported by Spencer (1991) for the period following my study.

Male offspring of red-neck wallabies disperse from their mother's home range whereas female offspring inherit it (Johnson 1986). Although we do not have the data to test whether this pattern of dispersal occurs in *P. assimilis* at Black Rock, it is consistent with the observations of Horsup (*personal communication*) who studied the home ranges of rock wallabies at Black Rock over two years. He found that the home range of each female was stable while those of males changed if they paired with a new female. However, I consider it unlikely many male (or female) offspring emigrated from Black Rock and believe the low numbers of juveniles at Black Rock are the result of mortality not emigration. Rest sites are usually considered the ultimate resource limiting the size of rock wallaby colonies (Briscoe *et al.* 1982, Short 1982). When population density is high and available rest sites are occupied, independent young may be under more pressure to immigrate. However, this is unlikely to have occurred during my observational period as almost no independent young were surviving to replace the adults which died (Chapter 5).

8.4.3 *Variation in PY survival*

Although neither seasons nor years seemed to affect the timing of PY deaths at Black Rock during my study (Figure 8.2), the chances of surviving early pouch life were strongly influenced by the season of birth as well as the individual mother, whereas survivorship in late pouch life appeared to be governed by the individual mother *per se*. Young born in the late dry season were twice as likely to survive total lactational dependence as those born in the wet and early dry seasons combined. Although in a drought year like 1987, a young born in the late dry season is born when the mother's condition is worst (Chapter 6), it places a low energetic demand on its mother at this time. As this demand becomes greater some four months later, its mother can take advantage of the improvement in environmental conditions in the months during and after the wet season. After the wet season breaks, food (particularly the preferred forbs) is more abundant (Horsup and Marsh 1992) and water more available. Both are important to the growing PY. Kennedy and Heinsohn (1974) observed that lactating *P. assimilis* had a 17% higher water turnover rate than non-lactating animals. It is likely that water turnover rates of lactating macropodids are highest in late pouch life when milk production peaks (Green 1989).

Despite the strong influence of season of birth on the survivorship of PY, *P. assimilis* breeds continuously (Chapter 7), suggesting that other factors also influence offspring survival. The unpredictability of rainfall and pasture growth at Black Rock may partially account for this pattern of survival. For example, a reproductive strategy in which the birth of offspring was timed to occur in October in the expectation of the imminent arrival of the wet season would be inappropriate in this uncertain climate when the wet season can arrive anywhere between October and February, or not at all (Chapter 2).

Variation between individual mothers was a significant factor in PY survivorship during both total lactational dependence and late pouch life. The negative correlation between the probabilities of the offspring of an individual mother surviving the two stages of pouch life suggest that different factors may be operating at each stage. I failed to identify phenotypic correlates of PY survivorship at either stage except that smaller-framed females were more successful in rearing young through late pouch life than larger females. However, this effect disappeared if the identity of the mother was included in the model, suggesting that the overall influence of 'mother' was much greater than the influence of body size *per se*. While the greater reproductive success of smaller framed females during late pouch life may be considered a surprising result, a variety of inter-related explanations are possible.

Natural selection theories generally predict that larger mothers are selected for as they are more reproductively successful (Ralls 1976). This premise is based on the widely documented phenomenon that larger females have larger litters (e.g. see Lewin 1989). However, the 'litter size' of macropodids is invariant and constrained to one young. Unless larger females can be shown to have some other advantage (e.g. better access to resources), then they have no advantage over their smaller framed conspecifics. Indeed, if we accept the cost hypothesis (Bell 1984), that (in an environment where resources may be limiting) energy trade-offs occur between growth and reproduction, then smaller females have expended less energy on growth and may have more energy to expend on reproduction earlier in their lives. The potentially longer reproductive life span of smaller females may mean they are more successful over their lifetime than their larger conspecifics.

Life history theory predicts that traits should evolve to maximise lifetime reproductive success, rather than instantaneous reproductive success (such as litter size *per se*). The data presented here represent only a proportion of a female's reproductive lifetime and therefore may be a distorted view of each female's lifetime reproductive success. Once data on lifetime reproductive success on known-age animals become available, the hypothesis that adult female size is negatively correlated with lifetime reproductive success, can be tested.

Another possible explanation for the success of small females lies in the scaling of metabolic requirements with body size. While an animal with a smaller body size may require relatively more energy for maintenence than a larger conspecific, in absolute terms it requires less energy. There is a growing body of evidence that within species, the gut capacity of mammalian herbivores is very plastic (e.g. Gross, Wang and Wunder 1985; Hammond and Wunder 1991; reviewed in Foley and Cork 1992). If this is true for *P. assimilis*, and if there is no difference between different sized individuals in their foraging ability when resources such as food are limiting, then small females should be able to process similar amounts of food (and therefore energy) as large females. Given a smaller maintenence energy requirement, smaller females could then devote more energy to reproduction and may consequently be more successful. Smaller females may also have smaller offspring which demand less investment than their larger conspecifics. Thus PY of smaller females may weigh less at PEP or weaning than those of larger-framed females. Too few young reached these stages in this study for this hypothesis to be tested.

The finding that smaller framed females may be more successful in rearing PY through late lactation than their larger conspecifics could be an artefact of the sample size or the individual females sampled. For example, smaller sized females may have come from cohorts born in nutritionally poorer years, and these females may not have grown to the same adult size as females born in better years. The observed effect may therefore be an effect of age rather than body size *per se*. While none of the above hypotheses are exclusive, they are potentially testable, with a larger data set than this one.

Maternal factors such as age and social dominance, which have been implicated in reproductive success in other species (e.g., primates, Silk *et al.* 1981; deer, Clutton-Brock *et al.* 1982; elephant seals, Le Boeuf and Reiter 1988), could not be examined in this study. Most of the core females had full MES and could not be distinguished on the basis of age. Of the two youngest females, one (#111) was amongst the least successful females for rearing young in early pouch life (Table 8.1) while the other (#013) had a much higher rearing success during this period. This pattern of success was reversed for PY during late pouch life. The only known primiparous female (#159) successfully weaned her first and possibly second, offspring (P. Spencer *personal communication*). However, little can be drawn from this observation as it occurred after my study period when many other females were also successfully rearing young to weaning.

The survivorship of 255 offspring from Black Rock has now been monitored from June 1986 until February 1993. Comparison of the remaining data (made available by Peter Spencer) with the data for my core 15 females (collected between June 1986 and June 1990) indicates that there was no significant difference between the two data sets in the proportion of PY dying during the period of total lactational dependence (Yates' corrected $\chi^2=0.01$, df=1, $P=0.928$) or between the end of this period and mean PEP (201 days) (Yates' corrected

$\chi^2=0.01$, df=1, $P=0.928$). However, the proportion of young dying between mean PEP and 242 days (i.e. early YAF stage) was significantly higher for my 15 core females than for the remaining portion of the data set (Yates' corrected $\chi^2=7.13$, df=1, $P=0.008$). This suggests that the PY mortality observed for the 15 core females during the years of my study were perhaps typical for this colony and that the major change in survivorship with the changes in the seasons has been in the increased survival of young at foot. This is consistent with other studies of macropodids which show that the greatest variation in offspring survivorship occurs between late in pouch life and weaning when the lactational load on the mother is considered greatest (Cork and Dove 1989).

There was too little overlap between the females reported in this chapter and those regularly observed during the parallel behavioural study conducted by Alan Horsup to examine the effects of the stable linear dominance hierarchy established by females on their reproductive success. There is some suggestion that higher ranked female *P. penicillata* have a higher reproductive success (Joblin in Jarman 1989). This may be confounded by age, with dominant females tending to be older than their subordinates (e.g. Clutton-Brock, Albon and Guinness 1988). An individual's position in the dominance hierarchy may also change over time (Gouzoules, Gouzoules and Fedigan 1982) resulting in less variation between individual females over their lifetime than originally may otherwise have been predicted. The relationship between reproductive success and social rank is frequently complex and correlations may not be causative: a female's rank affects her access to feeding resources, territories or superior partners (Clutton-Brock 1988b), all of which may influence the survivorship of offspring.

Although all females at Black Rock are affected by any large scale environmental stresses (see Chapter 6), individual differences between females in resources may result in differential survivorship of PY. There are significant dietary differences between individuals (Horsup and Marsh, 1992) and food availability may vary between home ranges. Higginbottom (*personal communication*) found a strong correlation between the quality of the mother's diet and PY survivorship in *M. rufogriseus*. This relationship needs to be examined in detail at Black Rock.

Despite a large variation between females in PY survivorship, most of the surviving offspring died before maturity and I was unable to study maternal differences in offspring survival after weaning, the period identified by Clutton Brock (1988b) as the principal source of variation in reproductive success among breeding adults in several species of mammals. Most females at Black Rock had an effective reproductive success of zero during my study. This devastatingly high level of offspring mortality is presumably the result of the environmental conditions prevalent during the study period (Chapters 2 and 6) and perhaps the feral cat.

In years with a high food abundance, there may also be little individual variation between females in rearing offspring. This has been suggested for female macaque monkeys (*Macaca fuscata*) which have a strong social heirarchy (Gouzoules *et al.* 1982). Data from *M. giganteus* suggest that while no PY survive during drought years, survivorship is much higher under better environmental conditions (Kirkpatrick and McEvoy 1966). In *M. rufus*, drought conditions cause most PY to die, but most PY survived if favourable conditions continued for at least eight months (Newsome 1965, 1975).

