

**EFFECTS OF HUNTING AND RAINFALL ON
BENNETT'S WALLABY AND TASMANIAN
PADEMELON POPULATIONS**

by

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DECLARATION

This thesis contains no material which has been accepted for the award of any other higher degree or diploma in any tertiary institution, and to the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except when due reference is made in the text of this thesis.

A handwritten signature in cursive script, appearing to read 'Driessen Driessen', written in dark ink.

Michael Driessen



Plate 1: Bennett's wallaby, *Macropus rufogriseus*.



Plate 2: Tasmanian pademelon, *Thylogale billardierii*.

ABSTRACT

This study investigated the effects of hunting and rainfall on populations of Bennett's wallabies, *Macropus rufogriseus*, and Tasmanian pademelons, *Thylogale billardierii*, and represents the first major field based study on the biology of these species in their native environment. Three aspects of their biology were considered: body condition, breeding and population structure. Neither body condition nor population structure have been previously studied in either species.

This study was based on animals shot by commercial and non-commercial hunters. Study areas were located throughout Tasmania and represented a wide range of hunting and rainfall levels.

The start of the study coincided with the end of one of Tasmania's longest droughts. This drought provided an opportunity to investigate the effects of low rainfall on macropod populations in Tasmania.

Hunting had a direct effect on the age structure of the two wallaby species. High levels of hunting reduced the average age in populations of both wallaby species as a result of selective shooting of larger and hence, older individuals. In Bennett's wallabies, the effect of selective shooting of large animals was greater on males than on females and this caused a reduction in the proportion of males in the population. By comparison, there was no evidence that hunting caused a difference in the sex ratios of Tasmanian pademelons. This suggests that discrimination between male and female pademelons by hunters was minimal. It may also reflect the fact that Tasmanian pademelons are hunted less intensively than Bennett's wallabies.

The loss of reproductively mature animals as a result of hunting was largely compensated for by increases in breeding performance. In areas subjected to high hunting pressure, wallabies of both species reproduced at a younger age than wallabies in areas subjected to low hunting pressure. Moreover, wallabies in areas subjected to high hunting pressure

showed little decline in breeding success during the drought. The higher breeding performance in areas subjected to high hunting pressure was attributed to a decrease in density and subsequently an increase in the quantity of resources available for the surviving individuals.

The results of this study indicate that hunting had a greater impact on Bennett's wallabies than on Tasmanian pademelons. At present, the two species of wallaby are managed by the Department of Parks, Wildlife and Heritage as one species in relation to hunting. This greater vulnerability of Bennett's wallabies to hunting should be taken into consideration in its management, especially given that the reproductive rate of Bennett's wallabies is lower than that of Tasmanian pademelons.

The 1987/88 drought was shown to reduce the body condition (as measured by kidney fat index) of both wallaby species which, in turn, reduced breeding performance. The drought had less effect on Tasmanian pademelons than on Bennett's wallabies and this was attributed to differences in diet and breeding patterns. Survival of dependent young was lower during the year of the drought than during the year of normal rainfall. Fewer male Bennett's wallaby pouch young survived than females during the year of the drought. The drought also delayed the onset of maturity with males being more affected than females. For Tasmanian pademelons, this resulted in first-time breeders giving birth late in the breeding season.

The effects of drought on the biology of the two wallaby species were, in general, similar to those reported for other macropods on mainland Australia. Although the 1987/88 drought was severe by Tasmania's standards, it did not produce the same level of response seen in macropods experiencing severe drought in arid and semi-arid areas of Australia. This reflects the fact that the rainfall of Tasmania is characterised by low variability. Nevertheless, the drought did significantly reduce the breeding performance of both species and this should be taken into account in their management.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

Bennett's wallaby, *Macropus rufogriseus rufogriseus*, (Desmarest 1817) and the Tasmanian pademelon, *Thylogale billardierii*, (Desmarest 1822) are two species of macropod marsupial which are widespread and abundant in Tasmania and on many of its larger off-shore islands. Bennett's wallaby, together with the mainland subspecies, the red-necked wallaby, *Macropus rufogriseus banksianus*, ranges from central Queensland to south-eastern South Australia and into Tasmania. The Tasmanian subspecies differs from its mainland counterpart in that it is a seasonal breeder, whereas the mainland subspecies produces young in all months (Merchant and Calaby 1981). Bennett's wallaby has been introduced to the south island of New Zealand (Tyndale-Biscoe 1973, Gilmore 1977) and to some parts of Britain (Gilmore 1977). The Tasmanian pademelon once occurred in South Australia and Victoria (Wood Jones 1925) but is now restricted to Tasmania (Calaby 1971, Frith 1973).

Both Bennett's wallaby and the Tasmanian pademelon occur in a variety of habitats but show different preferences. Bennett's wallabies are most common in habitats with an open understorey whereas the Tasmanian pademelon is typically found in habitats with a dense understorey. Both species are particularly abundant where their natural habitat occurs adjacent to pasture. Although extensive land clearing for agriculture results in a reduction in numbers of both species through a loss of habitat, land clearance which produces a mosaic of cleared land and forest has lead to an increase in wallaby densities (Frith 1973, Johnson 1977a).

Both Bennett's wallaby and the Tasmanian pademelon have been hunted for skins, meat and sport since the earliest times of European settlement. Statistics on commercial hunting of

wallabies have been collected by the Department of Parks, Wildlife and Heritage since the 1920s (Anon 1984). Prior to the 1950s a considerable trade in wallaby skins existed with an average of 150 000 skins traded each year. Approximately 66% of these skins were of Tasmanian pademelons. No figures are available for the sale of meat during this period, but according to Guiler (1957) it was "...a rather spasmodic and casual business".

Since the 1950s the trade in wallaby skins has dropped considerably with an average of 50 000 skins traded every year between 1950 and 1988. This is despite an increase in the length of shooting season from 2-3 months prior to 1957 to 10-12 months since 1958. This decline in trade was associated with depressed skin prices (Anon 1984). An increase in skin prices in 1979/80 lead to 244 918 skins, worth over \$780 000, being traded. However, the price of skins soon fell and the number of skins traded in 1987/88 was 4574. The proportion of Tasmanian pademelons taken in relation to Bennett's wallabies dropped over this period to 50%. This may reflect a lesser demand for the use of fur in clothing for which the Tasmanian pademelon was sought. In recent years a reasonable trade in meat has been developed, with commercial operators selling both species to butchers for human and pet consumption (Anon 1984). In general, Bennett's wallaby is the preferred species for the meat trade due to its larger size.

Since the decline in skin prices most hunting of wallabies has been conducted by recreational shooters. However, even when skin prices were high, both species were extensively shot for sport (Guiler 1957) and wallaby hunting is considered to be a traditional past-time for many Tasmanians (Frith 1973). Estimates of the non-commercial harvest by postal questionnaire between 1979 and 1982 indicate that approximately 621 000 wallabies were taken every year (Anon 1984). On average 57% of this harvest comprised Bennett's wallabies.

Both species are regarded as significant pests in forestry and agricultural areas where their grazing and browsing activities cause extensive damage. As a consequence, both species have been subject to substantial control programs involving snaring (the use of

snare is now outlawed), shooting and poisoning. In the past much of the control has been undertaken by commercial shooters, but with decreased skin prices culling is now mainly conducted by recreational shooters or by farmers using 1080 poison. In spite of the widespread use of these control methods over the last 50 years only short-term relief has been achieved and both species still represent an economic threat to forestry and agriculture.

Macropods have been hunted throughout Australia since the earliest times of European settlement. Historical evidence suggests that hunting in the last 200 years has had little effect on reducing numbers or distribution of macropods (Robertshaw and Harden 1989). The exceptions to this are the forester kangaroo, *Macropus giganteus tasmaniensis*, in Tasmania and the toolache wallaby, *Macropus greyi*, in South Australia (Robertshaw and Harden 1989).

Most studies have shown that current hunting levels have little effect in regulating macropod abundance. Studies by Bayliss (1985, 1987), Caughley *et al.* (1979) and J. Caughley *et al.* (1984) found that hunting pressure had little impact on red and grey kangaroos. In contrast, Driessen and Hocking (1992) found that very high levels of hunting during the late 1970s and early 1980s reduced the abundance of both the Tasmanian pademelon and Bennett's wallaby.

A few studies have demonstrated some effects of hunting on the population structure of macropods. Russell and Richardson (1971) found that hunting pressure led to a younger age structure in wallaroos, *M. robustus*, *M. antilopinus* and *M. bernardus*, as a result of selective shooting of older animals. Newsome (1977a) demonstrated that selective hunting for male red kangaroos, *M. rufa*, caused a sex ratio biased towards females. Wilson (1975) compared the survival rates of grey kangaroos, *M. giganteus* and *M. fuliginosus*, red kangaroos and wallaroos, *M. robustus*, based on the age structures of skulls obtained by professional hunters. Survival rates were lowest for grey kangaroos and highest for red kangaroos, a difference that was attributed to greater tolerance by graziers for the latter.

The start of the present study coincided with the end of one of the longest droughts on record for Tasmania. This drought provided an opportunity to investigate the effects of low rainfall on the biology of macropod populations in Tasmania.

Several studies have shown that rainfall can regulate the abundance of various species of macropods (Newsome *et al.* 1967; J. Caughley *et al.* 1984; Caughley *et al.* 1985; Bayliss 1985; Robertson 1986; Driessen and Hocking 1992). The most common effect of rainfall on macropod populations is through its influence on plant growth and, hence, on food supply. This, in turn, will effect body condition, breeding and survival of a population. Shepherd (1987) was able to demonstrate a relationship between rainfall, pasture biomass, pasture quality and the condition of red and grey kangaroo populations. These rainfall induced changes in body condition were also linked to changes in fecundity and survival. Other studies have also demonstrated that rainfall influences the fecundity and survival of macropods (Newsome 1965, 1977b; Frith and Sharman 1964; Robertson 1986; Norbury *et al.* 1988).

1.2 AIMS OF STUDY

The aim of this study was to investigate differences in condition, breeding and age structure in Tasmanian pademelon and Bennett's wallaby populations in relation to hunting pressure and rainfall.

1.3 NOMENCLATURE

Bennett's wallaby is the common name used to distinguish the Tasmanian subspecies from its mainland counterpart, the red-necked wallaby. Bennett's wallaby is locally known as "kangaroo" or just "roo". The Tasmanian pademelon is also known in the literature as the

red-bellied pademelon or rufous wallaby. I have chosen to use the former based on the terminology used in Strahan (1983). This species is locally referred to as "wallaby".

When referring collectively to Bennett's wallaby and the Tasmanian pademelon in this study, the term 'wallabies' will be used. The term, 'macropods' is used to refer to members of the superfamily Macropodoidea (Strahan 1983; Grigg *et al.* 1989).

1.4 PAST STUDIES ON BENNETT'S WALLABY AND THE TASMANIAN PADEMELON

Despite the abundance of wallabies in Tasmania and the large numbers shot every year, there have been very few field studies investigating the biology of either species. Most field studies on Bennett's wallabies and Tasmanian pademelons have been concerned with investigating their effect on regeneration forests (Cremer 1960, 1962, 1969; Gilbert 1959, 1961; Mollison 1960; Statham 1983) and pastures (Gregory 1988), and with developing a means for their control (Elgie 1961; Tustin 1971; Statham 1983; Gregory 1988; Warburton 1990).

As a result of the concern expressed about the high level of culling of both species of wallaby, an investigation of census methods was undertaken by Johnson (1977a, 1978) and Mooney and Johnson (1979). Apart from reporting on methods of assessing abundance, they also examined their spatial and temporal use of habitat using radio tracking. Driessen and Hocking (1992) reviewed the method of census established by Johnson (1977a) and analysed the trends in abundance of both wallaby species from 1975 to 1990.

Aspects of Bennett's wallaby reproduction have been described from free-ranging populations in New Zealand (Catt 1977) and Britain (Fleming *et al.* 1983). Only one study has been conducted in Tasmania (Curlewis 1989) and this described the breeding season of Bennett's wallaby based on a small sample of young taken from three areas in Tasmania.

McCartney (1978) and Rose and McCartney (1982a) described the breeding season of the Tasmanian pademelon from samples taken from eastern and south-eastern Tasmania which included unpublished data collected by Bill Mollison in the late 1950s and early 1960s. Mollison collected data on the biology of both wallaby species whilst investigating the problem of wallaby and brushtail possum, *Trichosurus vulpecula*, damage to forest regeneration in the Florentine Valley (Mollison 1960). The data on the Tasmanian pademelon were later analysed by McCartney (1978), however most of Mollison's data, including information on Bennett's wallaby, remain both unpublished and apparently unlocatable.

For both wallaby species, the majority of information on their biology has been based on captive populations with aspects of reproduction and development receiving most attention.

Most of the research on Bennett's wallaby reproduction has been conducted by Merchant and Calaby (1981) who compared the reproductive biology and development of Bennett's wallaby with the mainland subspecies, the red-necked wallaby, in captive colonies in Canberra. In Britain, Bennett's wallabies have been the subject of a number of studies investigating seasonal and lactational quiescence (Loudon *et al.* 1985; Curlewis *et al.* 1986; Curlewis *et al.* 1987; Loudon and Curlewis 1987; Curlewis and Loudon 1988; Brinklow and Loudon 1989). In Tasmania, Walker (1977) and Walker and Rose (1981) described prenatal development in this species.

Walker (1977) made a preliminary investigation of delayed gestation length, oestrous cycle and pouch young growth following the birth of a diapausing blastocyst in the Tasmanian pademelon. This work was investigated further by McCartney (1978) and Rose and McCartney (1982a). Horak (1980) studied embryonic growth and development and aspects of delayed gestation with emphasis upon the analysis of ovarian and uterine interrelationships.

There have been a small number of behavioural studies conducted on captive populations of both species. Morton and Burton (1973) made observations on Tasmanian pademelons kept at the Melbourne Zoological Gardens and a similar study was conducted by Clancy (1982) at the University of Tasmania. Lafollette (1968, 1971) reported on agonistic behaviour and dominance in Bennett's wallaby in Ohio, U.S.A., and Merchant and Calaby (1981) noted the breeding behaviour of Bennett's wallaby held in captivity in Canberra.

Methods of aging Bennett's wallaby and Tasmanian pademelon pouch young have been developed by J. Merchant (unpublished data) and Rose and McCartney (1982b) respectively. Catt (1979) developed a means of aging Bennett's wallabies from counting annuli laid down in the periosteal zone of the mandible. J. Merchant (unpublished data) also established a relationship between age and molar eruption.