At Black Rock, the proportion of young surviving has increased recently and more of these animals are becoming reproductively active (P. Spencer *personal communication*). This coincides with two above average wet seasons and the death of the feral cat in June 1990. In April 1991, after the first above average wet season since 1984 and one of the highest wet season rainfalls ever recorded, 19 of the 43 rock-wallabies caught were pre-reproductive animals (P. Spencer *personal communication*). Equal numbers of both sexes were caught and of the adult animals, approximately half were in their first year of sexual maturity. Perhaps, like the red and grey kangaroos, *P. assimilis* is severely affected by drought conditions but the population recovers during good years when most females are able to successfully rear young.

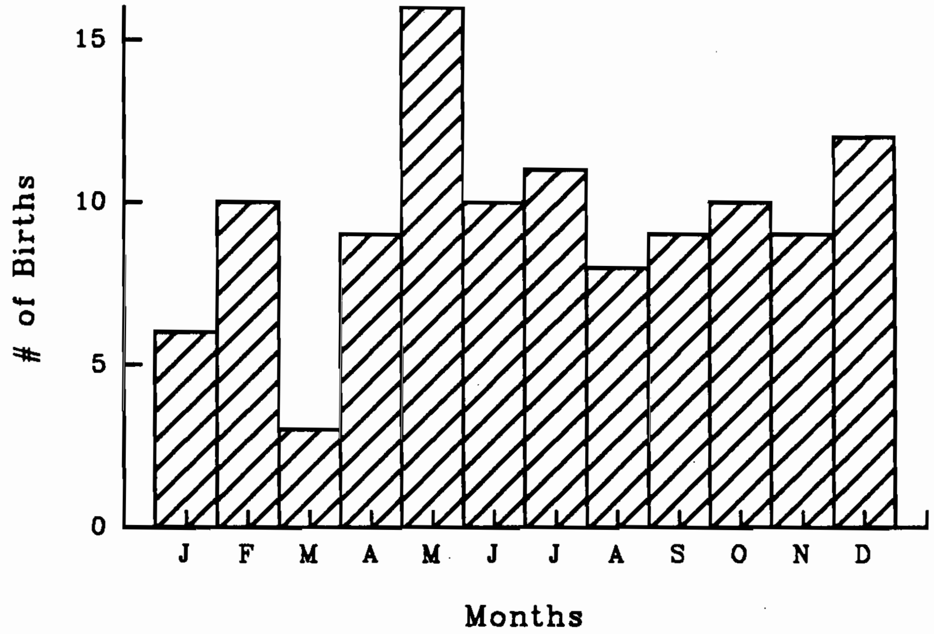

Figure 8.1 Temporal distribution of all births recorded at 'Black Rock' (June 1986 - June 1990) for the 15 females which were caught regularly (*c.f.* Figure 7.1). No adjustments were made for the unequal sampling effort across months.

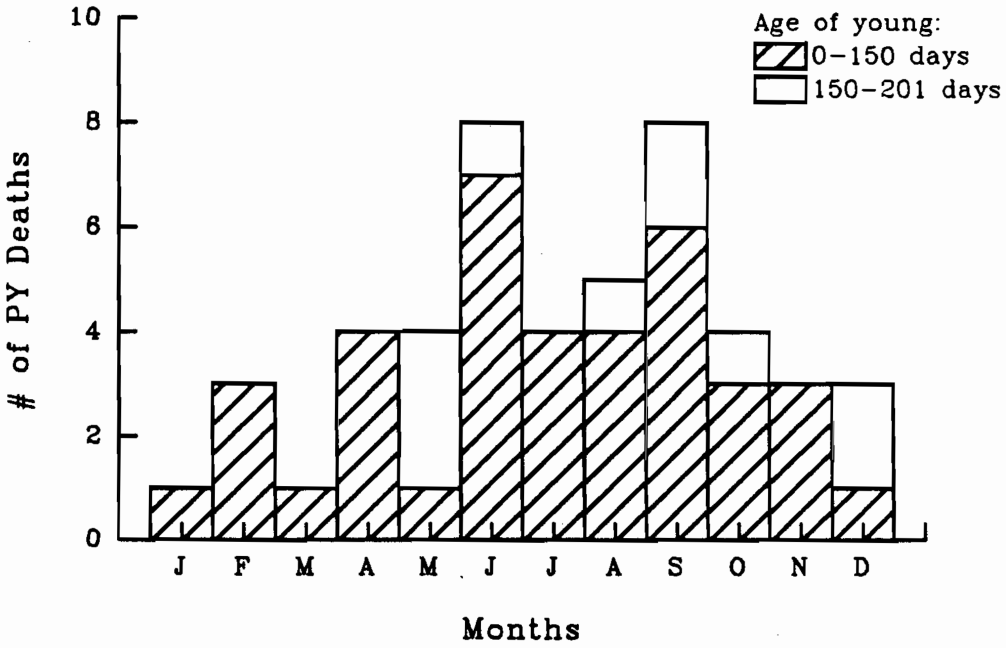

Figure 8.2 Temporal distribution of all PY deaths recorded at 'Black Rock' (June 1986 - June 1990) for the 15 females caught regularly. No adjustments were made for the unequal sampling effort across months.

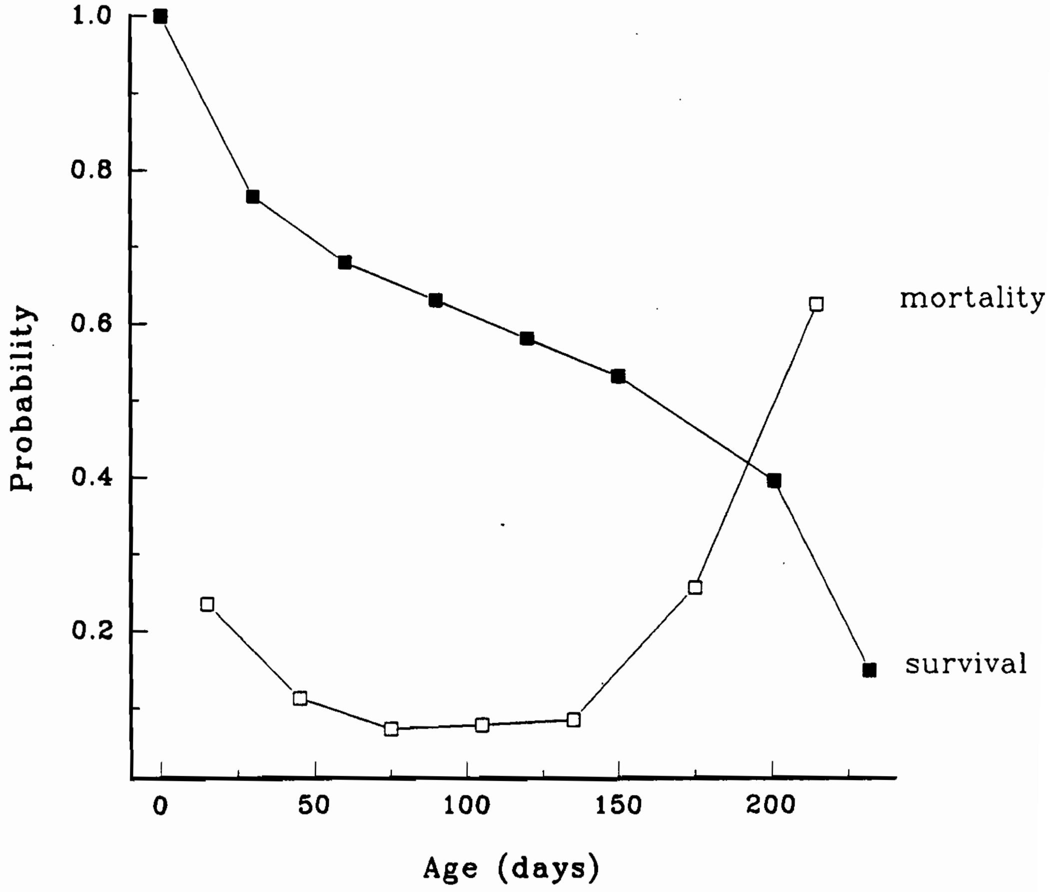

Figure 8.3 Schedules of survivorship (solid squares) and probability of dying mortality (open squares) for PY (n=81) of the 15 females which were regularly caught.

Chapter 9

General Discussion

Much of the life history of a species can be predicted from knowledge of its phylogeny and body size (Stearns 1983). The remaining aspects of a species' life history are related to its immediate environment, to other selection pressures or to vicariance (Gould and Lewontin 1979). In this concluding chapter, I will review the findings of this study in the light of current knowledge of the life histories of mammals (particularly macropodids), the response of *P. assimilis* to the seasonality of the habitat in which it lives and the variation between individuals in life history strategies. I will then speculate on what this means for the population dynamics of *P. assimilis* colonies and for speciation in *Petrogale*. Finally, I will propose directions for future research.

9.1 Phylogenetic and body size constraints on *P. assimilis*

While membership of a taxonomic group constrains some life history traits, other traits have been shown to be related to body size (Stearns 1983, Lee and Cockburn 1985, Lee and Ward 1989). Like other marsupials, *P. assimilis* is a lactation specialist, expending proportionately more time (and presumeably more energy) on lactation rather than on gestation. In contrast, most eutherian mammals expend relatively more time and energy on gestation than lactation (Lee and Cockburn 1985). The gestation period of *P. assimilis* (approximately one month) is much shorter than the length of time from birth to PEP (approximately seven months) or to weaning (approximately 8 months).

Table 9.1 Summary of some life history traits of tropical macropodids, with species arranged by increasing adult female body weight. N.B. Most of the distribution of *M. agilis* is in the tropics, and *M. robustus* is not restricted to the tropics, but is included for comparative purposes.