In contrast to Bennett's wallaby, a considerable amount of information has been published on the mainland subspecies, the red-necked wallaby. Most of this research was from studies conducted at Wallaby Creek in north-eastern New South Wales (Jarman *et al.* 1987). These studies have investigated; philopatry, reproductive success in females and maternal investment (Johnson 1986); the density and distribution of this species in relation to environmental variables (Southwell 1987); effect of fire on pasture utilisation (Southwell and Jarman 1987); home range and movements (Johnson 1987a); use of dung pellet counts for measuring absolute densities (Johnson and Jarman 1987, Johnson *et al.* 1987); relationships between mother and young (Johnson 1987b); social interactions and reproductive tactics (Johnson 1989a); grouping and the structure of association (Johnson 1989b) and mortality of immature red-necked wallabies (Johnson 1989c).

McEvoy (1970) described the subspecies as it occurs in Queensland, providing information on distribution, habitat types, breeding and conservation.

CHAPTER 2

DESCRIPTION OF STUDY AREAS

2.1 LOCATION OF STUDY AREAS

Wallabies were collected from a total of 12 areas distributed throughout Tasmania (Figure 2.1) representing different levels of hunting and rainfall. The selection of study areas was, in part, dependent upon the availability of hunters to regularly shoot wallabies. The Styx, Lemont, Maria Island and Nunamara study areas were not sampled regularly and the data collected from them were used only where relevant.

2.2 RAINFALL

Average annual rainfall data for all study areas are given in Table 2.1. The long-term average represents data gathered over at least the last 50 years. The average annual rainfall for the years 1977-1986 and the rainfall for 1987, 1988 and 1989 are given as an indication of more recent rainfall conditions. Total rainfall in 1987 was lower than the long term annual average at all study areas (Table 2.2). This lower rainfall in 1987 is associated with a drought which is described below.

A drought or rainfall deficiency is defined by the Australian Bureau of Meteorology as a period of at least three months when the level of rainfall fell below the 10th percentile. Using the results of Shepherd (1991) it is possible to put the drought which occurred prior to the start of the present study into historical perspective. Shepherd determined the number of droughts which occurred between 1910 and 1991 for three regions of Tasmania and ranked

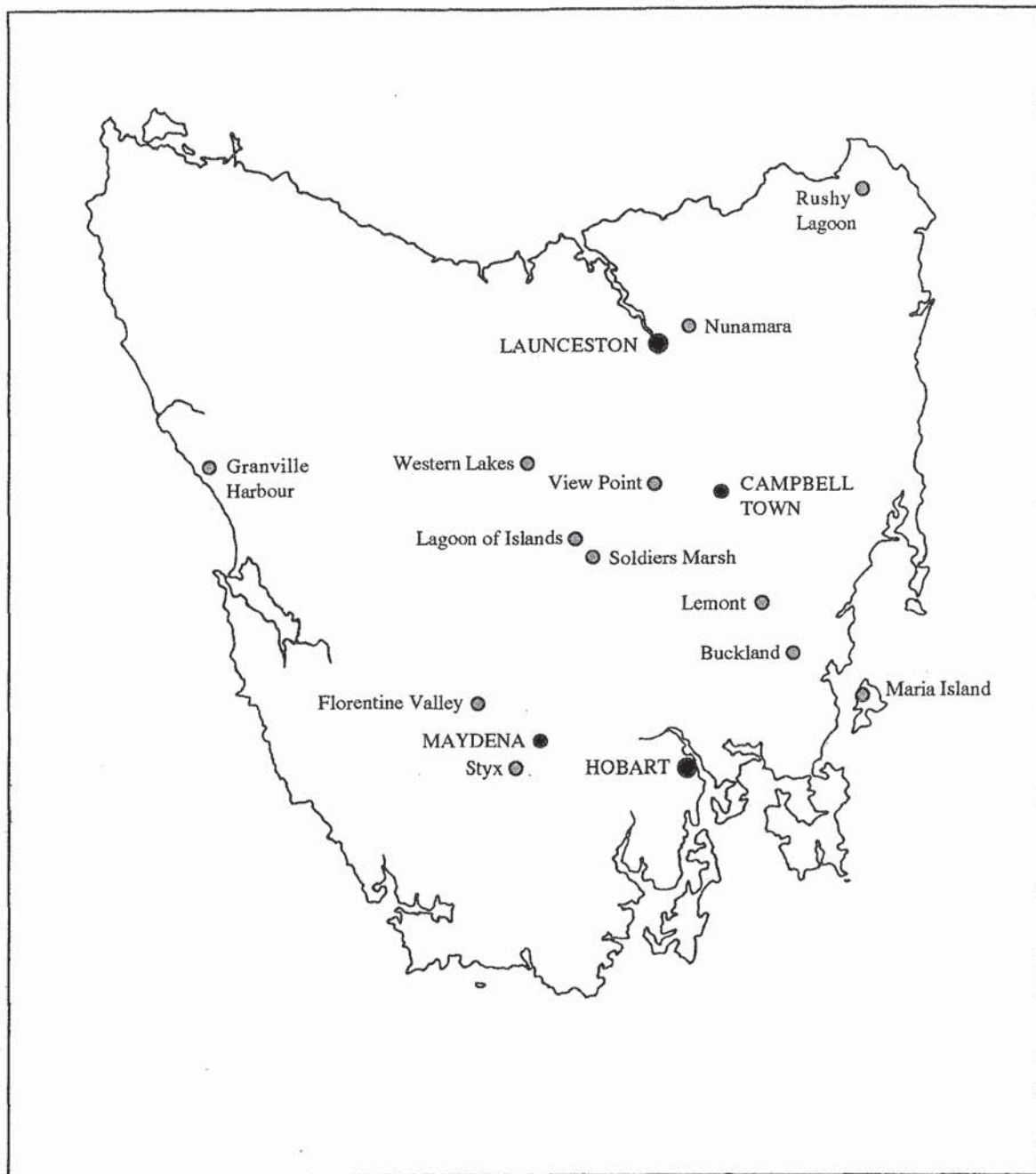


Figure 2.1 Location of study areas (●)

Table 2.1 Annual rainfall (mm) data for each study area.

Study Area	Long-Term Average	Average for 1977-1986	1987	1988	1989
Lemont	561	503	403	492	-
View Point	630	633	505	643	739
Buckland	657	635	477	596	574
Maria Island	663	623	443	614	594
Rushy Lagoon	745	703	-	732	802
Soldiers Marsh	840	793	691	857	800
Lagoon of Islands	840	793	691	857	800
Western Lakes	1291	1259	1051	1372	1290
Styx	1208	1157	1112	1192	-
Florentine Valley	1208	1157	1112	1192	-
Nunamara	1352	1084	1216	1112	1268
Granville Harbour	1515	1426	1348	1417	1294

Table 2.2 Rainfall in 1987 as a percentage deficit of the long-term average annual rainfall.

Study Area	Rainfall Deficit in 1987 (%)
Lemont	28
View Point	20
Buckland	27
Maria Island	33
Rushy Lagoon	-
Soldiers Marsh	18
Lagoon of Islands	18
Western Lakes	19
Styx	8
Florentine Valley	8
Nunamara	10
Granville Harbour	11

them in terms of length and in terms of the magnitude of the departure of rainfall from the median (severity). Only information from northern and eastern Tasmania will be discussed here as there were no study areas in southeastern Tasmania (as defined by Shepherd (1991)). In northern Tasmania, the drought occurred from March 1986 to June 1988. For this region, the drought was the longest on record and the 7th most severe. In eastern Tasmania, the drought occurred from April 1977 until July 1988. For this region, it was the 2nd longest on record and the 11th most severe. No information is available for western Tasmanian where three study areas, Florentine Valley, Styx and Granville Harbour, were located. However, the results in Table 2.2 suggest that the effect of the drought was less severe.

Long-term, mean monthly rainfall distributions for each study area are given in Figure 2.2. In low rainfall areas, rainfall is evenly distributed throughout the year, whereas in high rainfall areas rainfall peaked in winter.

Plant growth in Tasmania is restricted by low temperatures in winter and low effective rainfall, due to high evapotranspiration in summer and early autumn (Scott 1965; Kirkpatrick *et al.* 1988). Hence, growth mainly occurs in spring and late autumn. In high rainfall areas the growing season is extended into summer, whilst in inland areas and areas of high elevation the growing season is shortened by lower temperatures.

The study areas covered much of the range of rainfall that occurs in Tasmania. For the purposes of the present study, the study areas were divided into the three groups shown below.

Low Rainfall	< 700 mm a year	Lemont, View Point, Buckland, Maria Island
Medium Rainfall	700-1000 mm a year	Rushy Lagoon, Soldiers Marsh, Lagoon of Islands
High Rainfall	> 1000 mm a year	Western Lakes, Styx, Nunamara, Florentine Valley, Granville Harbour

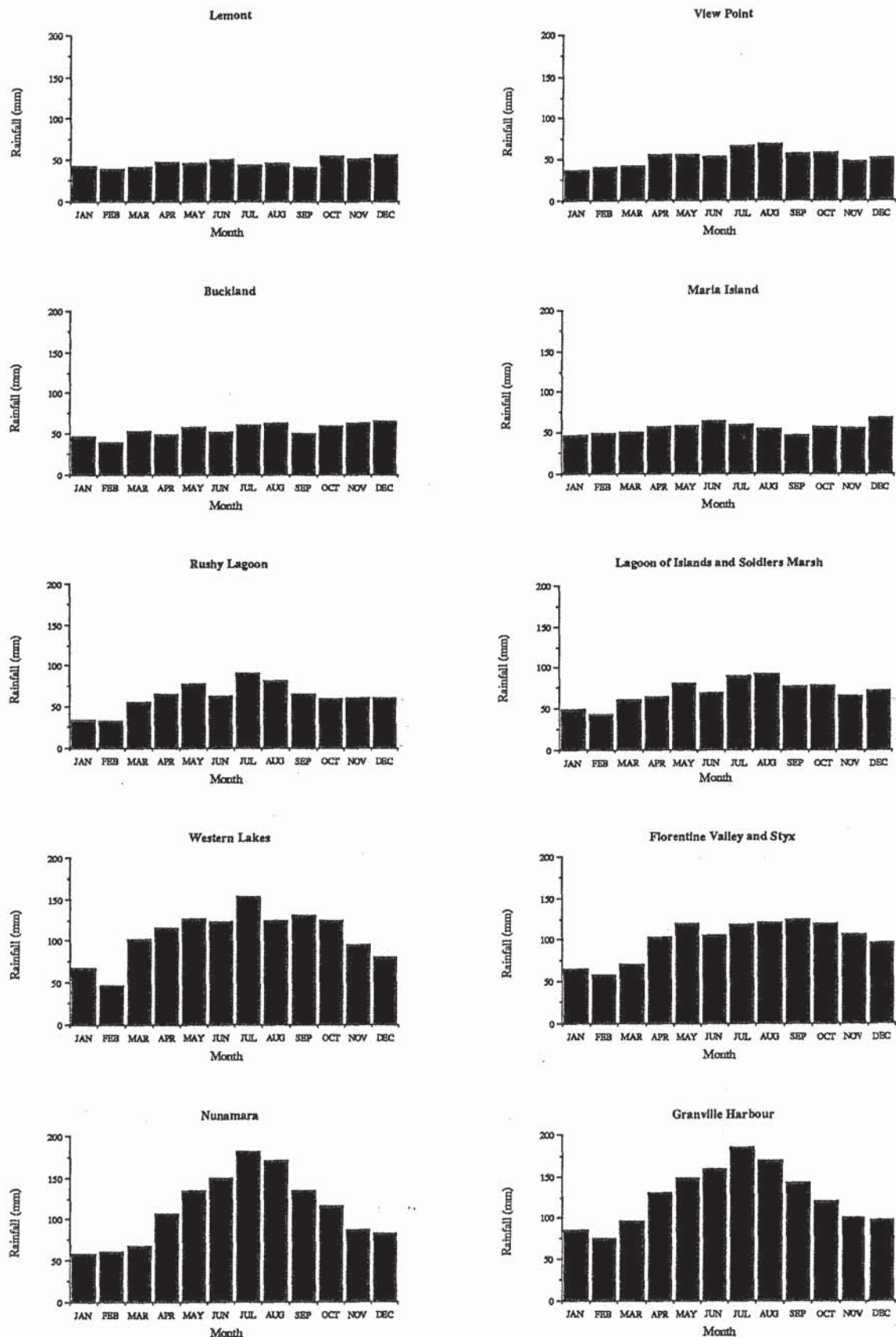


Figure 2.2 Long-term mean monthly rainfall distribution for all study areas.

2.3 TEMPERATURE AND ALTITUDE

Temperature and altitude statistics for each study area are given in Table 2.3. The minimum and maximum temperatures at each study area were a function of altitude. Thus, as altitude increased, the temperature decreased.

Table 2.3 Altitude and temperature data for each study area.

Study Area	Altitude (m)	Temperature (°C)			
		mean minimum	mean maximum	extreme minimum	extreme maximum
Maria Island	10	-	-	-	-
Granville Harbour	20	7.8	16.4	-3.0	37.2
Rushy Lagoon	60	10.3	16.7	-1.1	36.1
Buckland	200	7.3	17.8	-5.3	39.4
Nunamara	200	6.2	16.8	-7.1	37.3
Lemont	300	5.0	15.5	-12.8	40.0
View Point	200	5.2	17.2	-9.4	37.8
Florentine Valley	300	4.8	15.6	-6.7	39.4
Styx	300	4.8	15.6	-6.7	39.4
Soldiers Marsh	700	3.9	16.6	-12.5	37.5
Lagoon of Islands	800	3.9	16.6	-12.5	37.5
Western Lakes	1150	2.3	11.4	-13.0	33.4

2.4 VEGETATION, LAND USE AND HUNTING OF WALLABIES

(a) Lagoon of Islands

Lagoon of Islands is located on the lower slopes of the Central Plateau. It consists of a mosaic of pasture, subalpine woodlands and forests and marshes.

The canopy of the forests and woodlands is open and common *Eucalyptus* spp. present include *E. dalrympleana* (mountain white gum), *E. pauciflora* (weeping gum) and *E. rodwayi* (swamp peppermint). The tall shrub layer is usually sparse containing regenerating eucalypts and *Acacia dealbata* (silver wattle). The low shrub and ground layer varies from open areas dominated by native grasses to dense sedgey and heathy areas. Species include *Cyathodes juniperina* (pink berry), *Leucopogon hookeri*, *Hakea microcarpa*, *Lomatia tinctoria* (guitar plant) and various sedges in the poorly drained areas. Large areas of habitat suitable for both species of wallaby occur beyond the study area.