	Petrogale concinna[1]	*Petrogale assimilis*[2]	*Petrogale inornata*[3]	*Macropus agilis*[4]	*Macropus robustus*[5]
Adult ♀ weight (g)	1400	3500	4000	12000	16000
Number of teats	4	4	4	4	4
Litter size	1	1	1	1	1
Oestrous cycle length (days)	-	>gestation	32	32.4	-
Gestation (days)	-	*c.* 27-34	31	29.4	-
Attachment/ first off teat (days)	-	*c.* 127	127	-	-
Permanent pouch exit (days)	180	201	204	219	256
Weaning (days)	360	267-389	290	328	380
♀ sex. maturity (months)	12 - 24	18-23	18	12	27
♂ sex. maturity (months)	-	23-25	20	14	-
Birth season	all year	all year	all year	all year	all year
Life span (years)	-	≥ 12	-	-	-
Sexual dimorphism[6]	♂ < ♀	♂ > ♀	♂ > ♀	♂ >> ♀	♂ >> ♀

[1]Sanson in Lee & Cockburn 1985, [2]Delaney, this study, [3]Johnson 1979, [4]Kirkpatrick & Johnson 1969, Merchant 1976, Bolton *et al.* 1982, [5]Ealey 1967, [6]Jarman 1989.

Like other macropodid marsupials, female *P. assimilis* are iteroparous, have four teats, a litter size of one, and give birth to an altricial young which is carried in a pouch (Table 9.1). Like most other macropodids, the gestation period is probably slightly shorter than the oestrous cycle and relatively independent of body size, and birth is almost certainly followed by a post-partum oestrus and subsequent lactational quiescence. Individuals may become sexually mature at 18 months of age and adults may breed for more than 10 years, as the maximum life span is at least 12 years. The sequence of growth and the developmental times for *P. assimilis* are typical of a macropod of its size (Table 9.1). The length of time from birth to PEP, weaning and sexual maturity is between that observed for smaller and larger species of macropodid, and comparable to that described for a similar sized macropodid, *P. inornata* (Johnson 1979).

Comparisons of growth rates in marsupials are difficult. Past inter-specific comparisons have used weights from captive populations measured at regular intervals (Lee and Cockburn 1985, Cockburn and Johnson 1988, Lee and Ward 1989). Such measures are not possible from field populations of *P. assimilis*, but the growth models which were developed in Chapter 3 predict head and pes lengths and these can be converted to proportions of mean adult female lengths. These proportions are close (e.g. within 10%) to those calculated from data for similar-aged captive *Macropus parma* (Maynes 1976) and *Thylogale billardierii* (Rose and McCartney 1982). These two macropodid species are of similar size to *P. assimilis*, and have Gompertz constants for growth in body weight either side of the regression line for Gompertz constant versus body mass in marsupials (Lee and Ward 1989). By extrapolation, *P. assimilis* probably has growth rates similar to those predicted for a marsupial of its size.

While many species of marsupial have an unbiased sex ratio at birth (Cockburn 1990), others, including *P. xanthopus* (Poole *et al.* 1985, Lim *et al.* 1987), do not. The sex ratio of a species may be related to such factors as the differential mortality of a particular sex, or it may reflect the social organisation of that species. There was no deviation from parity in the sex ratio at any stage in the life history of *P. assimilis*, which is consistent with its level of sexual dimorphism and social organisation. Smaller mammals are less likely to be sexually dimorphic than their larger relations (Kleiman 1977, Jarman 1989) and like the other smaller macropodoids (Jarman 1989), *P. assimilis* exhibits only limited sexual dimorphism in its external morphology and growth during adult life. On average, males are slightly larger (<10%) than females. In *P. assimilis*, sexual dimorphism is most pronounced in upper limbs (and presumably in their associated musculature) and in weight (Chapter 4), just as it is in the larger heteromorphic species of macropodoid (Jarman 1989). *P. assimilis* at Black Rock (Horsup 1989) and elsewhere (Barker 1990), are considered to form long-term pair bonds. Such a social organisation is consistent with its limited sexual dimorphism, its size and parity of sex ratio (Kleiman 1977), but has only been suggested for one other macropodid, *Setonix brachyurus* (Kitchener 1972).

9.2 Environmental variation and the life history of *P. assimilis*

The distribution and general habitat requirements of *P. assimilis* indicate it that is a typical member of the genus, living as it does on rocky outcrops in the wet-dry tropics region of northern Australia. The seasonality of this region is defined by the unpredictability of the onset, magnitude and duration of the wet season. The wet-dry tropics of Australia are also defined by low soil fertility and variability of soil moisture (Ridpath 1985). The harshness and variability of this climate may be ameliorated by the rocky outcrops (Mares and Lacher 1987;

Freeland, Winter and Raskin 1988) in which *P. assimilis* lives. Rocks may help retain moisture, increase runoff to the surrounding soils and support a more diverse vegetation. In turn this may increase local soil fertility in the immediate vicinity. However, drought conditions prevailed during the years prior to and during my study. Under these conditions, it is possible that patterns emerged which would have been concealed during more favourable conditions.

The influence of the seasons on changes in the body condition of adult rock wallabies reflected the availability of water and quality of forage. Although below average annual rain fell at Black Rock in both the full weather years of my study, the pattern of rainfall was quite different during each of these years. Changes in the body condition of adult rock wallabies were reflected in this rainfall pattern. In the extreme dry season of 1987, rock wallabies were starving and became anaemic. In 1988, a higher proportion of the year's rain fell during the dry seasons, plant growth increased and green forage was available throughout the year (Horsup and Marsh 1992). Consequently, rock wallabies maintained weight and their blood packed cell volume remain relatively constant during this period. Thus to a rock wallaby, not all 'drought' years are equal. As Wolda (1978) noted, small variations in rainfall pattern may have a large effect on populations of herbivores.

Both the seasonality of the environment and body condition potentially affect an animal's ability to reproduce. In *P. assimilis*, adults of both sexes are capable of breeding continuously throughout the year. This pattern is typical of all male macropodids investigated to date (Tyndale-Biscoe 1989). This contrasts with the pattern in female macropodids, with females of some species breeding seasonally and others continuously (Table 1.1). Continuous reproduction, whereby births may occur at any time of year, is considered to be the ancestral characteristic of female macropodids and is the most common strategy in this family (Tyndale-Biscoe 1989).

Most terrestial mammalian populations studied in the wet-dry tropics of the world exhibit at least some seasonality of reproduction (e.g. South American rodents, Ojasti 1983; African rodents and lagomorphs, Happold 1983; and African ungulates, Sinclair 1983). In the wet-dry tropics of Australia, the introduced ruminants, *Bos taurus* and *Bubalis bubalis* (Williams and Newsome 1991), at least one rodent, *Rattus sordidus colletti* (Redhead 1979) and two dasyurid marsupials, *Parantechinus* (formerly *Antechinus*) *bilarni*, and *Dasyurus hallucatus* (Begg 1981a,b) breed seasonally. However, neither the potoroid, *Aepyprymnus rufescens* (Johnson 1978), nor any of the macropodids living in this region and studied to date, have births restricted to a particular season (Table 9.1). Since females of some species of Macropodidae breed seasonally elsewhere in Australia (Table 1.1), this is not a phylogenetic constraint of females for this family.

Continuous breeding appears to be typical of members of the genus *Petrogale*. All known species of *Petrogale* breed continuously (*P. inornata*, Johnson 1979, *P. xanthopus*, Poole *et al.* 1985, Lim *et al.* 1987; *P. concinna*, Sanson in Lee and Cockburn 1985; *P. lateralis*, Kinnear, Onus and Bromilow 1988; and *P. assimilis*, this study), although Sharman and Maynes (1983a) initially suggested that some species of rock wallaby may be seasonal breeders. However, there are too few data to distinguish whether the continuous pattern of reproduction observed in *P. assimilis* is a phylogenetic constraint for this genus, a response to the environment in which this species lives, or an ancestral habit which has not been changed by evolutionary pressures.

Although breeding is continuous, conditions suitable for survival of young are not. The cost hypothesis predicts that if a resource is limited, less energy can be devoted to growth or reproduction (Bell 1984). That is, adult females which have limited energy and which can expect to breed again, should redirect energy from reproduction to maintenance of their own bodily health. The reduction of litter size is a trade-off between such resource limitations and the need to successfully reproduce (e.g. see Happold 1983, Lee and Cockburn 1985 and Dobson 1988). However, this trade-off is not available to species of macropodids as they are essentially constrained to one young per litter. In such cases, if energy is limiting we can expect (1) reproduction to cease, (2) the development and growth of young to slow, and/or (3) young to die.

There is no evidence that reproduction in all individuals of a colony of *P. assimilis* ceases totally in poor environmental conditions, as has been documented for populations of *M. rufus* and *M. robustus* in arid Australia (Ealey 1967, Newsome 1975). Young of *P. assimilis* were born at all times of the year and there was no time period when PY were not present (Chapters 7, 8). However, there is anecdotal evidence that several individual female *P. assimilis* stopped breeding for periods of up to ten months. Whether or not these were periods of anoestrus is unknown, and until this question is examined in detail, the role of anoestrus in the reproductive strategy of *P. assimilis* will remain unknown. Periods of anoestrus were not found in *M. agilis* until its reproduction was examined in detail (Bolton, Newsome and Merchant 1982 *cf* Kirkpatrick and Johnson 1969, and Merchant 1976).

There is also no evidence that detrimental changes in female body condition affected the growth rates of PY of *P. assimilis*. While sample sizes are limited, the growth of PY of *P. assimilis* at Black Rock was compared with that of captive animals maintained at Macquarie University, Sydney (Chapter 3). A marked nutritional difference potentially existed between these two populations of mothers: captive females were fed and watered *ad libitum*, and wild females were nutritionally stressed during at least part of the year. Although individual PY had different growth curves, comparisons of the two populations of captive and wild PY showed no significant differences in growth parameters between these two nutritional regimes. Ealey (1967) and Taylor and Rose (1987) suggested that poorer nutrition caused slower growth rates in PY of *M. robustus* and *Bettongia gaimardi* respectively. While there was individual variation between PY of *P. assimilis* in their rate of growth, the data were too limited to examine potential causes of this occurrence. More data on the growth of wild PY born at different times of the year or on young reared in captivity with mothers fed on different planes of nutrition may further confirm or deny these factors affect PY growth.