Sampling took place on part of an 11 000 ha property. The property included 1500 ha of pasture which had been fertilised with super phosphate every year for at least the past 15 years. The main pasture species were rye grass and clover. During the last 5-6 years sheep have grazed on the property and cattle have been present during the summer months. Large areas have been selectively logged during the past 4 years with 20 ha clearfelled in the last 15 years. In 1985, 1080 poison was laid to control wallabies in one of the paddocks. This was the only use of this poison in the last 20 years.

Over the last 15 years, intensive wallaby shooting has been conducted by a local hunting club, the Steppes Wildlife Trust, on a weekly basis. Club records indicate that an average of nearly 3000 wallabies have been shot every year and that hunters prefer to shoot Bennett's wallabies despite Tasmanian pademelons being more abundant.

(b) Soldiers Marsh

Soldiers Marsh is also located on the lower slopes of the Central Plateau. The habitat is similar to that of the Lagoon of Islands except that there is no improved pasture and there are larger areas of marshes.

The structure and floristics of the native vegetation of this study area are similar to that described for Lagoon of Islands. However, there are noticeably more *E. delegatensis* (gum-

topped stringybark) and *E. gunnii* (cider gum). Large areas of suitable habitat for both species of wallaby, particularly Bennett's wallaby, extend beyond the study area.

The area where sampling occurred is owned by a logging company but little logging has occurred. Sheep graze on the study area all year round. In at least the last 10 years no 1080 poison has been laid and no super phosphate has been applied.

The Bagdad Field and Game Club has been shooting in the area for the last 15 years. Members estimate that around 500-800 wallabies are shot each year and that 75-90% are Bennett's wallabies. Tasmanian pademelons, although present in the area, have never been common.

(c) *Western Lakes*

Western Lakes is a high altitude study area in the Central Plateau Protected Area. Samples were taken from the stretch of land adjacent to the 16 km road between the settlement of Liawenee and Double Bay Lagoon.

The vegetation includes woodland dominated by *E. coccifera* (snow gum) but alpine heath is the most extensive plant community comprising xeromorphic species such as *Orites revoluta*, *O. acicularis*, *Epacris serpyllifolia*, *Olearia ledifolia* and *Helichrysum hookeri*. These woody shrubs form rounded bushes which are usually less than a metre high but in places reach 2 m high. Other common species are *Richea sprengelioides*, *Diselma archeri*, *Microcachrys tetragona* (Strawberry pine) and the cushion plants *Abrotanella forsteroides* and *Donatia novae-zelandiae*.

No poisoning, logging or grazing occurs within the study area. Bennett's wallabies were common and Tasmanian pademelons were uncommon. However, according to the local ranger the number of Tasmanian pademelons has been slowly increasing in recent years.

It was difficult to assess the hunting pressure in this extensive area. The local ranger, from the Department of Parks, Wildlife and Heritage, estimated that a couple of hunting parties would arrive every weekend over winter but their success rate was not high, rarely taking more than a half dozen Bennett's wallaby. Thus it is likely that less than 500 wallaby are taken in a year.

(d) Granville Harbour

Granville Harbour is located on the west coast of Tasmania. It comprises 80 ha of pasture bounded on one side by the sea and on the remaining sides by extensive tracts of forest.

The forest consists of an emergent stratum of *E. obliqua* (stringybark) over a tall rainforest understorey which includes tree species such as *Nothofagus cunninghamii* (myrtle), *Atherosperma moschatum* (sassafrass), *Phyllocladus aspleniifolius* (celery-top pine), *Pomaderris apetala* (dogwood), *Olearia argophylla* (musk), *Phebalium squameum* (lancewood) and *Pittosporum bicolor* (cheesewood). Ferns such as *Blechnum wattsii*, *Polystichum proliferum* and *Dicksonia antarctica* (manfern) are common in the understorey as is the cutting grass, *Gahnia grandis*.

Cattle were run on the pasture for ten years up until 1987. Since then it has not been grazed by stock, and bracken, *Pteridium esculentum*, has begun to take over. In at least the last ten years no fertiliser has been applied and no 1080 poison has been laid.

Tasmanian pademelons are far more common in the area than Bennett's wallabies. The number of wallabies shot in the area was difficult to assess due to unauthorised shooters hunting on this remote property. The owner and one regular shooter estimates that about 500 are known to be shot each year.

(e) Buckland

The Buckland study area is located in the Buckland Military Training Reserve on the east coast of Tasmania. It comprises extensive areas of mature heathy and sedgy dry sclerophyll forest and approximately 20 ha of pasture.

The open eucalypt canopy includes *E. obliqua* (stringy bark), *E. amygdalina* (black peppermint), *E. ovata* (swamp gum) and *E. globulus* (blue gum). The tall shrub layer is sparse and includes *Acacia dealbata* (silver wattle) and *Exocarpos cupressiformis* (native cherry). The low shrub and ground layer is dominated by the bracken, *Pteridium esculentum*, the sagg, *Lomandra longifolia* and the sedges *Lepidosperma* spp., *Juncus* spp. and *Restio* spp. Shrub species include *Pultenaea juniperina* (prickly beauty) and *Cyathodes glauca* (cheeseberry).

Sheep grazed on the small area of pasture all year round and super phosphate was added every year for at least the last 10 years. No logging has occurred and no 1080 poison has been laid in the last decade.

Approximately 500 wallabies, of which approximately 75% are Tasmanian pademelons, are shot annually by the caretaker of the reserve. Tasmanian pademelons are more common adjacent to the pasture areas, whereas, Bennett's wallabies are more common in the native forest.

(f) Rushy Lagoon

Rushy Lagoon is located in northeastern Tasmania. The area consists of large areas of pasture interspersed with native vegetation.

The native forest on the property is mostly heathy dry sclerophyll forest dominated by *E. amygdalina* (black peppermint). The tall shrub layer is usually open and is dominated by *Casuarina littoralis* (bull-oak) but also includes *Banksia marginata* and *Exocarpos cupressiformis* (native cherry). The low shrub and ground layer are dominated by *Pteridium*

esculentum (bracken), *Lomandra longifolia* (sagg) and *Lepidosperma concavum* (sedges). Shrubs present include *Epacris impressa* (common heath), *Leptospermum scoparium* (tea tree) and *Aotus ericoides* (golden pea).

Sampling occurred on part of a property which covers 28 000 ha including 16 000 ha of pasture. The property is grazed by sheep and to a lesser extent cattle. Lime and super phosphate are applied annually. Crops grown include species of rye grass, cocksfoot, turnips, wild white clover, sub-clover and strawberry clover.

Wallabies at this study area are subjected to a high harvesting pressure. A commercial shooter has taken approximately 5000 wallaby annually since 1985. Of these less than 200 Tasmanian pademelons were shot a year. Additionally, the local shooting club accounts for approximately 3000 wallabies shot every year since 1974. Club shooters generally shot equal numbers of both species. Other shooters account for another 500-1000 wallabies. In all, approximately 9000 wallabies are shot each year. Prior to 1985, 1080 poison was laid regularly. The neighbouring property shoots and lays poison each year.

(g) View Point

View Point is located in the northern Midlands and comprises large areas of pasture interspersed with native woodlands.

Both grassy and shrubby open dry sclerophyll forest occur on the study area as well as small areas of wetter forests on southern slopes. *E. amygdalina* (black peppermint) and *E. viminalis* (white gum) are the most common eucalypts present, although *E. obliqua* (stringybark) dominates on wetter areas. The tall shrub layer is generally sparse and is dominated by *Acacia dealbata* (silver wattle) and also includes *Banksia marginata*, and *Bursaria spinosa* (prickly box). The low shrub and ground layer is dominated by native and introduced grasses as well as the sagg, *Lomandra longifolia*.

Sampling took place on part of a 2500 ha property which includes 1000 ha of pasture. The main stock on the property are sheep (90%) but cattle are also present. Fertiliser has been added to the pasture nearly every year over the last ten. Main pasture species are rye grass and clover. In recent years no 1080 poison has been laid in the area due to the presence of deer farming. Some logging has occurred.

The Bagdad Field and Game Club has conducted shooting on the property since 1988. Up to 2000 wallabies have been shot annually over the last 10 years with neighbours culling at a similar level. In 1988 and 1989 hunting was restricted to less than 1000 due to deer trapping operations.

(h) Florentine Valley

This study area is located in southwest Tasmania. It contains a mosaic of pine plantations and *Eucalyptus* spp. regrowth forest at various stages of development and is surrounded by mature mixed forest.

The mixed forest consists of emergent eucalypts such as *E. dalrympleana*, and *E. obliqua* (stringy bark) over a tall dense shrub layer which includes *Phebalium squameum* (lancewood), *Pittosporum bicolor* (cheesewood), *Pomaderris apetala* (dogwood), *Zieria arborescens* (stinkwood), *Nothofagus cunninghamii* (myrtle), *Phyllocladus aspleniifolius* (celery-top pine) and *Olearia argophylla* (musk). Ferns such as *Dicksonia antarctica* (manfern), *Pteridium esculentum* (bracken), *Polystichum proliferum* and *Blechnum wattsii* are common. *Gahnia grandis* (cutting grass) is also common.

The study area is controlled by Australian Newsprint Mills (ANM). Most of the pines in the study area were planted in 1982 and 1987. The eucalypt regrowth was cleared in 1989 just before sampling finished. The pine plantation was fertilised once after planting. 1080 poison was laid twice in the year after planting and once every year thereafter. The study area also included a site which has been cleared and replanted 4 times in the last 10 years.

Shooting pressure has varied over the last ten years. Just before and after planting, in 1982, the hunting pressure was particularly high with 1000-2000 being shot annually. Between 1983 and 1986 approximately 6-700 were shot and since then less than 500 a year were shot.

(i) *The Styx*

This study area is also located in the southwest of Tasmania. Samples were taken from a stretch of road about 17 km long through mostly mixed forest similar to that described for the Florentine Valley. This study area is also controlled by ANM.

Hunting pressure is very low with less than 50 wallabies shot a year. No 1080 poisoning has occurred in the area of sampling. This study area was sampled only in the winter of 1988. It was not sampled again due to the difficulty in obtaining adequate samples of wallaby in the dense vegetation which occurred adjacent to the road. Tasmanian pademelons were the most common of the two species in this area with only one Bennett's wallaby being seen during seven nights of sampling.

(j) *Maria Island National Park*

This study area is located on Maria Island off the east coast of Tasmania. The island includes large areas of dry sclerophyll forest and pasture.

The main eucalypts which dominate the native vegetation where sampling took place include *E. pulchella* (white peppermint), *E. globulus* (blue gum) and *E. obliqua* (stringybark). The open tall shrub layer is dominated by *Acacia dealbata* (silver wattle) *Casuarina littoralis* (she-oak) and *Bursaria spinosa* (prickly box). Grasses dominate the ground layer along with *Lomandra longifolia* (sagg) and *Lepidosperma* spp. (sedges).

A small number of Tasmanian pademelons and Bennett's wallabies were shot in this National Park as part of a monitoring program involving these species. The island suffers from chronic over-population and in times of drought abnormally high juvenile mortality has

occurred due to starvation (G. Hocking, unpublished data). Highest densities of wallabies occur around the settlement at Darlington where there are large areas of pasture. Samples of Bennett's wallabies were taken from this area as well as from native forest south of Darlington. Tasmanian pademelons were only taken from around Darlington.

Small numbers of Bennett's wallabies have been shot in the past to control numbers and to remove sick animals. No 1080 poison has been laid on the island and fertiliser has not been used in the past decade.

(k) *Lemont*

This study area is located in the southern Midlands near the town of Lemont. Only a small sample of Bennett's wallabies was taken from this study area. The area consists of a mosaic of large open pastures and small patches of native dry sclerophyll forest. The area is heavily hunted by commercial shooters and local residents.

(l) *Nunamara*

This study area is located in northern Tasmania. A small number of wallabies (skulls, testes and pouch young and skins) were collected from a number of properties in this area by Mr L. Smith. The area includes a mosaic of pasture and dry and wet sclerophyll forest. The area is regularly hunted.

2.5 SUMMARY

A summary of rainfall, altitude, vegetation, land use and hunting pressure is given in Table 2.4. Hunting pressure was estimated based on the following:

- (i) The number of wallabies shot per year within and around the immediate study area.
- (ii) The number of years wallabies were subjected to hunting.
- (iii) The distribution and abundance of wallabies within and around the study area.

Table 2.4 Summary of study area descriptions

Study Area	Rainfall	Altitude (m)	Vegetation	Stock	Poison	Shooting
Lemont	low	<500	Dry Sclerophyll / Improved Pasture	sheep	?	high
View Point	low	<500	Dry (& Wet) Sclerophyll / Improved Pasture	sheep	no	medium
Buckland	low	<500	Dry Sclerophyll (some Improved Pasture)	(sheep)	no	low
Maria Island	low	<500	Dry Sclerophyll / Unimproved Pasture	no	no	very low
Rushy Lagoon	medium	<500	Dry Sclerophyll / Improved Pasture	sheep/cattle	no ^a	very high
Soldiers Marsh	medium	500-1000	Subalpine Dry Sclerophyll	sheep	no	low
Lagoon of Islands	medium	500-1000	Subalpine Dry Sclerophyll / Improved Pasture	sheep/cattle	no ^b	high
Western Lakes	high	>1000	Alpine Heath (and Woodland)	no	no	low
Styx	high	<500	Mixed Forest	no	no	very low
Florentine Valley	high	<500	Mixed Forest / Pine Plant. / Regenerating Eucalypts	no	yes	low
Nunamara	high	<500	Dry and Wet Sclerophyll Forest	sheep/cattle	yes	medium
Granville Harbour	high	<500	Mixed Forest / Unimproved Pasture	no	no	low

a poisoned once in recent years, regular poisoning occurs on neighbouring properties.

b poisoned once in last 15 years.

CHAPTER 3

GENERAL METHODS

3.1 FIELD METHODS

Commercial shooters, non-commercial shooters and officers from the Department of Parks, Wildlife and Heritage were used to obtain samples of Bennett's wallabies and Tasmanian pademelons. Sampling occurred in winter (May-September) and summer (November-February) of 1988 and 1989. The actual timing of sampling within these periods depended on the availability of shooters and weather conditions. At the View Point study area, deer trapping also restricted sampling times.

Unless otherwise stated, all shooters were instructed to shoot wallabies regardless of sex or size in order to minimize any sampling bias imposed by the hunters themselves.

In most cases, shooting occurred from a vehicle with the aid of a spotlight. The exception to this was those samples collected on foot in the Nunamara study area. Shooting normally commenced once it was dark and usually continued for three hours, but ranged from one to five hours. In most cases the wallabies were examined after the shooting period. However, if large numbers were shot or the vehicle was small, shooting and examination occurred alternately.

All animals had their sex determined and were weighed with a Salter 25 kg spring balance. Head lengths were measured using 210 mm vernier callipers. Skulls, testes, pouch young, kidneys and their associated fat were removed, placed in labelled plastic bags and were placed in a freezer within 24 hours of collection. The size of all four teats and whether the teats were lactating or not was also recorded.

3.2 AGING

Ages of pouch young were calculated from head length using the following equations.

Tasmanian pademelon
(McCartney 1978)

$$\text{Age (days)} = \frac{\text{Head Length (mm)} - 8.03}{0.347}$$

Bennett's wallaby
(derived from J.Merchant, unpublished data)

$$\text{Age (days)} = \frac{\text{Head Length (mm)} - 16.75}{0.310}$$

The ages of animals which had left the pouch were estimated by molar eruption (Sharman *et al.* 1964). The stages of eruption were given decimal notations accumulating in fifths, as described by Newsome *et al.* (1977). There are two potential sources of error when using this method. Firstly, molar progression is a direct function of the amount of chewing (Sanson 1982). Hence, the relationship between age and molar eruption may differ between captive and free-ranging animals and between populations with different diets. Secondly, some sex-related differences in molar eruption have been shown to occur in the agile wallaby, *M. agilis*, (Newsome *et al.* 1977) and these differences may occur in the wallabies used in this study. As a consequence of these potential sources of error the data derived from this technique must be viewed conservatively.

The relationship between molar eruption and age of Bennett's wallabies (J. Merchant, unpublished data) is shown in Figure 3.1. This method is limited by the fact that animals cannot be aged once all the molar teeth have erupted. Thus for Bennett's wallabies, individuals could not be aged beyond six years.

Up until the present study there was no means of determining the age of Tasmanian pademelons after pouch vacation. McCartney (1978) examined the relationship between age and cementum annulation in the teeth but found no consistent relationship.

In an effort to determine a relationship between age and molar eruption; known age, hand reared young held by wildlife parks and private individuals were examined. Molar eruption stages were determined by examining the teeth of the live animal with the aid of an ophthalmoscope. The results are presented in Figure 3.2. Tasmanian pademelons could not be aged beyond 30 months using this method.

During the winter sampling period of 1988 a reference collection of 281 Bennett's wallaby and 251 Tasmanian pademelon skulls was established. Skulls were boiled, cleaned and then aged. In the remaining sampling periods the semi-thawed skulls were aged after prising open the jaw.

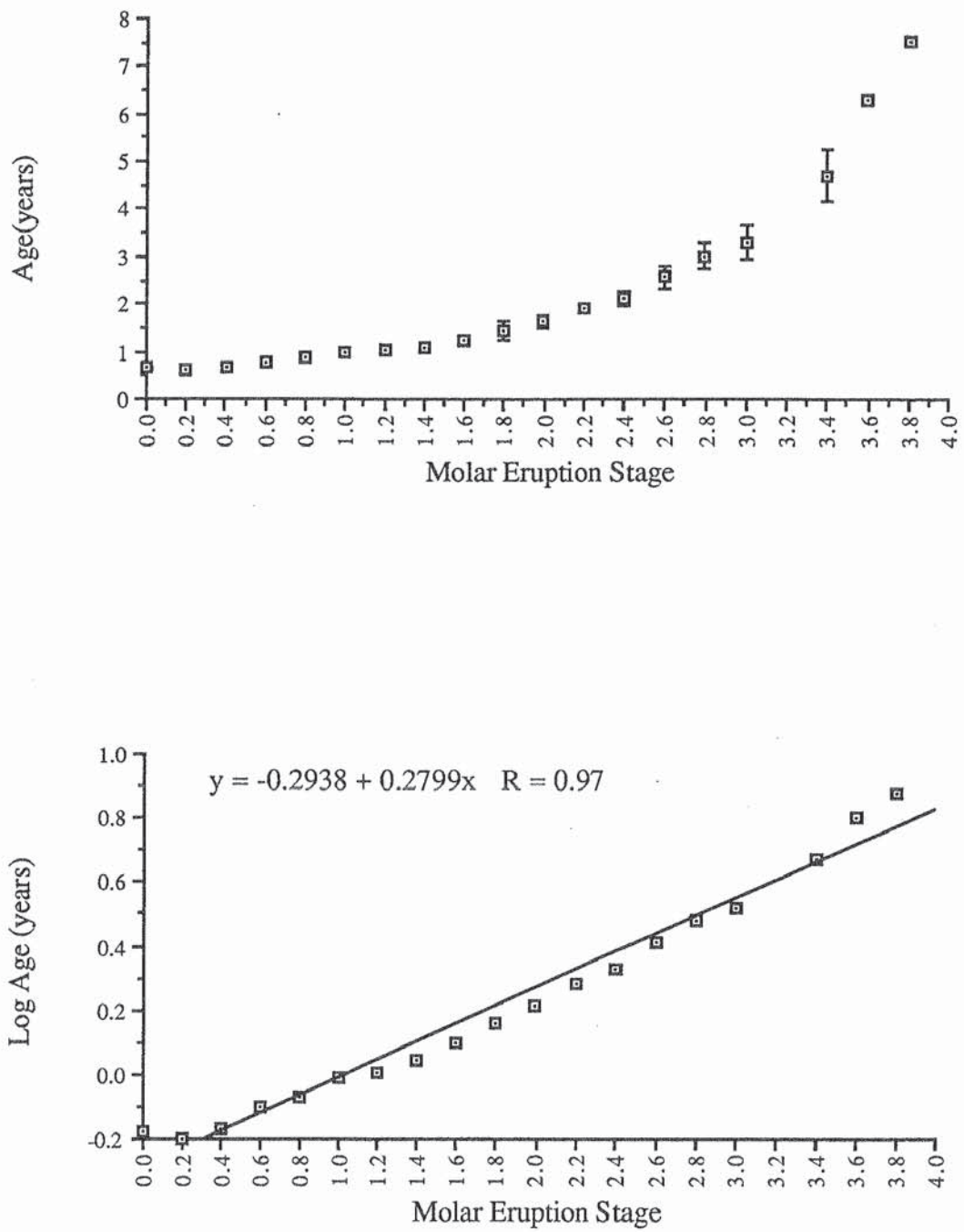


Figure 3.1 Relationship between age and molar eruption stage for Bennett's wallabies.
Data supplied by Dr. J.Merchant, CSIRO, Canberra.

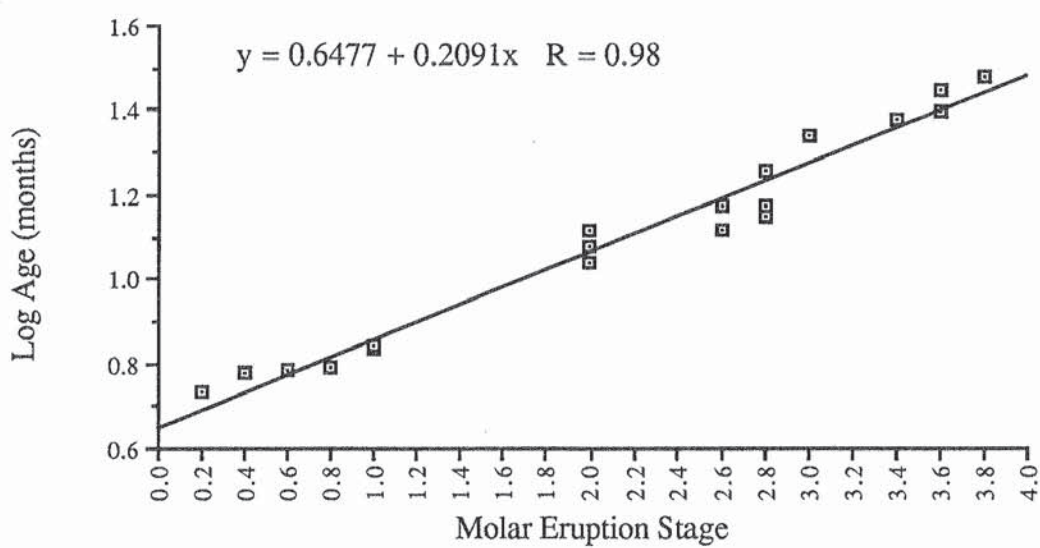
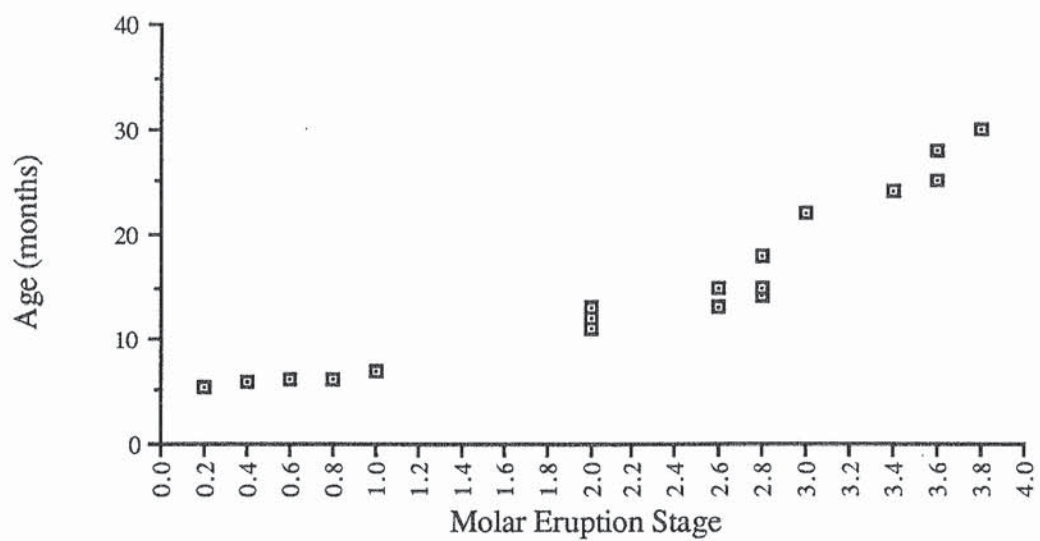


Figure 3.2 Relationship between age and molar eruption stage for the Tasmanian pademelon. Data was obtained from examination of hand reared young of known age.

CHAPTER 4

BODY CONDITION

4.1 INTRODUCTION

The body condition of members of a population reflects the quality of the environment in which that population lives (Klein 1970; Riney 1982; Bailey 1984; Shepherd 1987). Inferred in the use of this term is the idea that body condition is closely related to the chances of an animal's survival (Caughley 1971a). The most common measures of body condition are body size, usually body weight, and measures of fat reserves (Bailey 1984). This follows from the knowledge that when environmental conditions are favourable and an animal's intake of food exceeds its daily requirements, deposits of protein, fat and other metabolites are built up and body weight increases. This does not necessarily imply that fat animals are in good health, but the assumption is normally made that animals with relatively high levels of fat also have adequate levels of other resources within the body (Johns *et al.* 1984). Shepherd (1987) found that body condition in red and western grey kangaroos was linked to some components of rate of increase such as fecundity and survival, and concluded that body condition was a useful summary statistic of a kangaroo's response to their environment.

There have been numerous studies investigating the body condition of a wide range of mammal species. Some studies have shown that within a population there are differences in body condition between adults and juveniles (Riney 1955; Dunham and Murray 1982; Lindstrom 1983; Henderson and Clarke 1986; Pepin 1987) and between males and females (Johns *et al.* 1984; Anderson 1985; Boyd and Myhill 1987). The body condition of animals will also vary throughout a year (Caughley 1962, 1970, 1971a; Flux 1971; Attwell 1982; Dunham and Murray 1982; Johns *et al.* 1984; Waid and Warren 1984; Boyd and Myhill

1987; DeLiberto *et al.* 1989) and has often been shown to be related to the reproductive cycle which, in turn, is influenced by environmental conditions.

Rainfall has been shown to be a significant factor influencing the body condition of animals (Sinclair 1977; Anderson 1985; Shepherd 1987) due to its effect on food availability and quality. Shepherd (1987) was able to show that body condition of red and western grey kangaroos was correlated with rainfall, pasture biomass and dietary quality.

Few studies have compared body condition of populations in relation to hunting pressure. Studies on red deer, *Cervus elaphus*, (Challies 1973), white-tailed deer, *Odocoileus virginianus*, (Kie *et al.* 1983) and chamois, *Rupicapra rupicapra*, (Storch (1989) have shown that populations subject to hunting are in better condition than those which are not hunted. This has been attributed to the lower density of animals in the hunted areas and hence greater resources for the survivors.

The body condition of Bennett's wallabies and Tasmanian pademelons has not been previously studied. The aim of this chapter is to assess the body condition of these two species and to determine whether hunting and rainfall influences their body condition. The Kidney Fat Index or KFI (Riney 1955) was used to assess the short term response of wallabies to the quality of their environment and growth in body weight was used to assess the longer term response.

4.2 METHODS

The routine measurement of body weight and the collection of kidneys and their associated fat has been described in Chapter 2. KFI was calculated for the left and right kidney using the formula below and then averaged.

$$\text{KFI} = \frac{\text{kidney fat weight}}{\text{kidney weight}} \times 100$$

There are two assumptions in using KFI. Firstly, the amount of kidney fat is proportional to total body fat and, secondly, kidney weight is proportional to body weight. The first assumption is assumed to be true for both wallaby species based on other studies on macropods (Caughley 1962) as well as other mammal species (Smith 1970; Havera 1977). The second assumption will be tested in section 4.3.1.

The frequency distribution of KFIs for both species showed a Poisson distribution and consequently a variance stabilising transformation (square root) was applied to the data (Zar 1984).

For both species, at each study area, mean KFIs were calculated for adult females, adult males and juveniles over winter (June-August) and summer (November-February) of 1988 and 1989.

Mean KFIs for male and female juvenile Tasmanian pademelons were combined as they were not significantly different ($F_{(1,348)}=2.43$, $P>0.1$). Mean KFI for juvenile male Bennett's wallabies was slightly higher (3 KFI units) than that of females ($F_{(1,386)}=8.24$, $P>0.005$). However, in order to reduce the number of comparisons, the juveniles of both sexes were combined.

In all comparisons using adult females, only those which showed evidence of successful reproduction were used as those which failed to produce a pouch young or had lost a pouch young had much lower KFIs (see results in Section 4.3.2).