Finally, and in contrast, almost all offspring of *P. assimilis* born at Black Rock during my study period died before they were weaned (Chapter 8). The highest probability of dying during pouch life occurred during the beginning and end of this period (0.234 and 0.256 respectively; Figure 8.3). However, the probability of dying increased greatly after the young left the pouch (0.625; Figure 8.3). This late stage of lactation is the most energetically demanding period of reproduction for a marsupial mother (e.g. see Cork and Dove 1989, and review by Cockburn and Johnson 1988). As offspring died, they were usually replaced within a month by a new young.

Sharman, Frith and Calaby (1964) first suggested that growth of PY of macropodids is an 'all or none' phenomenon. Data from both *M. rufus* (Newsome 1965), and *P. assimilis* (this study), highlight the high mortality of PY reared during poor environmental conditions. This, together with the probable lack of variation in growth of PY due to maternal nutrition suggest that Sharman *et al.* (1964) may be correct in their interpretation.

The seasons were also crucial to the survivorship of PY. Young born in the late dry season were twice as likely to survive total lactational dependence as those born at any other time of the year (Chapter 8). This was probably because the mother was able to take advantage of the flush of green forage and water after the wet season started, and meet the increasing energetic demands of her young. However, the length and timing of the late dry season is, by definition, dependent on when the wet season begins and this is an unpredictable event. This may explain why loss of PY is so great during total lactational dependence. If the wet season is delayed, a mother may lose her PY early in pouch life when her investment in that young is low. The next PY is then more likely to survive as it (or, probably more correctly, its mother) can take advantage of the wet season flush when it does arrive.

9.3 Individual variation in life history strategies

The probability of offspring survivorship was not only related to the season of birth of the PY. Variation between individual mothers strongly influenced the survivorship of PY during both total lactational dependence and late pouch life. My data (albeit limited) suggest that individual females may adopt different strategies in rearing PY (Chapter 8). Some females had a high probability of rearing PY during total lactational dependence but most of these young die during late pouch life. Others had a low probability of PY survivorship during total lactational dependence, but most of these young survived to the end of pouch life. Extrapolation of data from *M. eugenii* on the energetic cost of different phases of lactation to females (Cork and Dove 1989) suggest that there will be little difference between the two strategies in energy investment, as young dying in early pouch life will have received little investment of energy from the mother. I suggest that perhaps the real importance of this finding is not in energetic terms, but rather in the phenotypic plasticity which is present within a population which allows that population to survive in an unpredictable environment. This is supported by a growing number of studies that are finding considerable variation in reproductive strategies and success between individual females within a population (Clutton-Brock 1988b).

I was able to identify only one maternal correlate of PY survivorship: that smaller-framed females were more successful in rearing young in late pouch life. However, this factor is less important than mother *per se*. This is contrary to most generally accepted theories which predict that bigger mothers are better than smaller mothers (Ralls 1976, Wilson 1975), but there are several reasons why this could be so (Chapter 8.4.3). These include differential energy allocation and requirements and the production of smaller young. Alternatively, the observed result may be the product of unmeasurable factors such as age or the effect of measuring instantaneous rather than lifetime reproductive success.

I was unable to examine the influence of some other factors (such as maternal age and position in the dominance hierarchy) which have been shown to influence the survivorship of young in other mammals (e.g. Silk *et al.* 1981; Clutton-Brock, Guinness and Albon 1982b; Gouzoules, Gouzoules and Fedigan 1982; Stuart-Dick and Higginbottom 1989). However, techniques for determining the age of post-PY animals were investigated and developed (Chapters 4, 5) so that such information on maternal age can be readily obtained in the future. The eruption and forward movement of the teeth were used to age rock wallabies between weaning and full molar eruption (Chapter 5). Since full eruption probably occurs at about seven years in *P. assimilis* and the maximum life span was at least 12 years, molar eruption is a useful tool for ageing animals during a major proportion of their adult life.

The existence of stable home ranges of female *P. assimilis* (Horsup *personal communication*) and the individual variation in their diet (Horsup and Marsh 1992) suggest that the nutritional status of a mother may influence survivorship of her PY. The mechanism controlling PY growth and perhaps mortality is unknown, although it is likely to be via limitations of either the quantity or quality of milk supplied. Anecdotal evidence suggests that lack of dietary sodium strongly influences PY survivorship of macropodids in early pouch life by limiting the mother's conversion of food intake into milk (B. Green *personal communication*).

The mother's ability to obtain and convert the food available would then be a major influence on the survival potential of the PY. Such a mechanism provides a way in which a female's reproductive effort may be 'controlled' via lactation. However, there is no data on the chemical composition of the diet of adult females which have PY of different ages or offspring survivorship at Black Rock.

As the environmental conditions improve, I would expect the probabilities of offspring survivorship to also improve. However different probabilities of mortality occur at different phases of lactation and this will probably continue to occur during improved conditions. The probability of offspring mortality was greatest between during the YAF stage (0.625) compared with that during total lactational dependence (0.234) and late pouch life (0.256). As different factors influence the various phases of lactation to different extents, it is unlikely that the improved environmental conditions will change the probabilities of dying equally. However, even if they are changed equally, the greatest potential for improved survivorship of young is between PEP and weaning. A halving of the mortality recorded during the drought years of this study would see the survivorship of PY to PEP increase from approximately 75% to 87%. However, the same change in probabilities of mortality between during the YAF stage would see 69% of young survive this phase compared with 38% previously, a far more significant increase.

It must be remembered that observed life history traits, which are 'solutions' to environmental variability, may not be the optimal response to such variability. Rather, they are the best compromise given the constraints of phylogeny (Stearns 1976). The high mortality of offspring of *P. assimilis* may be such a compromise whereby a continuously breeding species can survive and successfully reproduce in an unpredictable and not always benign environment. What is important is for the population to contain the phenotypic plasticity to cope with the unpredictable environment.

Pouch young were not the only rock wallabies to die during the study period; some 25% of tagged adults also died. No causes could be determined for most of these deaths and rock wallabies died in equal numbers regardless of sex, season and of year. As recruitment into the adult population was negligible during this time, the net result was a decline in the number of rock wallabies at the Black Rock colony.

9.4 Population dynamics of a colony of *P. assimilis*

During the drought years of my study period, offspring mortality was high and recruitment into the adult population was neglible. The age structure of the population was skewed towards very young animals (PY) and very old animals (≥7 years). Almost no sub-adults or young adults were present in the population. Few animals had been recruited to the breeding population in at least the previous five years. This low recruitment approximately coincides with the sequence of below average rainfall years which preceded my study period (Figure 2.6). While the older animals could not be aged, I speculate that these animals may be part of a cohort which was born during the above average rainfall years in the late 1970's and early 1980's.

Previous and subsequent research at Black Rock occurred during years of average to above average rainfall. During the high rainfall years of the early 1970's PY survivorship was high and a high proportion of pre-reproductive animals were present in the population (W. Davies, *personal communication*). Above average wet seasons and favourable conditions also occurred after my study period. By April 1991, the population had increased, almost half of the animals caught were pre-reproductive and new adults were being recruited (P. Spencer *personal communication*).

I suggest that the population age structure of *P. assimilis* at Black Rock fluctuates in response to the quality of seasons (as defined by the amount and pattern of rainfall). In good years, a high proportion of young survive to become members of the breeding population and the size of the population increases, since recruitment exceeds mortality. In drought years, few or no young survive to breed and the population declines as adult mortality exceeds recruitment.

Thus recruitment into the breeding population may be spasmodic, reflecting the irregular pattern of good seasons. While adult *P. assimilis* may be capable of breeding for ten or more years, the adult population of a colony may consist of animals born during relatively few good years.

Many relevant studies of macropodids which have examined changes in reproduction, offspring survivorship, recruitment, or the age structure of the population examined these factors in isolation from each other (e.g. Ealey 1963; Frith and Sharman 1964; Sadleir 1965; Kirkpatrick and McEvoy 1966; Poole 1973, 1975; Caughley, Bayliss and Giles 1984). Few studies have examined the inter-relationships between these changes and the long term pattern of rainfall. Newsome (1977) examined these factors in a population of *M. rufus* in central Australia. The age structure of this population of kangaroos was also found to be skewed towards older animals which had been born almost 20 years previously.

Additional animals had been recruited four and eight years previously. The years of recruitment coincided with years of high rainfall and good pasture growth. Newsome (1977) concluded that in the unpredictable climate of arid Australia, *M. rufus* relies on the infrequent favourable years to regenerate populations and allow these populations to survive long periods of intermittent drought. This pattern is similar to that which I think is occurring in the population of *P. assimilis* at Black Rock and may be typical of populations of this and other species of macropodids living in unpredictable environments.

The pattern of pulsing of animal numbers within a colony over time which I have hypothesised above, has implications for the conservation biology of rock wallabies. If true, rock wallaby populations in this region regularly pass through periods of low numbers and demographic instability. This needs to be monitored carefully as additional factors, such as feral cats (Spencer 1991) and foxes (Kinnear, Onus and Bromilow 1988), could have a devastating impact at particular points in the cycle when the population has been driven to precarious levels by local climatic factors. Relatively large numbers of habitats need to be protected to compensate for the asynchronous pulsing of populations and the need for populations to be regenerated from each other.