The effect of variation in hunting pressure and rainfall between study areas on KFI was tested by correlation analysis. Total rainfall for the 12 months prior to collection of KFIs was used for the correlation. As hunting pressure could not be quantified on a parametric scale, a

non-parametric test, Kendall's Rank Correlation Coefficient, was used to investigate the effect of this factor on KFI. Annual hunting pressure was ranked from very low to very high (refer to Table 2.4 in Section 2.5)

4.3 RESULTS

4.3.1 Variation in Kidney Weight to Body Weight Ratio

The use of kidney weight (KW) in KFI allows for comparison between animals of different size. The underlying assumption is that kidney weight is proportional to body weight (BW). This assumption is tested below for different sexes, age groups, seasons and study areas.

Variation between sexes and age groups

The regressions given in Figure 4.1 shows that there are linear relationships between kidney weight and body weight for Bennett's wallaby ($r^2=0.82$, $p<0.001$) and for the Tasmanian pademelon ($r^2=0.85$, $p<0.001$). There were no significant differences between males and females for either species (Bennett's wallaby: slope, $t=0.71$, $p>0.50$, elevation, $t=0.01$, $p>0.90$; Tasmanian pademelon: slope, $t=0.27$, $p>0.50$, elevation, $t=1.77$, $p>0.05$).

For both species, the Y-intercept was not equal to zero (Bennett's wallaby: $t=6.4$, $p<0.001$; Tasmanian pademelon: $t=14.6$, $p<0.001$). This indicates that young wallabies have proportionally larger kidneys than old wallabies. This is clearly demonstrated in Table 4.1 where mean kidney weight to body weight (KW/BW) ratios are given. Thus, there were no significant differences in mean KW/BW ratios for Bennett's wallabies older than 2 years ($F(4,656) = 2.02$, $p>0.05$) or Tasmanian pademelons older than 30 months ($F(2,506) = 0.04$, $P>0.90$).

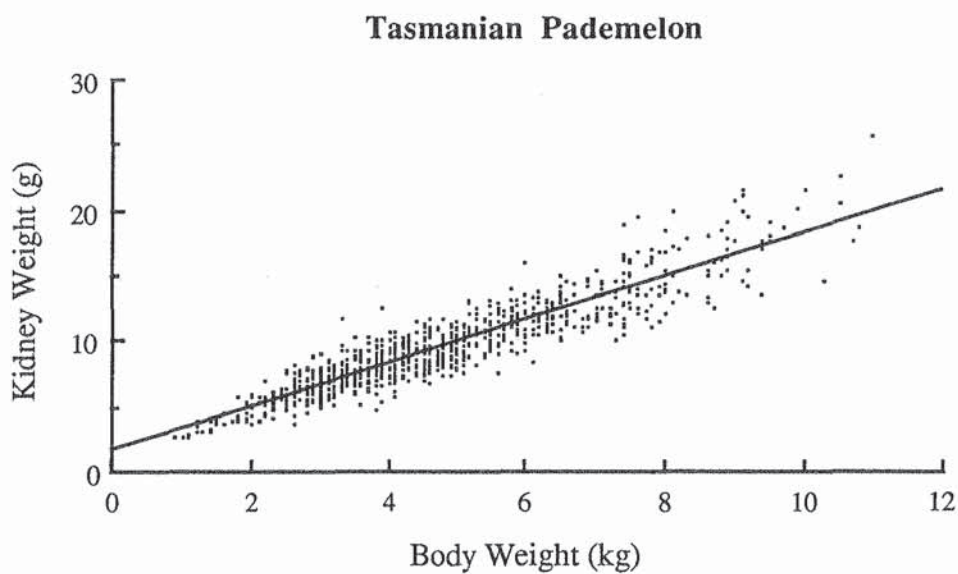
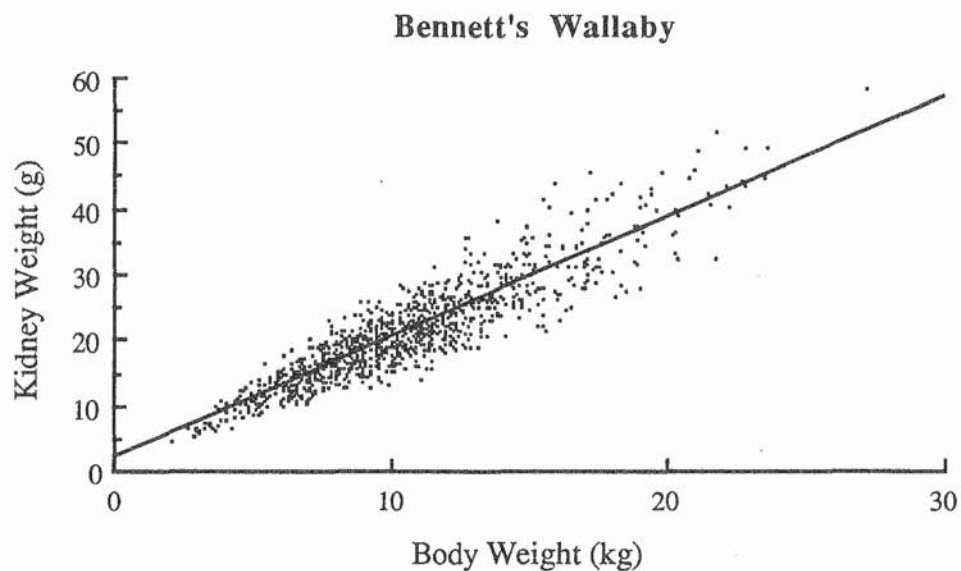


Figure 4.1 Relationship between kidney weight and body weight for Bennett's wallaby ($y = 1.851 + 1.842x$, $R = 0.91$) and the Tasmanian pademelon ($y = 1.672 + 1.660x$, $R = 0.92$).

Table 4.1. Variation in mean kidney weight (KW) to body weight (BW) ratios (\pm s.d.) by age. Numbers in rounded parentheses indicate sample size.

Bennett's Wallaby			Tasmanian Pademelon		
Age	KW / BW Ratio		Age	KW / BW Ratio	
(years)	(g/kg)		(months)	(g/kg)	
0.75-1	2.23 \pm 0.27	(45)	6-12	2.33 \pm 0.35	(202)
1-2	2.18 \pm 0.30	(343)	12-18	2.14 \pm 0.31	(265)
2-3	1.99 \pm 0.28	(300)	18-24	1.96 \pm 0.26	(189)
3-4	1.91 \pm 0.26	(121)	24-30	1.92 \pm 0.26	(144)
4-5	1.94 \pm 0.30	(119)	30+	1.93 \pm 0.26	(164)
5-6	1.98 \pm 0.27	(34)			
6+	1.98 \pm 0.33	(87)			
F-test	F [6,1041] = 23.81			F [4,959] = 71.58	
Significance	p < 0.001			p < 0.001	

Variation between study areas

As KW/BW ratios varied between age groups, only adult age classes (>2 years for Bennett's wallabies and >18 months for Tasmanian pademelons) will be used to compare variation in mean KW/BW ratios between study areas and months.

For both wallaby species, mean KW/BW ratios varied significantly between study areas (Table 4.2). The maximum difference in mean KW/BW ratios between study areas was 23% for Bennett's wallabies and 12% for Tasmanian pademelons.

Table 4.2. Variation in mean kidney weight (KW) to body weight (BW) ratios between study areas. Solid lines indicate study areas which were not significantly different from each other at the 0.05 level. Numbers in rounded parentheses indicate sample size.

Bennett's Wallaby

Study Areas	KW / BW Ratio	No Significant Differences
Western Lakes	2.17 ± 0.27 (113)	
Florentine Valley	2.07 ± 0.26 (118)	
Soldiers Marsh	2.02 ± 0.24 (95)	
Lagoon of Islands	1.96 ± 0.29 (77)	
Maria Island	1.93 ± 0.25 (51)	
Rushy Lagoon	1.87 ± 0.22 (96)	
View Point	1.78 ± 0.25 (38)	
Buckland	1.66 ± 0.17 (61)	
F-test Significance	F [7,641] = 33.17 p < 0.001	

Tasmanian Pademelon

Study Areas	KW / BW Ratio	No Significant Differences
Soldiers Marsh	2.09 ± 0.24 (47)	
Granville Harbour	2.07 ± 0.23 (58)	
Maria Island	2.07 ± 0.23 (20)	
Rushy Lagoon	1.99 ± 0.21 (50)	
Lagoon of Islands	1.95 ± 0.29 (81)	
Florentine Valley	1.93 ± 0.24 (116)	
Buckland	1.91 ± 0.25 (35)	
View Point	1.83 ± 0.21 (76)	
F-test Significance	F [7,471] = 54.65 p < 0.001	

Variation between months

As mean KW/BW ratios varied between study areas, only those study areas which were not significantly different from each other will be used to compare variation in KW/BW ratios between months. Thus for Bennett's wallaby, Soldiers Marsh and the Florentine Valley study areas were used, and for the Tasmanian pademelon, Rushy Lagoon, Florentine Valley, Lagoon of Islands and Buckland study areas were used.

Mean KW/BW ratios varied between months for both Bennett's wallaby ($F_{(13,205)} = 3.63, p < 0.001$) and the Tasmanian pademelon ($F_{(14,267)} = 2.46, p < 0.005$) (Figure 4.2). For Bennett's wallaby this variation was attributed to the decrease in the ratio in June 1988 and May 1989. When these two months were excluded from the analysis there was no difference between months ($F_{(11,161)} = 1.14, p > 0.25$). For the Tasmanian pademelon the ratio was less in June and July of 1988. When these two months were excluded from the analysis there was no significant difference between months ($F_{(12,224)} = 1.14, p > 0.25$). The mean KW/BW ratio for Tasmanian pademelons in April 1989 was low but was not significantly different from other months.

4.3.2 Kidney Fat Index

Bennett's wallaby

Comparison between sexes, age groups and seasons

Mean KFIs for adult females, adult males and juveniles in winter and summer are shown in Table 4.3. The data have been pooled over all study areas and both years.

For adult females, adult males and juveniles, mean KFIs in winter were significantly higher than in summer. During winter, mean KFIs for adult females were 17% higher than adult males and 40% higher than juveniles. During summer, mean KFIs for adult males were 13% higher than adult females and 26% higher than juveniles.

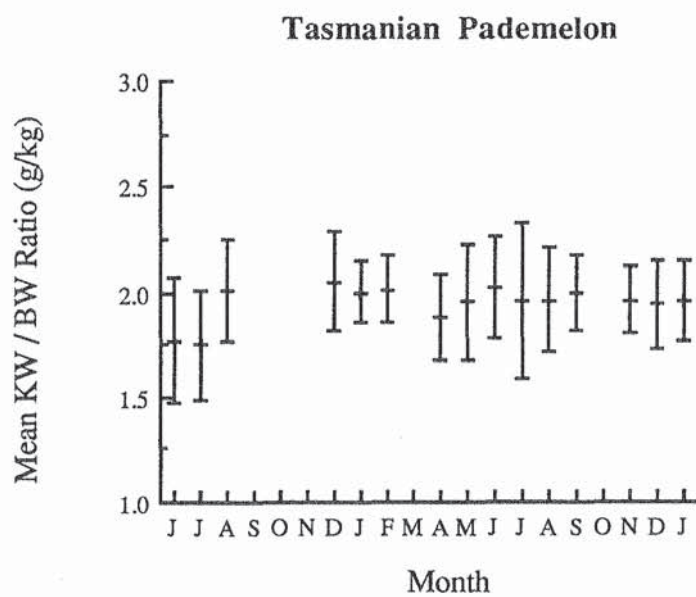
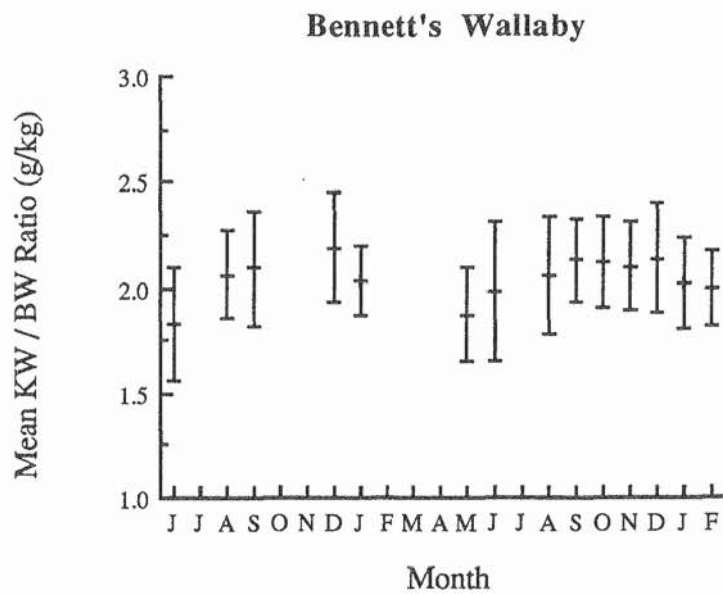


Figure 4.2 Monthly variation in mean kidney weight (KW) to body weight (BW) ratios from June 1988 to February 1990. Standard deviations are given.

Table 4.3 Comparison of mean KFIs between sexes, age groups and seasons for Bennett's wallabies (\pm s.d.) (square root transformed). The data were pooled over all study areas and both years. Numbers in rounded parentheses indicate sample size.

	Winter	Summer	F-Test	Significance
Adult Female	5.6 \pm 2.3 (159)	3.9 \pm 1.6 (114)	F[1,271]=43.19	p<0.0001
Adult Male	4.8 \pm 1.5 (156)	4.4 \pm 1.5 (176)	F[1,330]=5.18	p<0.05
Juvenile	4.0 \pm 1.1 (149)	3.5 \pm 1.1 (142)	F[1,289]=13.28	p<0.001
F-Test	F[2,461]=31.31	F[2,429]=17.34		
Significance	p<0.0001	p<0.0001		

Comparison between study areas

Mean KFIs for adult females, adult males and juveniles at each study area are shown in Table 4.4. During winter of 1988 mean KFIs differed significantly between study areas for adult females, adult males and juveniles. Mean KFIs were lower in low rainfall study areas than in high rainfall study areas. Mean KFIs were positively correlated with total rainfall for the 12 months prior to the sampling period (adult females: $r=0.95$, $df=5$, $p=0.0009$; adult males: $r=0.79$, $df=4$, $p=0.05$; juveniles $r=0.84$, $df=4$, $p=0.04$) (Figure 4.3)

During winter of 1989 mean KFIs did not differ significantly between study areas for adult females, adult males or juveniles. Furthermore, there were no significant correlations between mean KFIs and total rainfall for the 12 months prior to the sampling period (adult females: $r=0.08$, $df=6$, $p=0.8$; adult males: $r=0.39$, $df=5$, $p=0.4$; juveniles: $r=0.22$, $df=5$, $p=0.6$).

Table 4.4 Comparison of mean KFI's between study areas for Bennett's wallabies (\pm s.d.) (square root transformed). Numbers in rounded parentheses indicate sample size. ns=not significant.

WINTER 1988					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
Lemont	Low	High	3.8 ± 1.0 (7)	3.1 ± 0.3 (6)	2.9 ± 0.4 (5)
View Point	Low	Medium	4.7 ± 0.7 (6)	-	3.5 ± 0.6 (8)
Buckland	Low	Low	4.8 ± 0.6 (6)	4.0 ± 0.6 (7)	3.5 ± 0.1 (5)
Soldiers Marsh	Medium	Low	4.8 ± 0.3 (5)	4.9 ± 1.2 (12)	-
Lagoon of Islands	Medium	High	5.0 ± 1.3 (6)	4.2 ± 1.0 (6)	3.5 ± 1.0 (11)
Western Lakes	High	Low	6.9 ± 2.2 (8)	5.8 ± 2.1 (22)	4.6 ± 1.1 (15)
Florentine Valley	High	Low	5.9 ± 0.9 (7)	4.3 ± 1.3 (5)	3.7 ± 1.1 (11)
F-Test			F [6,38]=5.11	F [5,52]=3.65	F [5,49]=3.76
Significance			p < 0.002	p < 0.02	p < 0.02
SUMMER 1988					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	low	Medium	-	5.8 ± 1.6 (6)	3.5 ± 0.6 (8)
Lagoon of Islands	Medium	High	3.8 ± 1.4 (10)	4.3 ± 1.5 (18)	2.8 ± 0.4 (13)
Western Lakes	High	Low	2.9 ± 0.9 (13)	3.1 ± 1.1 (12)	3.0 ± 0.9 (8)
Florentine Valley	High	Low	4.6 ± 1.3 (16)	5.2 ± 1.7 (28)	3.6 ± 0.8 (16)
F-Test			F [2,36]=6.96	F [3,60]=6.61	F [3,41]=3.58
Significance			p < 0.01	p < 0.002	p < 0.05
WINTER 1989					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	Low	High	5.1 ± 1.9 (7)	-	-
Buckland	Low	Low	7.1 ± 2.0 (11)	5.3 ± 1.1 (10)	4.3 ± 1.1 (15)
Maria Island	Low	Very Low	5.5 ± 2.0 (29)	4.0 ± 1.0 (15)	3.8 ± 1.2 (23)
Rushy Lagoon	Medium	Very High	7.1 ± 3.2 (18)	4.7 ± 1.3 (25)	4.0 ± 1.1 (9)
Soldiers Marsh	Medium	Low	6.0 ± 1.8 (17)	5.4 ± 0.8 (11)	4.2 ± 0.9 (19)
Lagoon of Islands	Medium	High	6.3 ± 1.7 (8)	4.8 ± 1.4 (11)	4.3 ± 1.2 (7)
Western Lakes	High	Low	5.7 ± 2.4 (10)	5.1 ± 2.0 (15)	4.0 ± 1.3 (9)
Florentine Valley	High	Low	6.7 ± 2.2 (14)	5.0 ± 2.1 (7)	4.5 ± 1.3 (12)
F-Test			F [7,106]=1.52	F [6,87]=1.49	F [6,87]=0.59
Significance			ns	ns	ns
SUMMER 1989					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	Low	Medium	4.0 ± 1.0 (8)	5.1 ± 1.1 (9)	3.4 ± 1.1 (11)
Buckland	Low	Low	3.3 ± 0.3 (10)	4.5 ± 1.1 (16)	3.6 ± 0.6 (17)
Rushy Lagoon	Medium	Very High	4.6 ± 2.9 (10)	4.9 ± 1.6 (11)	-
Soldiers Marsh	Medium	Low	3.3 ± 0.6 (10)	4.3 ± 1.4 (19)	3.1 ± 0.3 (7)
Lagoon of Islands	Medium	High	3.8 ± 1.0 (9)	4.0 ± 1.0 (11)	3.4 ± 0.6 (11)
Western Lakes	High	Low	3.5 ± 1.6 (11)	3.4 ± 0.6 (21)	3.3 ± 1.3 (16)
Florentine Valley	High	Low	4.9 ± 1.8 (17)	5.0 ± 1.3 (25)	4.2 ± 1.5 (35)
F-Test			F [6,68]=1.99	F [6,105]=4.67	F [5,91]=2.34
Significance			ns	p < 0.001	ns

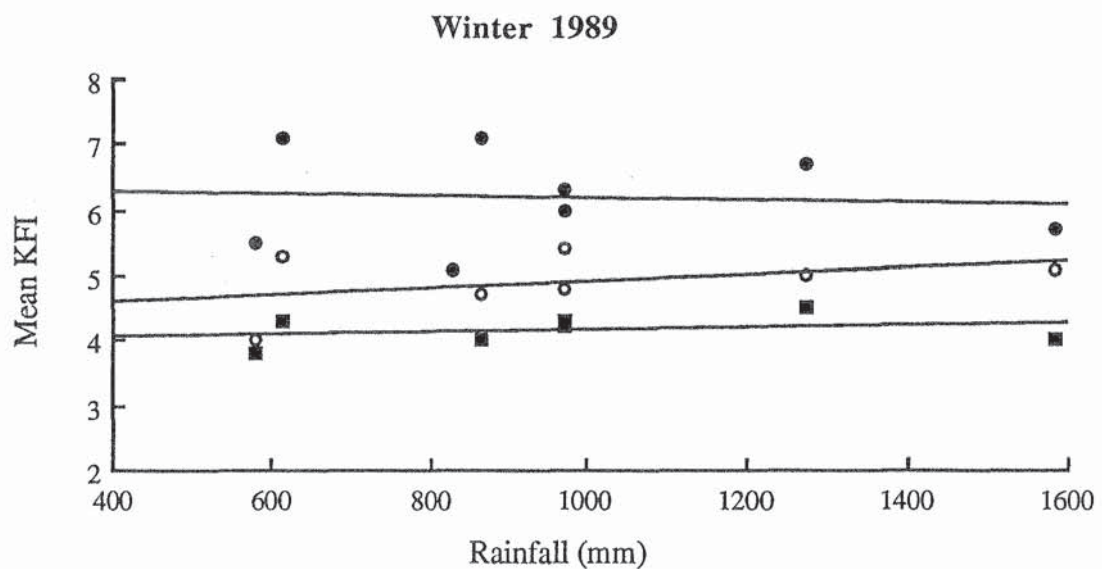
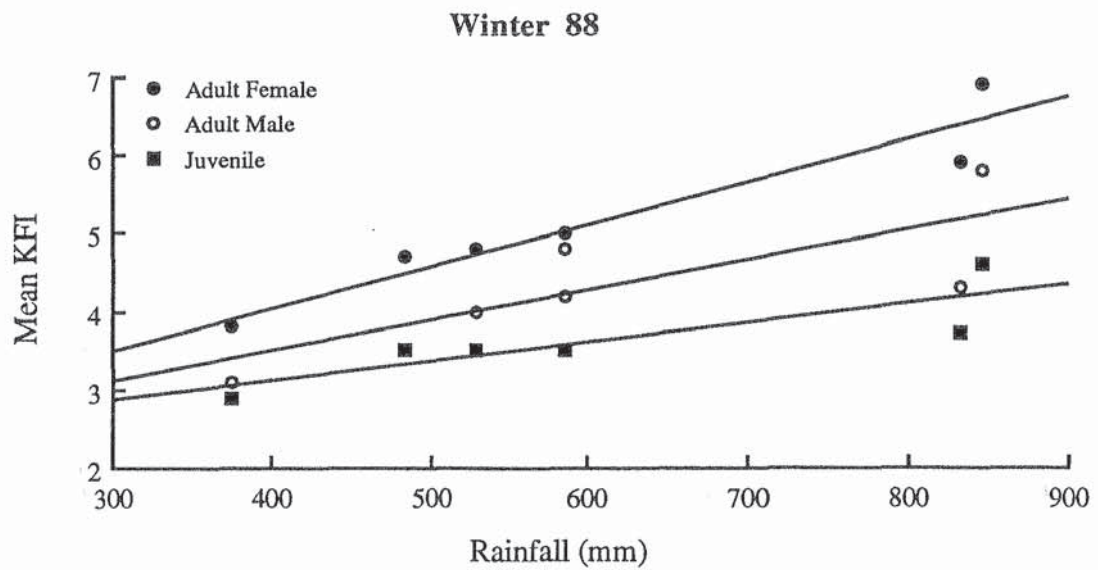


Figure 4.3. Correlation between mean KFI and rainfall (12 months prior to sampling periods) for Bennett's wallaby during winter 1988 (adult females: $r=0.95$, $df=5$, $p=0.0009$; adult males: $r=0.79$, $df=4$, $p=0.05$; juveniles $r=0.84$, $df=4$, $p=0.04$) and 1989 (adult females: $r=0.08$, $df=6$, $p=0.8$; adult males: $r=0.39$, $df=5$, $p=0.4$; juveniles: $r=0.22$, $df=5$, $p=0.6$). Means and standard deviations are given in Table 4.4.

During summer of 1988 mean KFIs differed significantly between study areas for adult males, adult females and juveniles (Table 4.4). For adult males and females this can be attributed to the low mean KFIs at the Western Lakes study area. For juveniles, KFIs were lowest at Lagoon of Islands and Western Lakes. No correlations were undertaken between rainfall and mean KFI during summer of 1988 due to insufficient data.

During summer of 1989 mean KFIs for adult males differed significantly between study areas. This can be attributed to the low mean KFI at Western Lakes. Mean KFIs for adult females and juveniles did not differ significantly between study areas. However, it should be noted that mean KFIs for Western Lakes were amongst the lowest for these groups. There were no significant correlations between mean KFI and total rainfall for the 12 months prior to the sampling period (adult females: $r=0.09$, $df=5$, $p=0.8$; adult males: $r=0.69$, $df=5$, $p=0.08$; juveniles: $r=0.28$, $df=4$, $p=0.6$).

No correlations were found between annual hunting pressure and mean KFI in winter 1988 (adult females: $\text{Tau}=-0.47$, $z=1.5$, $p=0.07$; adult males: $\text{Tau}=-0.35$, $z=1.1$, $p=0.1$, juveniles: $\text{Tau}=-0.53$, $z=1.5$, $p=0.07$), winter 1989 (adult females: $\text{Tau}=0.29$, $z=1.0$, $p=0.2$; adult males: $\text{Tau}=-0.17$, $z=0.53$, $p=0.3$, juveniles: $\text{Tau}=-0.18$, $z=0.56$, $p=0.3$) or summer 1989 (adult females: $\text{Tau}=0.40$, $z=1.28$, $p=0.1$; adult males: $\text{Tau}=0.17$, $z=0.53$, $p=0.3$, juveniles: $\text{Tau}=0.0$, $z=0.0$, $p=0.5$). No correlations were undertaken for summer 1988 data.

It should be noted that mean KFIs for Rushy Lagoon, which was the most heavily hunted study area, were amongst the highest of all study areas.

Comparison between years

Comparisons of mean KFIs between years are given in Table 4.5. Only winter data were compared due to insufficient sampling in summer 1988. Mean KFIs were significantly lower in 1988 than in 1989.

Table 4.5 Comparison of mean KFIs between years for Bennett's wallabies (\pm s.d.) (square root transformed). The data were pooled over study areas which were sampled in both years and which were not significantly different from each other. Numbers in rounded parentheses indicate sample size.

	Winter 88	Winter 89	F-Test	Significance
Adult Female	5.1 \pm 0.9 (30)	5.9 \pm 0.8 (39)	F _[1,67] =15.89	p<0.001
Adult Male	4.4 \pm 1.1 (30)	5.1 \pm 1.3 (39)	F _[1,67] =5.41	p<0.05
Juvenile	3.6 \pm 0.9 (27)	4.3 \pm 1.4 (35)	F _[1,60] =5.91	p<0.05

Tasmanian pademelon

Comparison between sexes, age groups and seasons

Mean KFIs for adult females, adult males and juveniles in winter and summer are shown in Table 4.6. The data have been pooled over all study areas and both years.

For adult females, adult males and juveniles, mean KFIs in winter were significantly higher than in summer. During winter, mean KFIs for adult females were 18% higher than adult males and 45% higher than juveniles. During summer, mean KFIs for adult females were 19% higher than adult males and 47% higher than juveniles.

Table 4.6 Comparison of mean KFIs between sexes, age groups and seasons for Tasmanian pademelons (\pm s.d.) (square root transformed). The data were pooled over all study areas and both years. Numbers in rounded parentheses indicate sample size.

	Winter	Summer	F-Test	Significance
Adult Female	7.7 \pm 3.1 (191)	5.6 \pm 3.1 (107)	F _[1,296] =31.06	p<0.0001
Adult Male	6.5 \pm 2.1 (242)	4.7 \pm 1.6 (123)	F _[1,363] =67.80	p<0.0001
Juvenile	5.3 \pm 2.0 (217)	3.8 \pm 1.2 (104)	F _[1,319] =48.62	p<0.0001
F-Test	F _[2,647] =50.50	F _[2,331] =20.05		
Significance	p<0.0001	p<0.0001		

Comparison between study areas

Mean KFIs for adult females, adult males and juveniles at each study area are shown in Table 4.7. During winter of 1988 mean KFIs differed significantly between study areas for adult females and adult males. Mean KFIs were lower in low rainfall study areas than in high rainfall study areas. Mean KFIs were positively correlated with the total rainfall for the 12 months prior to the sampling period (Figure 4.4). For adult females ($r=0.99$, $df=3$, $p=0.002$) and adult males ($r=0.99$, $df=2$, $p=0.002$) the results were statistically significant. Mean KFIs did not vary between study areas for juveniles and there was no correlation between mean KFI and rainfall for juveniles ($r=0.58$, $df=2$, $p=0.4$).

Table 4.7 Comparison of mean KFI's between study areas for Tasmanian pademelons (\pm s.d.) (square root transformed). Numbers in rounded parentheses indicate sample size. ns=not significant.