9.5 A possible model for speciation in *Petrogale*

As a result of this work at Black Rock, the ecology of *P. assimilis* is better understood than that of most species of *Petrogale* and indeed tropical Macropodidae. *Petrogale assimilis* is a typical member of its genus; it lives on rocky outcrops which ameliorate the harshness of the surrounding environment and its distribution is restricted to the wet-dry tropics of northern Australia. Thus our knowledge of *P. assimilis* may provide some insights into speciation in *Petrogale* generally.

Speciation in *Petrogale* has fascinated marsupial biologists for some time because of the relatively high species diversity of the genus in comparison to other marsupial genera and the incomplete reproductive isolation between taxa. An understanding of the mechanisms involved has implications for understanding evolutionary theory generally. As yet, no detailed ecological mechanism has been proposed. Sharman, Close and Maynes (1990) suggested that since the distribution of each species could be delineated on climatic criteria, climate was probably an important influence. My study reinforces their suggestion and hints at a mechanism which may enhance species diversity in the wet-dry tropics.

The major centre of *Petrogale* speciation is located in the wet-dry tropics of north eastern Australia. Freeland *et al.* (1988) have suggested that in the wet-dry tropics, rocky outcrops are islands of higher species diversity and a more benign environment in the 'sea' of an otherwise harsher environment.

I hypothesise that the number of *P. assimilis* at Black Rock pulses in response to rainfall. A similar phenomenon was shown for *M. rufus* in central Australia (Newsome 1977). However, unlike *M. rufus*, *Petrogale* spp. are bound to rocky outcrops which are often spatially isolated and movement between these islands is probably quite limited, even in good years.

It seems likely that genetic exchange between populations will be higher when environmental conditions are favourable. As the population expands, shelter sites may become limiting, forcing young animals from the main colony. Even away from the rocky outcrop, water and suitable high quality forage would be available for longer periods in favourable conditions, making successful migration between outcrops more likely. In contrast, little genetic exchange is likely during more unfavourable environmental conditions. In such times, water and forage are limited even around the normally diverse rocky outcrops, animals lose body condition and probably adopt energy saving strategies, precluding long range movements. Mortality of all age classes is high during such times. Smaller populations may die out altogether if these conditions persist and populations on larger outcrops such as at Black Rock, would be greatly diminished. With a cycle of more favourable seasons, the remaining populations would recover, and dispersal and repopulation of other areas may occur.

A series of introgressions has been postulated as a genetic mechanism of speciation in rock wallabies (Sharman *et al.* 1990, Eldridge *et al.* 1988, 1989). It is less likely that such genetic differences would be fixed in populations during good years due to increased dispersal between populations. However, if the heterozygote formed from individuals from two parent populations exhibits hybrid vigour, then the genetic changes postulated by Eldridge *et al.* (1988, 1989) and Sharman *et al.* (1990) may become fixed when these populations are isolated and reduced in numbers during cycles of unfavourable years. These introgressions would then be spread throughout the local region when population expansion occurred in good years. This would result in the high genetic diversity which is evident in colonies of rock wallabies today (P. Spencer *personal communication*), particularly in the wet-dry tropics. The pulses of recruitment within populations postulated earlier (Chapter 9.4) would reinforce spatial isolation between outcrops. The spatial variability of rainfall in the wet-dry tropics (Ridpath 1985) could result in nearby colonies pulsing asynchronously with each other and this would also serve to increase genetic diversity. The above interpretation is based on limited evidence and further studies are necessary to test its validity (see Chapter 9.6).

9.6 Future directions

This study of the life history of *P. assimilis* suggest several fruitful areas for future research. These will provide insights for the species, macropodids and for animal populations in the wet-dry tropics generally. For *P. assimilis*, these may be split into questions which address differences at the individual level and the population level.

9.6.1 *Individual level*

This study has established that females differ in their abilities to raise young successfully. Several factors may contribute to this variation, and each requires further attention. Studies at Black Rock are continuing and will increase the variety and number of individuals for which we have information on reproductive success. They will also allow investigation of lifetime rather than just instantaneous reproductive success. This variety among mothers needs to be associated with measurable differences between them. In particular, the greater success of small framed females at raising PY from total lactational dependence to PEP should be investigated. Strategies of energy allocation are currently being addressed by Jim Merchant and Helene Marsh. The behavioural ecology of *P.*

assimilis at Black Rock (Horsup 1989 and *personal communication*) and elsewhere (Barker 1990) also provides a number of interesting avenues of research. There are potential differences between females in both the quality of mates and food supplies. Age, position in the local dominance hierarchy, and regular measures of forage quality and quantity and soil moisture within feeding territories need to be correlated with growth, survivorship and reproductive success.

As an adjunct, the paternity studies currently being undertaken by P. Spencer will provide important information on the strength of the pair-bonding, and on the variation in reproductive success of males, which has not been addressed in the present study.

While many studies, including this one, detail changes in PY mortality, few have addressed the proximate factors causing this mortality. Factors such as nutrition have been postulated but others such as disease also require attention. This would most profitably be examined in captive colonies where such variables as the quality and quantity of forage could be manipulated.

9.6.2 *Population level*

Our understanding of the population dynamics of *Petrogale* is, at best, weak. Dispersal is often cited as important in the life history strategy of *Petrogale* yet remains unstudied in this genus. Knowledge of exactly which sex and age-class will disperse and how and when this occurs is a vital ecological link to understanding speciation in *Petrogale*, as postulated earlier.

Finally, the hypothesis presented here, that the population numbers of *P. assimilis* fluctuate markedly in response to environmental parameters needs to be tested. This could be achieved in either of two ways. Firstly, by continuing observations at the Black Rock study site over a number of years and monitoring . the changes in the population age structure with respect to the pattern of rainfall. Alternatively, the age-sex distribution of a number of carefully chosen populations could be examined using the techniques of age determination developed in Chapter 5. This could be then correlated with the climatic history of each colony.

Past reviews of the ecology of macropodids have highlighted the paucity of information on small tropical species (Sadleir 1965, Lee and Cockburn 1985, Lee and Ward 1989). This study has in part redressed this imbalance. Future studies of *Petrogale* such as those suggested above, will not only increase our knowledge of tropical marsupials, but will also further our understanding of this fascinating genus.

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Appendix 1: Comparison of Black Rock and Lyndhurst Rainfall (mm).

Year	Month	Black Rock	Lyndhurst
1988	January	21.2	11.8
	February	175.0	182.0
	March	2.3	10.4
	April	0.0	0.0
	May	1.0	0.0
	June	17.7	10.0
	July	15.0	11.6
	August	61.0	60.0
	September	0.0	0.0
	October	6.5	9.2
	November	8.5	17.5
	December	18.0	73.6
1989	January	145.3	49.6
	February	131.5	177.4
	March	104.0	132.4
	April	39.0	12.0
	May	69.0	80.4
	June	29.5	38.0
	July	39.5	30.0
	August	0.0	0.0
	September	0.0	0.0
	October	0.0	0.0
	November	290.5	>210.0
	December	?	30.0
1990	January	>3.0	73.0
	February	3.0	9.0
	March	83.0	87.0
	April	83.5	95.0
	May	69.0	50.0
	June	85.5	93.4

N.B. Researchers were only present at Black Rock for 12-15 days per month and hence the rainfall records for this location can be considered as a minimum only.

Appendix 2: Trap Success

Year	Field Trip	# Trap Days	# Post-PY *P. assimilis* caught
1986	June	92	?21
	July	98	?23
	September	88	17
	October	82	16
	December	111	13
1987	February	110	24
	March	112	17
	April	119	22
	May	110	33
	June	111	37
	July	144	34
	August	140	34
	September	123	33
	October	112	30
	November	115	35
	December	100	32
1988	January	83	32
	February	64	28
	March	106	40
	April	104	35
	May	115	33
	June	148	27
	July	116	26
	August	106	26
	September	115	25
	October	121	27
1989	February	244	30
	July	152	22

Appendix 3
Capture data for each marked rock wallaby for each trapping trip at Black Rock.

Only those months sampled are included. Legend to capture data: 1=alive, captured, 0=dead (since last capture, see Appendix 8 for more detail on adult mortality),and for females, ^{p}=PY present, $_{f}$=YAF present. Rock wallabies were first caught as adults unless otherwise noted: * PY, $^{+}$ YAF, $^{\#}$ sub-adult, $^{\bullet}$ orphaned (see Table 2.2), ^{b} caught at Little Black Rock. # Identification number for individual rock wallabies, those in bold are the 'core adults' which were used in Chapters 6 and 8. (A) Females, (B) Males.

(A) FEMALES

	1986					1987											1988										1989	
#	**J**	**J**	**S**	**O**	**D**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**F**	**J**
001	1^p			1^p					1^p	1_f		1^p	1^p	1^p		1^p	1^p_f	1^p	1^p	1^p	1^p	1^p	1^p	1^p_f	1^p_f	1_f	1^p	1^p
005$^+$		1																										
006	1_f	0?																										
008	1^p	1^p	1^p	1^p	1^p_f	1^p	1^p	1^p	1^p	1^p_f	1_f	1	1^p	1^p	1^p	1^p	1^p	1	1^p	1^p	1^p	1^p	1^p	1^p	1^p_f	1^p	1^p	0
010	1^p	1^p	1	1^p		1^p				1^p	1^p	1^p	1^p	1^p	1_f	1_f	1^p		1^p	1^p	1^p	1^p	1^p_f	1_f	1^p	1^p	1_f	1
012	1^p								1^p	1^p	0^p																	
013	1^p	1^p				1^p	1^p	1_f	1^p_f	1^p	1^p	1^p	1^p	1	1	1	1	1	1^p	1^p	1^p	1	1^p	1^p	1^p	1^p	1^p	1^p
014	1^p			1^p	1^p	1^p				1^p_f	1^p	1	1^p	1^p	1^p	1^p	1^p	1^p	1_f	1^p_f	1^p_f	1^p_f	1^p	1^p	1^p	1^p_f	1^p	1
018	1			0																								
413	1																											
032		1^p	1^p						1^p	1_f	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1_f	1	1^p	1^p
035		1^p							1^p	1	1^p	1^p										0						
036		1^p	1^p	1^p	0																							
037		1^p	1^p_f		1^p	1^p	1^p	1^p	1	1	1	1	1^p	1^p	1^p	1^p	1^p	1^p	1^p_f	1^p	1^p	1^p	1^p	1^p	1^p_f	1	1^p	1^p
038*			1																									
043		1^p		1^p				1^p				1	1^p	1	0													
045$^+$			1																									
046		1^p	1^p	1^p				1^p	1^p_f	1^p	1^p	1^p	1^p	1	1	1	1^p	1^p	1^p	1^p	1^p	0						
049		1^p	1^p	1^p		1^p_f	1^p	1^p	1	0?																		
052		1^p	1		1	1^p		1^p	1^p	1	1	1	0															
053		1^p																1^p		1^p	1_f	1^p_f	1^p	1^p	1	1^p	1^p	1^p
054			1^p			1^p			1	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p_f	1^p	1^p	1^p	1_f	1^p	1^p	1^p	1^p	1^p	1^p	
061			1																	1	1							1^p
063*					1																							
068					1							1	1^p				1^p											
070					1^p	1^p			1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1	1^p	1^p	1^p	1^p	1^p	1^p	1_f	1^p_f	1^p	1^p	1^p

	1986					1987											1988										1989	
#	J	J	S	O	D	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	F	J
D*						1																						
074+							1																					
075+							1																					
076						1^p			1^p	1	1^p	1^p	1	1^p	1^p	1^p	1^p	1^p	1_f	1^p_f	1_f	1^p_f	1_f	1^p	1^p	1^p	1^p	1^p_f
079*							1^a																					
082							1				1^p	1							1^p		1^p							
089							1^p								1^p					1^p	1^p	1^p					1	
096*										1																		
097									1^p										1^p				1			1	1_f	1^p
F*									1																			
098*										1																		
102									1	1^p	1^p	1^p																
104									1^p_f					1^p														
107									1_f		1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p
108+											1																	
110										1																		
111										1^p			1^p	1^p	1^p	1^p	1^p	1^p	1^p	1^p		1^p	1^p	1^p	1^p	1^p	1^p	1_f
117										1^p	1^p				1^p				0									
J/121*											1	1																
125													1^p															
128*															1													
130															1^p_f	1^p	1^p	1^p	1^p									
132															1^p	1^p												
133															1^p	1^p	1^p_f	1^p_f	1	1	1^p	1	1	1	1	1	1	1
134#																1												
136															1^p										1^p			1^p
L/138*																1	1											

	1986					1987											1988										1989		
#	J	J	S	O	D	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	F	J	
142																1^p			1^p			1^p	1_f	1^p_f					
143*																	1												
144*																1													
145																1				1^p	1							1^p	
M/310[a]																	1												
149+																				1	1	1	1	1					
152																			1										
153																				1^p								1^p	
155*																					1								
159+																						1				1		1	1^p
160																					1^p						1^p	1^p	
164*																							1						
166*																							1						
167*																							1						
174*																									1	1			
R/176*																										1	1		
P*																										1			
181[b]																											1^p		
184[b]																											1_f		
192+																												1	
193																												1	1
197*																												1	
198*																												1	

(B) MALES

	1986					1987											1988										1989	
#	**J**	**J**	**S**	**O**	**D**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**F**	**J**
002	1			1		1	1		1	1	1	1	1	1	1	1	1	1	1	1	0							
003	1																											
004	1	0?																										
007	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
009	1	1	1						1	1																		
015	1																											
017	1						1	1	1	1	1		1	1	1	1	1		1	1	1	1	1	1	1	1	1	
019	1						1	1	1	1	1	1	1	1	0?													
023	1	1																										
024	1	1			1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		0		
025	1									1	1	1					0											
A*		1																										
026		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
034		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0							
H*									1																			
039		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
040		1							1	1	1	1	1	1		0												
041		1										0																
050		1	0																									
056			1					1	1	1	1	1		1	1	1	1	1	1	1	1		0?					
060*				1	1																							
071					1			1		1	1	1	1	1	0													
072					1	1				1	1	1																
C*						1																						
078						1		1	1	1		0?																
080						1	1	1	1	1	1	0?																

	1986					1987											1988										1989	
#	J	J	S	O	D	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	F	J
081						1								1														
085							1	1	1		1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	0	
086							1																					
087							1	1	1	1		1						0										
092*									1																			
093								1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	0				
103*										1																		
105									1	1																		
106*										1	1																	
109										1																	1	
F/112*										1	1																	
114										1																		
115										1					1			1	1	0								
116										1					1	0												
119											1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
120											1	1	1						1		1							
124													1		1	1	1	1										
126													1				1	1	1									
127													1		1		1		1	1	1		1		1	1	1	1
131															1	1	1	1	1	1					1			
135															1	1	1	1	1	1	1	1	1	1	1	1	1	1
137*																	1											
139*																	1											
K/141*																1	1											
146																	1											
148																	1				1			1			1	
150/N*																		1	1	1	1	1	1	1	1	1	1	

	1986					1987											1988										1989		
#	J	J	S	O	D	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	F	J	
O*																		1											
151*																				1									
154																				1									
157*																						1							
161*																							1	1	1	1	1	1	1
162																						1	1				1		
165*																							1	1					
168*																								1	1				
171																		1	1	1	1		1	1	1	1	1		
173*																									1				
175*[a]																									1				
177																									1	1			
179																										1	1		
180[b]																											1		
182																										1			
183[b]																											1		
185+[b]																											1		
188																											1		
195*																												1	
196*																												1	
199																											1		
U/316																												1	

Appendix 4: Pouch Young Growth

Measurements (mm) of pouch young from rock wallabies caught at Black Rock and used to develop age determination models (Chapter 3).

PY#	Sex[1]	Days[2]	Head length	Pes length
4	2	0	22.0	13.2
4	2	31	33.7	25.0
4	2	58	42.0	37.2
4	2	86	52.0	58.2
4	2	121	60.5	77.8
4	2	153	68.0	88.0
8	1	0	13.2	5.4
8	1	63	36.4	30.4
8	1	83	42.2	41.8
8	1	116	55.6	67.7
8	1	145	62.5	81.9
11	2	0	--	4.8
11	2	28	23.0	14.0
11	2	55	33.0	23.5
11	2	91	45.5	41.2
11	2	121	54.2	63.0
11	2	153	62.5	82.5
15	1	0	24.4	16.0
15	1	33	35.1	29.2
15	1	59	42.0	41.5
15	1	93	54.3	64.1
15	1	120	59.9	77.1
16	1	0	13.7	6.0
16	1	62	35.2	27.0
16	1	88	44.7	41.5
16	1	115	52.7	59.8
16	1	154	61.7	85.0
76	2	0	--	7.0
76	2	38	24.7	17.5
76	2	65	32.5	26.0
76	2	96	41.0	40.5
76	2	124	50.0	60.2
76	2	152	56.7	73.0

[1] 1=female; 2=male

[2] Days since first capture

Appendix 5: Growth of 'known-age' animals

Morphometric measurements (in millimetres and grams) of 'known-age' wild rock wallabies from Black Rock measured beyond pouch-life.

(A) Females

ID	Age^1	Head length	Arm length	Pes length	Body weight
149	78	34.8	-	-	-
149	116	-	-	-	85
149	143	55.5	-	-	-
149	176	65.5	-	-	420
149	206	71.0	50.0	101.5	650
149	236	75.5	53.0	103.5	920
149	267	77.5	51.0	105.0	1125
149	300	79.2	55.0	107.5	1150
159	166	77.0	55.5	110.5	1100
159	292	86.5	62.0	117.0	1750
159	385	91.0	69.0	124.0	2150
159	424	-	-	-	2350
159	448	89.8	73.0	129.5	2550
159	502	-	-	-	2800
159	534	-	-	-	2700
159	562	94.0	77.0	132.0	2750
159	599	-	-	-	3150
159	627	-	-	-	3350
159	660	-	-	-	3220
159	689	-	-	-	2270
159	716	-	-	-	3300
159	754	-	-	-	3110
159	808	100.5	80.0	132.5	3170
159	904	102.5	82.0	134.5	3650
159	927	-	-	-	3700
159	964	-	-	-	3430
159	986	-	-	-	3350
159	993	-	-	-	3350
159	1013	-	-	-	3520
159	1045	-	-	-	3550
159	1062	-	-	-	3550
159	1069	-	-	-	3510
159	1126	108.0	83.0	132.5	3500
176	27	15.5	-	-	-
176	121	46.5	-	-	-

176	153	54.8	-	-	150
176	180	60.2	-	-	250
176	217	66.5	46.0	94.5	470

[1] Age in days

(B) Males

ID	Age[1]	Head length	Arm length	Pes length	Body weight
150	147	52.0	-	-	125
150	173	60.8	-	-	220
150	206	67.0	-	-	470
150	233	72.0	49.5	101.0	670
150	263	74.5	52.5	105.0	885
150	299	77.5	52.5	108.0	950
150	329	78.2	54.0	108.2	1150
150	361	81.0	56.5	111.0	1250
150	388	82.0	56.8	111.0	1450
150	420	83.8	58.8	115.5	1550
161	168	60.5	-	-	235
161	200	68.0	-	-	430
161	232	73.8	50.5	97.5	705
161	258	76.0	51.8	101.2	920
161	291	81.2	56.0	107.8	1150
161	350	85.0	64.0	115.5	1500
161	393	-	-	-	1750
161	414	88.0	67.0	123.2	1950
161	443	-	-	-	2100
161	468	-	-	-	2100
161	500	-	-	-	2300
161	530	93.5	72.0	127.5	2300
161	566	-	-	-	2550
161	594	-	-	-	2600
161	627	-	-	-	2620
161	656	-	-	-	2980
161	684	-	-	-	2650
161	721	-	-	-	3100
161	776	-	-	-	3180
161	838	-	-	-	3300
161	871	-	-	-	3250
161	895	-	-	-	3600
161	932	102.2	87.0	136.5	3460
161	953	-	-	-	3500
161	960	-	-	-	3375