WINTER 1988					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	Low	Medium	4.8 \pm 0.5 (8)	4.5 \pm 0.7 (15)	4.6 \pm 1.2 (22)
Buckland	Low	Low	6.0 \pm 1.8 (5)	4.6 \pm 1.0 (7)	-
Lagoon of Islands	Medium	High	6.8 \pm 1.4 (7)	5.6 \pm 1.3 (8)	5.5 \pm 2.4 (12)
Florentine Valley	High	Low	9.7 \pm 3.1 (7)	7.8 \pm 2.2 (26)	6.4 \pm 1.6 (10)
Styx	High	Very Low	9.2 \pm 4.6 (8)	8.0 \pm 2.6 (16)	5.0 \pm 1.4 (8)
F-Test			F [4,30]= 28	F [4,67]=11.33	F [3,48]=2.89
Significance			p < 0.02	p < 0.001	ns
SUMMER 1988					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	Low	Medium	-	3.6 \pm 0.9 (6)	3.9 \pm 1.1 (8)
Lagoon of Islands	Medium	High	4.7 \pm 2.0 (15)	4.4 \pm 1.5 (27)	3.4 \pm 0.8 (12)
Florentine Valley	High	Low	4.3 \pm 0.8 (19)	4.5 \pm 2.0 (8)	3.3 \pm 0.5 (8)
F-Test			F [1,32]=5.44	F [2,38]=0.74	F [2,25]=1.41
Significance			ns	ns	ns
WINTER 1989					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	Low	Medium	7.9 \pm 2.5 (22)	6.4 \pm 1.8 (22)	4.4 \pm 1.2 (21)
Buckland	Low	Low	7.4 \pm 3.7 (7)	5.3 \pm 1.2 (15)	3.9 \pm 1.2 (8)
Maria Island	Low	Very Low	7.0 \pm 2.5 (14)	5.4 \pm 0.8 (5)	5.9 \pm 1.3 (6)
Rushy Lagoon	Medium	Very High	9.8 \pm 3.4 (26)	6.2 \pm 2.1 (43)	4.8 \pm 2.0 (21)
Soldiers Marsh	Medium	Low	5.9 \pm 1.7 (10)	4.9 \pm 1.3 (12)	3.9 \pm 1.4 (8)
Lagoon of Islands	Medium	High	6.5 \pm 3.3 (23)	6.3 \pm 1.8 (26)	4.7 \pm 1.2 (23)
Florentine Valley	High	Low	8.7 \pm 2.7 (25)	7.2 \pm 2.1 (26)	6.4 \pm 2.4 (23)
Granville Harbour	High	Low	8.4 \pm 2.2 (18)	7.4 \pm 1.8 (24)	6.1 \pm 2.4 (58)
F-Test			F [7,137]=3.77	F [7,165]=3.99	F [7,160]=4.74
Significance			p < 0.002	p < 0.001	p < 0.001
SUMMER 1989					
Study Area	Rainfall	Hunting	Adult Female	Adult Male	Juvenile
View Point	Low	Medium	7.2 \pm 2.7 (14)	4.5 \pm 1.0 (28)	4.7 \pm 1.2 (14)
Buckland	Low	Low	5.3 \pm 2.9 (8)	4.3 \pm 0.8 (9)	3.4 \pm 0.6 (5)
Rushy Lagoon	Medium	Very High	8.1 \pm 3.2 (11)	4.8 \pm 1.1 (7)	3.7 \pm 1.0 (12)
Soldiers Marsh	Medium	Low	5.0 \pm 2.5 (5)	4.0 \pm 1.1 (10)	3.9 \pm 1.1 (8)
Lagoon of Islands	Medium	High	5.5 \pm 3.0 (6)	-	3.6 \pm 0.3 (5)
Florentine Valley	High	Low	4.9 \pm 1.4 (7)	4.8 \pm 1.6 (8)	-
Granville Harbour	High	Low	8.3 \pm 3.5 (11)	7.0 \pm 1.9 (11)	3.8 \pm 1.4 (32)
F-Test			F [6,55]=2.03	F [5,67]=8.41	F [5,70]=1.82
Significance			ns	p < 0.001	ns

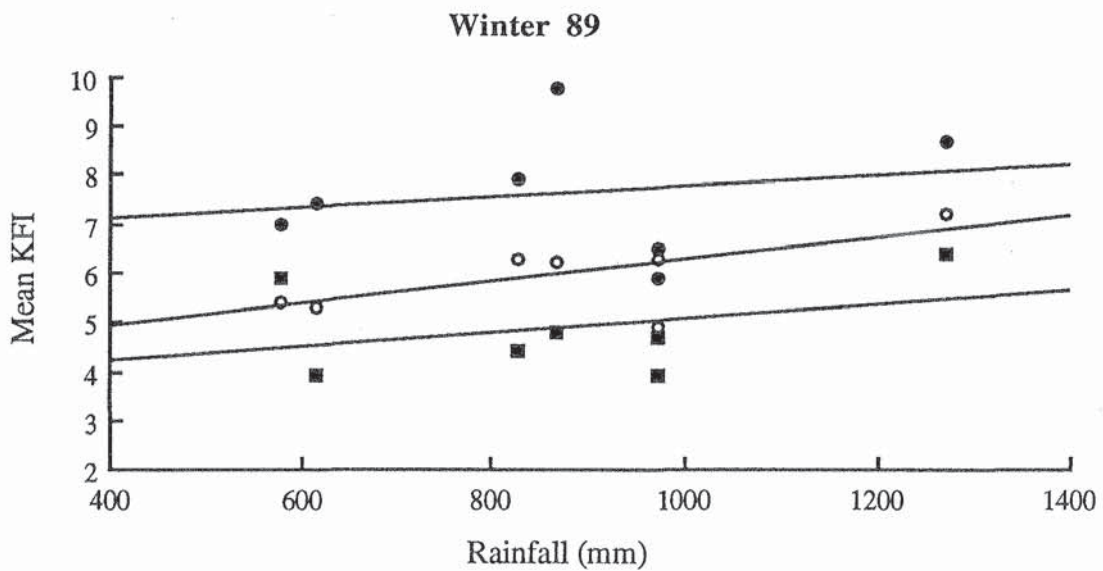
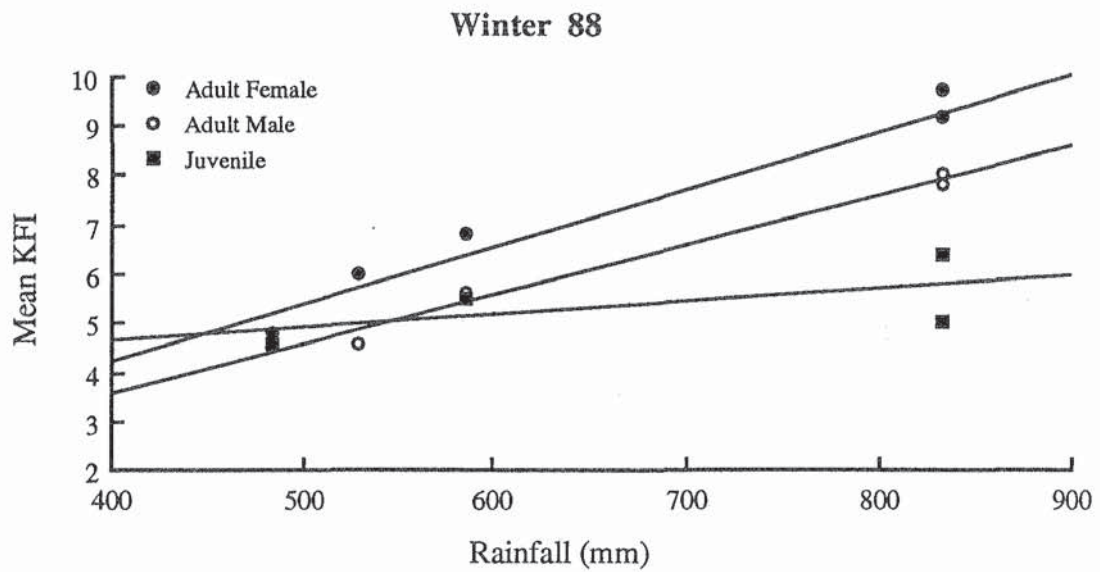


Figure 4.4. Correlation between mean KFI and rainfall (12 months prior to sampling periods) for the Tasmanian pademelon during winter 1988 (adult females: $r=0.99$, $df=3$, $p=0.002$; adult males: $r=0.99$, $df=3$, $p=0.0005$; juveniles: $r=0.58$, $df=2$, $p=0.4$) and 1989 (adult females: $r=0.19$, $df=5$, $p=0.7$; adult males: $r=0.67$, $df=5$, $p=0.1$; juveniles: $r=0.34$, $df=5$, $p=0.5$). Means and standard deviations are given in Table 4.7.

During winter of 1989 mean KFIs differed significantly between study areas for adult females, adult males or juveniles. For adult females the mean KFI at Rushy Lagoon was significantly higher than those for other study areas; for adult males the mean KFI for Granville Harbour was significantly higher; and for juveniles mean KFIs for Granville Harbour and the Florentine Valley were significantly higher. Mean KFIs were not correlated with total rainfall for the 12 months prior to the sampling period (adult females: $r=0.19$, $df=5$, $p=0.7$; adult males: $r=0.67$, $df=5$, $p=0.1$; juveniles: $r=0.34$, $df=5$, $p=0.5$) (Figure 4.4).

During summer of 1988 mean KFIs did not differ between study areas for adult females, adult males or juveniles (Table 4.7). No correlations were undertaken between rainfall and mean KFI during summer of 1988 due to insufficient data.

During summer of 1989 mean KFIs did not differ between study areas for adult females and juveniles. For adult males, the mean KFIs for Granville Harbour were significantly higher than those for other study areas. There were no significant correlations between mean KFI and total rainfall for the 12 months prior to the sampling period (adult females: $r=0.11$, $df=4$, $p=0.8$; adult males: $r=0.22$, $df=3$, $p=0.7$; juveniles: $r=0.34$, $df=3$, $p=0.6$).

There was no evidence of a correlation between annual hunting pressure and mean KFI for the Tasmanian pademelon in winter 1988 (adult females: $\text{Tau}=-0.32$, $z=0.8$, $p=0.2$; adult males: $\text{Tau}=-0.67$, $z=1.4$, $p=0.09$, juveniles: $\text{Tau}=0.0$, $z=0.0$, $p=0.5$), winter 1989 (adult females: $\text{Tau}=0.24$, $z=0.8$, $p=0.2$; adult males: $\text{Tau}=0.0$, $z=0.0$, $p=0.5$, juveniles: $\text{Tau}=-0.0$, $z=0.0$, $p=0.5$) or summer 1989 (adult females: $\text{Tau}=0.39$, $z=1.2$, $p=0.1$; adult males: $\text{Tau}=0.17$, $z=0.5$, $p=0.3$, juveniles: $\text{Tau}=0.0$, $z=0.0$, $p=0.5$). No correlations were undertaken for summer 1988 data.

Comparison between years

Comparisons of mean KFIs between years are given in Table 4.8. Only winter data were compared due to insufficient sampling in summer 1988. For adult males, mean KFIs were significantly lower in winter 1988 than in winter 1989. Mean KFIs for females in the winter of 1988 were 24% lower than in 1989, however, this difference was not statistically significant at the 0.05 level. There was no evidence that mean KFIs for juveniles differed between years.

Table 4.8 Comparison of mean KFIs between years for Tasmanian pademelons (\pm s.d.) (square root transformed). The data were pooled over study areas which were sampled in both years and which were not significantly different from each other. Numbers in rounded parentheses indicate sample size. ns=not significant.

	Winter 88	Winter 89	F-Test	Significance
Adult Female	5.8 \pm 1.5 (20)	7.2 \pm 3.1 (52)	F _[1,70] =4.78	ns (p=0.07)
Adult Male	4.8 \pm 1.1 (30)	6.1 \pm 1.7 (63)	F _[1,91] =13.23	p<0.001
Juvenile	4.9 \pm 1.7 (34)	4.5 \pm 1.2 (44)	F _[1,76] =1.31	ns

Comparison of mean KFIs between successful and unsuccessful breeders

Mean KFIs for adult females that were successful or unsuccessful in breeding are given in Table 4.9. Females which were unsuccessful in breeding had lower mean KFIs than those successful in breeding.

Table 4.9 Mean KFI's (\pm s.d.) (square root transformed) for successful (females with pouch young) and unsuccessful breeders (females which failed to breed or had lost pouch young). Numbers in parentheses indicate sample size.

Bennett's Wallaby

	Winter 88		Winter 89	
	Successful	Unsuccessful	Successful	Unsuccessful
Buckland	4.8 \pm 0.6 (6)	3.6 (1)	-	-
Maria Island	-	-	5.5 \pm 2.0 (29)	3.4 (1)
Rushy Lagoon	-	-	7.1 \pm 3.2 (18)	4.4 \pm 1.0 (3)
Soldiers Marsh	4.8 \pm 0.3 (5)	3.5 \pm 0.3 (4)	6.0 \pm 1.8 (17)	2.5 (1)
Lagoon of Islands	5.0 \pm 1.3 (6)	2.3 (1)	6.3 \pm 1.7 (8)	4.2 (1)
Western Lakes	6.9 \pm 2.2 (8)	1.8 \pm 0.1 (2)	5.7 \pm 2.4 (10)	3.7 (1)
Florentine Valley	5.9 \pm 0.9 (7)	3.3 (1)	-	-

Tasmanian Pademelon

	Winter 88		Winter 89	
	Successful	Unsuccessful	Successful	Unsuccessful
Maria Island	-	-	7.0 \pm 2.5 (14)	4.1 (1)
Rushy Lagoon	-	-	9.8 \pm 3.4 (26)	5.9 (1)
Lagoon of Islands	-	-	6.5 \pm 3.3 (23)	3.8 \pm 0.6 (3)
Florentine Valley	9.7 \pm 3.1 (7)	6.3 \pm 0.3 (2)	8.7 \pm 2.7 (25)	3.7 (1)
Styx	9.2 \pm 4.6 (8)	3.9 \pm 0.3 (2)	-	-
Granville Harbour	-	-	8.4 \pm 2.2 (18)	7.2 (1)

4.3.3 Growth

The increase in mean body weight with age for males and females of both species are shown in Figure 4.5. Mean body weights and statistical comparisons are given in Tables 4.10 and 4.11.

Both species showed strong sexual dimorphism. In the oldest age class male Bennett's wallabies were 48% heavier than females. Similarly, male Tasmanian pademelons in the oldest age class were 52% heavier than females. Female Bennett's wallabies attained maximum weight around 4-5 years of age whereas males continue growing at this age, albeit slowly. Female Tasmanian pademelons attained maximum weight by 2-3 years of age whereas males continue to increase in weight after this age. For both species, the greatest rate of growth occurred at a young age.

Tables 4.12 and 4.13 show the mean body weight of both species in each age class for each study area. There were significant differences in mean body weight and hence growth between study areas for both species.

Effect of hunting and rainfall on growth

The effects of hunting and rainfall on growth rate were investigated by correlation analysis. The oldest age class (6+ years for Bennett's wallabies and 30+ months for Tasmanian pademelons) was used for this analysis as these animals were considered most likely to give an 'average' indication of the condition of the habitat over an extended time period. Mean annual rainfall for 1977 to 1986 was used as an indication of rainfall conditions during the growth phase of these animals.