161	980	-	-	-	3520
161	1012	-	-	-	3620
161	1030	-	-	-	3575
161	1037	-	-	-	3605
161	1057	-	-	-	3630
161	1094	100.5	89.0	136.0	3565
179	341	89.8	65.5	123.2	2250
179	444	94.0	73.0	130.0	2550
179	465	93.8	74.0	128.8	2800
179	494	-	-	-	2450
179	520	-	-	-	2450
179	551	-	-	-	3200
179	581	93.8	72.2	127.8	2600
179	617	-	-	-	3400
179	646	-	-	-	3500
179	676	-	-	-	3400
179	707	-	-	-	3450
U/316	105	48.0	-	-	-
U/316	131	55.0	-	-	-
U/316	173	67.8	-	-	440
U/316	225	76.5	55.0	105.5	1000
U/316	251	-	-	-	1150
U/316	282	-	-	-	1550
U/316	312	85.5	63.2	116.0	1650
U/316	349	-	-	-	1900
U/316	375	-	-	-	1950
U/316	409	-	-	-	1960
U/316	438	-	-	-	2190
U/316	505	-	-	-	2450
U/316	558	96.5	76.0	129.5	2550
U/316	620	-	-	-	2780
U/316	653	-	-	-	2850
U/316	714	100.5	82.0	132.2	3100
U/316	735	-	-	-	3000
U/316	742	-	-	-	3050
U/316	761	-	-	-	3200
U/316	795	-	-	128.5	3180
U/316	813	-	-	-	3295
U/316	819	-	-	-	3200
U/316	839	-	-	-	3245
U/316	876	101.0	85.2	133.0	3270

[1] Age in days

Appendix 6

Molar eruption (MES) and molar progression (MI) status of 'known-age' animals used to calculate the regression curves for age determination.

PY#	Sex[1]	Age[2]	ME	MI	DAYS[3]	Wild[4]
79	1	408	1.8	1.2	--	0
79	1	449	1.8	1.2	41	0
79	1	526	2.0	1.4	77	0
79	1	534	1.8	1.4	85	0
79	1	610	2.0	1.5	76	0
79	1	694	2.2	1.7	84	0
79	1	806	2.4	1.9	112	0
79	1	948	2.6	2.2	142	0
146	2	385	1.4	1.0	--	1
149	1	206	0.8	0.7	--	1
149	1	268	1.0	0.9	62	1
150	2	175	0.8	0.7	--	1
150	2	234	1.0	0.7	59	1
150	2	299	1.2	0.9	65	1
150	2	361	1.4	1.0	62	1
150	2	421	1.8	1.3	60	1
161	2	232	0.8	0.5	--	1
161	2	350	--	1.0	118	1
161	2	384	1.6	1.1	44	1
161	2	520	1.8	1.4	136	1
174	1	199	0.4	0.4	--	1
177	2	296	1.2	1.0	--	1
177	2	508	1.6	1.4	212	1
179	2	341	1.8	1.4	263	1
179	2	581	2.0	1.4	240	1
182	2	252	0.8	0.5	--	1
182	2	432	1.6	1.4	180	1
182	2	461	1.8	1.4	29	1
182	2	492	1.8	1.5	31	1
185	2	235	0.6	0.3	--	1
310	1	354	1.6	1.0	--	0
311	2	297	1.2	0.7	--	0
311	2	409	1.6	1.2	112	0
312	1	273	1.2	0.6	--	1
313	2	240	0.8	0.4	--	1
314	1	297	1.4	0.8	--	0
314	1	348	1.6	1.2	51	0
314	1	425	1.8	1.3	77	0

314	1	507	2.2	1.5	82	0
314	1	593	2.4	1.6	86	0
314	1	705	2.6	2.0	112	0
315	2	177	--	0.3	--	1
316	2	224	1.0	0.9	--	1
316	2	310	1.4	1.0	86	1

[1] 1=female, 2=male

[2] in days

[3] Days since first radiograph

[4] 0=captive reared, 1=wild reared

Appendix 7

Anaesthetics trialled

It was necessary to anaesthetise the animals before radiographing them. Three drugs were chosen after consultation with local veterinary surgeons. These were tested during the initial trials to determine the best anaesthetic for the animals in the conditions at Black Rock. Initially four adult animals were randomly chosen for each drug. The dose rate, the recovery times and the corresponding effects for each drug have been summarised in Table 1.

Of the three drug regimes trialled, the barbiturate thiopentone sodium (Pentothal) was found be the best anaesthetic for this situation and was used throughout my study. With experience the initial dose rate for Pentothal was halved to 12.5 mg/kg. This amount was rarely injected, but was used as a safety measure to control the maximum amount of the drug injected. The advantages of this drug were that induction was rapid; recovery times were less than 1 hour; the observed effects were constant for a given dose and the depth of anaesthesia could be controlled. The handler must be experienced at locating and injecting into the venous system.

Saffan was the most effective of the intramuscularly injected drugs. The effects were less variable at the higher dose rate. Saffan has been known to cause anaphylaxis in some domestic mammals (e.g. cats) (Keep 1978) and it should be used with caution. It can be injected intravenously, but this would exacerbate any such effects. There is no evidence of this effect in macropodid marsupials, and as another suitable drug was available, it did not seem necessary to test Saffan intravenously.

A reversing agent (yohimbine) is available in some countries for xylazine-ketamine (Higginbottom 1989), which would reduce the recovery time for this drug mixture. This would make it more suitable where an intramuscular injection was preferred and short induction and recovery times were not critical.

References

Higginbottom K. (1989). Macropod studies at Wallaby Creek. VII. Capture of wild red-necked wallabies by 'blow-darting'. *Aust. Wildl. Res.* **16**, 173-8.

Keep J. M. (1978). Marsupial anaesthesia. In, *Post-graduate committee in veterinary science, Proceedings 36. Fauna.* **36**, 123-134.

Table 1 Effects of the anaesthetics trialled on wild *P. assimilis*.

Drug (commercial name)	Dosage (mg/kg)	Injection method	Recovery time	Comments
Xylazine (Rompun: Bayer) + Ketamine (Ketalar: Parke Davis)	8 15	i.m.	70 - 176 min	variable induction and recovery time; xylazine did not always negate the jaw champing induced by ketamine; spastic muscle spasms were occasionally observed in one animal;
Alphazalone + Alphadolene (Saffan: Glaxovet)	15	i.m.	> 105 x < 210 min	variable induction and recovery time; one animal did not go under completely;
"	18	i.m.	35 - 80 min	decreased induction and recovery time; effect less variable
Thiopentone sodium (Pentothal: Abbot)	25	i.v.	55 - 85 min	effect was constant (repeatable); could be given to effect recovery time was relatively constant;
"	12.5	i.v.	< 60 min	as above.

Appendix 8
Temporal Distribution of Deaths of Known Rock Wallabies at Black Rock

#	Month of death	Notes
002	April 1988	Empty radio-collar only.
004	June 1986	Disappearance after regular observations.
006	June 1986	Disappearance after regular observations.
008	February 1989	Poor health prior to disappearance.
012	July 1987	Trap death (cold stress).
018	October 1986	Body found.
019	November 1987	Disappearance after regular observations.
024	October 1988	Body found.
025	January 1988	Body found.
034	May 1988	Body found.
035	June 1988	Body found.
036	October 1986	Trap death (heat stress).
040	December 1987	Body found.
041	August 1987	Body found.
043	November 1987	Body found.
046	May 1988	Empty radio-collar only.
049	June 1987	Disappearance after regular observations.
050	September 1986	Body found.
052	August 1987	Body found.
056	July 1988	Disappearance after regular observations.
071	October 1987	Sick: jaws broken.
078	August 1987	Disappearance after regular observations.
080	August 1987	Disappearance after regular observations.
085	December 1988	Body found.
087	February 1988	Body found.
093	July 1988	Body found.
115	March 1988	Body found.
116	December 1987	Body found.
117	March 1988	Killed by male caught in same trap.
413	June 1986	Poor health: very old, ?post-capture stress myopathy.

Appendix 9

Monthly Variation in Adult Body Condition

(A1) Adult Female Weight (grams)

		All animals			R. M. Sub-sample[1]		
Year	**Month**	**N**	**Av.[2]**	**s.d.[3]**	**N**	**Av.[2]**	**s.d.[3]**
1986	J	4	3515	266			
	J	13	3842	542			
	S	4	3626	310			
	O	7	3666	512			
	D	6	3425	242			
1987	F	10	3578	92	8	3598	222
	M	5	3335	256			
	A	7	3471	261			
	M	16	3734	282			
	J	15	3552	354	13	3588	375
	J	16	3508	226			
	A	18	3537	346			
	S	16	3417	438			
	O	15	3352	443			
	N	18	3185	310	14	3279	383
	D	18	3337	378			
1988	J	15	3402	351			
	F	13	3488	333			
	M	20	3502	336	14	3543	349
	A	20	3423	747			
	M	21	3319	865			
	J	17	3447	741	14	3666	576
	J	14	3441	750			
	A	16	3675	337			
	S	8	3250	513			
	O	16	3581	441	13	3600	480
1989	F	17	3550	334			
	J	21	3294	480			

[1] Sub-sample of observations used in repeated measures ANOVA's (Chapter 6)

[2] Average value

[3] Standard deviation

(A2) Adult Male Weight (grams)

		All animals			R. M. Sub-sample[1]		
Year	Month	N	Av.[2]	s.d.[3]	N	Av.[2]	s.d.[3]
1986	J	3	4300	260			
	J	9	4247	290			
	S	6	4081	434			
	O	5	3966	409			
	D	7	3882	258			
1987	F	10	4090	280	10	4112	377
	M	10	4040	317			
	A	14	4145	315			
	M	16	4242	294			
	J	20	4072	258	12	4096	324
	J	18	4087	304			
	A	16	4138	227			
	S	17	3872	393			
	O	15	3872	341			
	N	19	3774	264	14	3747	270
	D	14	3871	203			
1988	J	17	3853	202			
	F	15	4030	186			
	M	17	4041	317	14	4127	249
	A	16	4116	271			
	M	14	4139	280			
	J	10	4100	284	14	4123	283
	J	12	4067	255			
	A	10	4075	248			
	S	7	4100	238			
	O	11	4077	415	10	4050	420
1989	F	10	4145	293			
	J	12	4050	345			

[1] Sub-sample of observations used in repeated measures ANOVA's (Chapter 6)

[2] Average value

[3] Standard deviation

(B1) Blood Packed Cell Volume (%) for Adult Female Rock wallabies

		All animals			R. M. Sub-sample[1]		
Year	Month	N	Av.[2]	s.d.[3]	N	Av.[2]	s.d.[3]
1987	F	9	41.56	3.43	8	42.87	1.67
	M	3	43.33	1.53			
	A	6	43.33	4.54			
	M	9	42.67	4.92			
	J	13	39.46	4.31	13	40.08	2.35
	J	14	39.71	4.41			
	A	18	44.61	4.26			
	S	15	43.13	5.23			
	O	15	38.2	5.20			
	N	17	36.94	2.95	14	37.79	1.72
	D	18	39.11	4.27			
1988	J	14	40.29	3.41			
	F	12	45.8	3.00			
	M	18	42.94	3.44	14	42.28	1.83
	A	19	44.53	4.08			
	M	19	45.62	4.28			
	J	17	42.24	4.43	14	42.28	2.16
	J	13	43.58	2.81			
	A	16	47.46	3.86			
	S	15	44.76	5.77			
	O	16	45.55	5.68	13	45.38	3.29
1989	F	17	43.74	5.39			
	J	19	41.62	3.53			

[1] Sub-sample of observations used in repeated measures ANOVA's (Chapter 6)

[2] Average value

[3] Standard deviation

(B2) Blood Packed Cell Volume (%) for Adult Male Rock Wallabies

		All animals			R. M. Sub-sample[1]		
Year	Month	N	Av.[2]	s.d.[3]	N	Av.[2]	s.d.[3]
1987	F	9	45.56	3.81	9	44.67	2.87
	M	9	45.22	4.71			
	A	13	49.38	5.38			
	M	16	46.69	5.08			
	J	20	41.85	5.65	12	43.92	3.27
	J	15	42.33	6.94			
	A	15	46.93	5.24			
	S	13	44.38	3.78			
	O	12	39.17	7.48			
	N	16	39.88	5.14	14	39.8	2.90
	D	14	42.36	5.66			
1988	J	17	41.88	6.33			
	F	14	50.00	4.38			
	M	17	46.71	4.07	14	47.00	2.29
	A	16	48.01	4.57			
	M	15	48.93	4.57			
	J	10	43.72	3.46	14	45.47	2.29
	J	12	49.56	4.29			
	A	10	51.93	5.07			
	S	10	50.04	4.01			
	O	11	50.04	4.40	10	49.40	3.14
1989	F	10	48.0	5.13			
	J	10	45.54	5.25			

[1] Sub-sample of observations used in repeated measures ANOVA's (Chapter 6)
[2] Average value
[3] Standard deviation

Appendix 10

Estimated Month of Birth for Pouch Young of All Females

♀ID#	SIB#	Birth Month
001	1	05-86
	2	10-86
	3	06-87
	4	12-87
	5	07-88
	6	12-88
	7	06-89
008	1	04-86
	2	11-86
	3	05-87
	4	07-87
	5	08-87
	6	02-88
	7	08-88
010	1	02-86
	2	10-86
	3	04-87
	4	12-87
	5	06-88
	6	08-88
	7	06-89
012	1	03-86
	2	03-87
013	1	04-86
	2	07-86
	3	09-86
	4	04-87
	5	07-87
	6	02-88
	7	06-88
	8	12-88
014	1	04-86
	2	10-86
	3	05-87
	4	07-87
	5	08-87
	6	03-88
	7	09-88
	8	12-88
	9	05-89
032	1	05-86
	2	11-86
	3	06-87
	4	01-88
	5	02-88
	6	10-88
	7	05-89
035	1	05-86
	2	12-86
	3	06-87
036	1	02-86
	2	08-86
037	1	01-86
	2	09-86
	3	11-86
	4	08-87
	5	02-88
	6	09-88
	7	11-88
	8	01-89
043	1	07-86
	2	01-87
	3	08-87
046	1	07-86
	2	10-86
	3	04-87
	4	12-87
049	1	07-86
	2	02-87
052	1	03-86
	2	12-86
053	1	07-86
	2	10-87
	3	09-87
	4	05-88
	5	03-89
054	1	09-86
	2	05-87
	3	12-87
	4	06-88
	5	01-89
061	1	02-89
068	1	09-87
	2	11-87

070	1	11-86
	2	06-87
	3	01-88
	4	08-88
	5	03-89?
	6	04-89
076	1	10-86
	2	06-87
	3	09-87
	4	03-88
	5	05-88
	6	07-88
	7	02-89
	8	05-89
082	1	04-87
	2	02-88
	3	08-88
089	1	01-87
	2	09-87
	3	11-87
	4	02-89?
097	1	12-86
	2	01-88
	3	08-88
	4	02-89
102	1	05-87
104	1	04-87
	2	10-87
107	1	10-86
	2	05-87
	3	11-87
	4	05-88
	5	11-88
	6	05-89
111	1	05-87
	2	08-87
	3	11-87
	4	12-87
	5	04-88
	6	09-88
	7	10-88
	8	06-89
117	1	01-87
	2	09-87
125	1	08-87
130	1	09-87
132	1	07-87
133	1	05-87
	2	12-87
	3	04-88
	4	10-88
136	1	10-87
	2	04-88
	3	11-88
	4	01-89
142	1	06-87
	2	12-87
	3	07-88
145	1	12-87
	2	01-89
153	1	01-88
	2	07-88
	3	01-89
159	1	05-89
160	1	02-88
	2	08-88
	3	09-88
	4	03-89

Appendix 11. Logistic regression analysis of variables influencing survivorship of PY. A Δ Deviance (or χ^2) and d.f. may be calculated by subtracting the Deviances and d.f. respectively of two related models, and this gives a test of the significance of the factor which has been omitted from the simpler model (Tabachnick and Fidell (1989).

(A) Seasonal factors possibly influencing PY survivorship during total lactational dependence (< 150 days of age).

Model	Deviance	d.f.
Mother + Season + Year	76.65	60
Mother + year	87.44	62
Mother + season	84.07	64
Season + year	100.8	74
Mother	91.69	66
Season	106.8	78
Year	106.9	76
Null model	110.8	80

(B) Mother variables possibly influencing PY survivorship during total lactational dependence (PY aged <150 days old). N.B. head and leg length were too highly correlated to include both in the full model.

Model	Deviance	d.f.
Mother + season + weight + head + PCV	42.93	35
Mother + weight + head + PCV	47.55	37
Weight + head + PCV	65.58	51
Weight + head	101.4	75
Weight + PCV	66.89	52
PCV + head	65.87	52
PCV	70.78	53
Head	108.0	79
Weight	101.8	76
Season + weight + head + PCV	62.56	49
Season + weight + head	94.16	73
Season + weight + PCV	63.25	50
Season + PCV + head	64.02	50
Season + PCV	69.89	51
Season + head	103.7	77
Season + weight	94.18	74
Season	106.8	78
Mother + weight	86.98	62
Mother + PCV	49.12	39
Mother + head	90.04	65
Mother	91.69	66
Null model	110.8	80

(C) Seasonal factors possibly influencing survivorship of PY during late pouch life (150-201 days of age).

Model	Deviance	d.f.
Mother + current season + current year	27.65	29
Mother + year	31.63	31
Mother + season	36.31	33
Season + year	61.59	42
Mother	37.23	35
Season	66.20	46
Year	62.19	44
Mother + season of birth + year of birth	29.55	29
Mother + season of birth	33.65	33
Season of birth + year of birth	57.80	42
Mother + year of birth	31.63	31
Season of birth	62.11	46
Year of birth	62.19	44
Null model	66.92	48

(D) Factors influencing survivorship of PY during late pouch life (150-201 days of age).

Model	Deviance	*d.f.*
Mother + weight	37.21	33
Weight	63.23	46
Mother	37.23	35
Weight + season	61.95	44
Season	66.20	46
PCV + mother	30.46	25
PCV	54.04	37
Leg + mother	37.23	35
Leg	61.48	47
Mother + body size index + fatness index	37.22	33
Mother + body size index	37.23	35
Mother + fatness index	37.22	33
Body size index + fatness index	59.39	45
Fatness index	65.67	46
Body size index	61.48	47
Null model	66.92	48

Delaney, Robyn, De'ath, Glenn 1990, Age estimation and growth rates of captive and wild pouch young of Petrogale assimilis, Australian Wildlife Research 17(5):491-499.