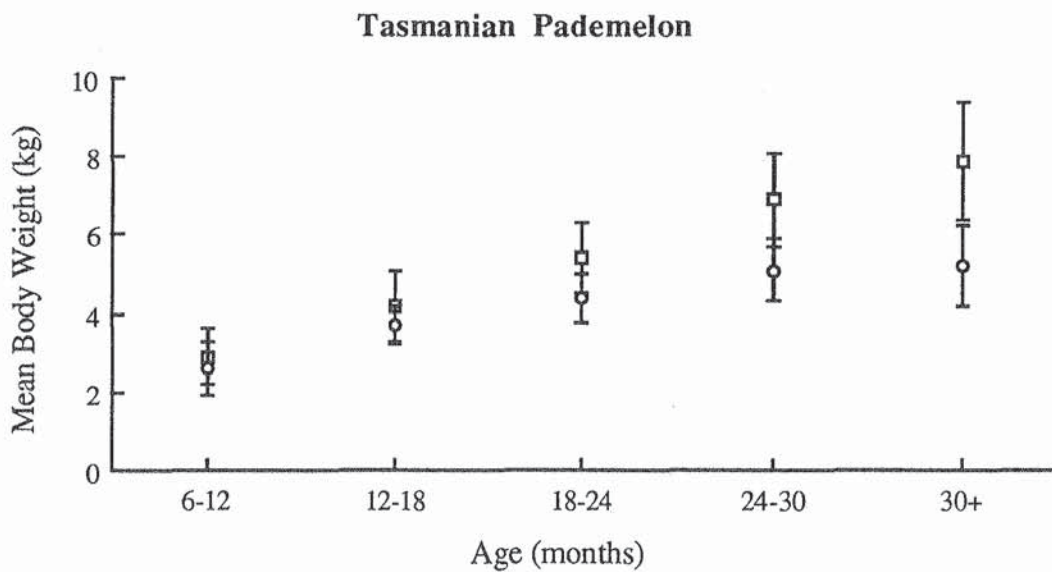
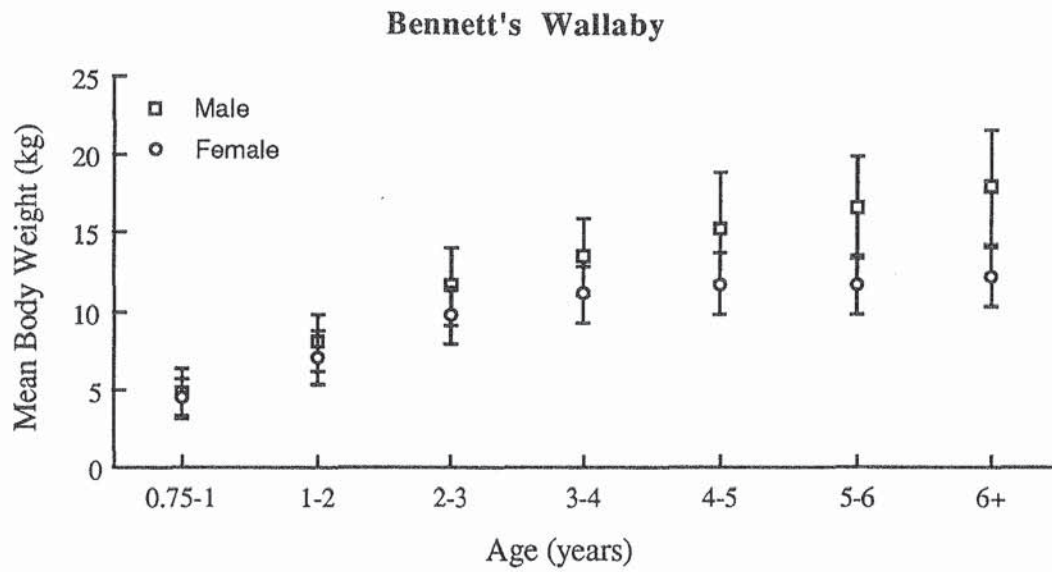


Figure 4.5 Comparison of mean growth rates (\pm s.d.) for male and female Bennett's wallabies and Tasmanian pademelons. All statistical information is given in Tables 4.10 and 4.11. Open squares denote males and closed squares denote females.

Table 4.10 Comparison of mean body weights between male and female Bennett's wallabies. The data were pooled over all study areas. Values in rounded parentheses refer to sample sizes.

Age (yrs)	Male		Female		F-test	Significance
	Weight (kg)	% increase	Weight (kg)	% increase		
0.75-1	4.8 ± 1.6 (31)		4.4 ± 1.3 (17)		F (1,46) = 0.66	ns
1-2	8.0 ± 1.8 (214)	66	7.0 ± 1.7 (159)	59	F (1,371) = 26.83	P < 0.001
2-3	11.6 ± 2.5 (191)	45	9.7 ± 1.8 (128)	39	F (1,317) = 50.62	P < 0.001
3-4	13.5 ± 2.5 (75)	16	11.1 ± 1.8 (58)	14	F (1,131) = 36.66	P < 0.001
4-5	15.3 ± 3.5 (70)	13	11.7 ± 2.0 (63)	5	F (1,131) = 51.34	p < 0.001
5-6	16.6 ± 3.2 (18)	8	11.7 ± 1.9 (16)	0	F (1,32) = 29.44	P < 0.001
6+	17.9 ± 3.7 (45)	8	12.1 ± 1.9 (57)	3	F (1,100) = 106.47	p < 0.001

Table 4.11 Comparison of mean body weights between male and female Tasmanian pademelons. The data were pooled over all study areas. Values in rounded parentheses refer to sample sizes.

Age (mths)	Male		Female		F-test	Significance
	Weight (kg)	% increase	Weight (kg)	% increase		
6-12	2.9 ± 0.7 (145)		2.6 ± 0.7 (119)		F (1,262) = 12.67	P < 0.001
12-18	4.2 ± 0.9 (171)	45	3.7 ± 0.5 (98)	43	F (1,267) = 25.54	P < 0.001
18-24	5.4 ± 0.9 (138)	29	4.4 ± 0.6 (78)	19	F (1,214) = 68.57	p < 0.001
24-30	6.9 ± 1.2 (121)	27	5.1 ± 0.8 (83)	16	F (1,202) = 145.70	p < 0.001
30+	7.9 ± 1.5 (95)	14	5.2 ± 1.0 (83)	1	F (1,176) = 198.19	p < 0.001

Table 4.12 Comparison of mean body weights (kg) between study areas for Bennett's wallabies.

Study Area	Age Class (years)						
	0-1	1-2	2-3	3-4	4-5	5-6	6+
MALE							
Maria Island		5.2 ± 0.4 (6)	8.0 ± 1.6 (4)	10.5 ± 1.4 (3)	11.4 ± 0.6 (9)		14.5 ± 0.8 (2)
View Point	2.9 ± 0.8 (3)	7.4 ± 1.8 (23)	9.8 ± 1.5 (18)	10.7 ± 0.8 (5)	11.5 ± 1.3 (3)		13.3 ± 2.7 (3)
Buckland	5.8 ± 1.8 (2)	6.6 ± 1.3 (19)	9.4 ± 1.1 (13)	11.0 ± 1.3 (6)	13.1 ± 1.4 (6)	14.0 ± 2.7 (3)	14.9 ± 1.3 (6)
Rushy Lagoon	4.7 ± 2.0 (5)	9.5 ± 1.5 (48)	14.5 ± 2.2 (30)	15.4 ± 1.4 (10)	19.0 ± 1.2 (5)		20.8 ± 2.5 (3)
Soldiers Marsh		7.3 ± 0.9 (26)	10.4 ± 1.2 (36)	12.5 ± 1.5 (18)	14.1 ± 2.0 (7)	18.4 ± 0.8 (2)	16.8 ± 1.6 (4)
Lagoon of Islands	3.8 ± 0.7 (5)	7.6 ± 1.5 (22)	11.3 ± 2.0 (25)	13.0 ± 1.4 (6)	14.2 ± 2.0 (8)	16.8 ± 0.9 (2)	16.3 ± 3.4 (8)
Western Lakes	5.7 ± 0.6 (2)	8.0 ± 1.4 (29)	12.1 ± 2.4 (30)	14.8 ± 2.0 (18)	16.0 ± 2.6 (12)	17.2 ± 3.0 (16)	19.4 ± 1.0 (7)
Florentine Valley	5.2 ± 1.8 (11)	8.6 ± 1.6 (33)	12.7 ± 2.0 (28)	16.5 ± 3.1 (7)	18.0 ± 3.6 (19)	16.9 ± 5.1 (4)	21.1 ± 3.6 (11)
F-test	F(5,22) = 1.7	F(7,198) = 15.9	F(7,176) = 21.2	F(7,65) = 11.1	F(7,61) = 10.4	F(4,12) = 0.6	F(7,37) = 5.6
Significance	ns	p < 0.001	p < 0.001	p < 0.001	p < 0.001	ns	p < 0.001
FEMALE							
Maria Island		4.9 ± 0.7 (10)	7.7 ± 1.0 (9)	8.7 ± 0.9 (5)	9.2 ± 0.9 (6)	10.0 ± 0.3 (3)	10.7 ± 2.5 (9)
View Point		5.9 ± 1.3 (17)	8.8 ± 1.8 (13)	9.8 ± 1.4 (5)	9.2 ± 1.2 (5)		10.6 ± 2.7 (5)
Buckland		5.9 ± 1.2 (14)	8.1 ± 1.2 (6)	9.3 ± 0.5 (5)	9.6 ± 1.4 (6)	10.4 ± 1.6 (2)	11.3 ± 0.9 (10)
Rushy Lagoon		8.8 ± 1.4 (33)	11.4 ± 1.6 (21)	12.8 ± 1.7 (10)	13.6 ± 1.0 (11)		13.6 ± 1.5 (12)
Soldiers Marsh		6.4 ± 0.8 (15)	9.4 ± 1.3 (18)	11.0 ± 1.2 (10)	12.2 ± 1.0 (9)		11.9 ± 1.0 (4)
Lagoon of Islands	3.8 ± 0.9 (4)	6.5 ± 1.4 (17)	8.9 ± 1.6 (13)	10.6 ± 0.7 (8)	11.5 ± 1.4 (7)	10.9 ± 0.3 (3)	12.1 ± 2.0 (4)
Western Lakes	4.4 ± 0.7 (2)	7.5 ± 1.8 (14)	10.2 ± 1.7 (19)	11.7 ± 0.7 (6)	11.8 ± 1.1 (8)	12.3 ± 0.8 (2)	13.2 ± 1.0 (8)
Florentine Valley	4.7 ± 1.7 (5)	7.6 ± 1.2 (31)	10.5 ± 1.4 (24)	12.5 ± 1.4 (9)	13.5 ± 1.3 (10)	14.2 ± 1.6 (4)	12.8 ± 0.7 (5)
F-test	F(2,8) = 0.5	F(7,143) = 17.4	F(7,114) = 10.0	F(7,50) = 10.2	F(7,54) = 17.5	F(4,9) = 7.8	F(7,50) = 2.99
Significance	ns	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.01	p < 0.025

Table 4.13 Comparison of mean body weights (kg) between study areas for Tasmanian pademelons.

Study Area	6-12	12-18	Age Class (months) 18-24	24-30	30+
MALE					
Maria Island	2.5 ± 0.3 (4)	2.4 ± 0.1 (2)		5.1 ± 0.6 (2)	6.3 ± 1.0 (3)
View Point	2.8 ± 0.5 (23)	4.0 ± 0.6 (43)	5.1 ± 0.8 (33)	6.0 ± 1.0 (23)	6.7 ± 1.2 (24)
Buckland	2.3 ± 1.1 (5)	3.9 ± 0.5 (11)	5.1 ± 0.7 (9)	6.5 ± 1.4 (8)	6.9 ± 0.9 (6)
Rushy Lagoon	3.3 ± 1.1 (18)	5.1 ± 0.9 (26)	6.3 ± 1.1 (12)	7.9 ± 0.8 (15)	9.4 ± 1.6 (4)
Soldiers Marsh	2.6 ± 0.7 (13)	3.7 ± 0.8 (15)	5.2 ± 0.9 (12)	6.5 ± 0.8 (8)	8.0 ± 1.2 (11)
Lagoon of Islands	3.1 ± 0.7 (22)	4.6 ± 0.8 (30)	5.6 ± 1.3 (19)	7.4 ± 1.3 (16)	8.1 ± 1.6 (7)
Western Lakes			5.8 ± 0.2 (2)	6.9 ± 0.6 (3)	
Florentine Valley	2.9 ± 0.9 (14)	4.3 ± 0.9 (13)	5.3 ± 0.7 (26)	7.1 ± 0.9 (28)	8.5 ± 1.4 (20)
Styx		3.5 ± 0.7 (6)	5.4 ± 0.4 (3)	7.3 ± 0.9 (9)	9.0 ± 0.6 (8)
Granville Harbour	3.0 ± 0.5 (43)	3.9 ± 0.6 (21)	5.3 ± 0.8 (20)	6.4 ± 0.4 (6)	8.4 ± 1.1 (10)
F-test	F (7,134) = 2.4	F (8,158) = 9.6	F (8, 127) = 2.8	F (9,108) = 5.47	F (8,84) = 6.2
Significance	p < 0.025	p < 0.001	p < 0.01	p < 0.001	p < 0.001
FEMALE					
Maria Island			3.4 ± 0.1 (3)	3.8 ± 0.2 (2)	4.4 ± 0.7 (10)
View Point	2.5 ± 0.5 (25)	3.6 ± 0.5 (28)	4.0 ± 0.4 (10)	4.3 ± 0.3 (14)	4.5 ± 0.5 (13)
Buckland	2.2 ± 0.6 (8)	3.9 ± 0.3 (3)	4.0 ± 0.2 (3)	4.4 ± 0.5 (4)	4.9 ± 0.6 (10)
Rushy Lagoon	3.0 ± 0.7 (19)	4.1 ± 0.4 (10)	4.9 ± 0.5 (7)	5.5 ± 0.8 (11)	5.7 ± 0.9 (5)
Soldiers Marsh	2.2 ± 0.5 (9)	3.3 ± 0.4 (5)	4.1 ± 0.5 (12)	4.9 ± 0.6 (5)	5.0 ± 0.4 (8)
Lagoon of Islands	2.7 ± 0.7 (15)	3.8 ± 0.5 (24)	4.3 ± 0.3 (14)	4.7 ± 0.5 (11)	4.8 ± 0.6 (8)
Western Lakes	3.2 ± 0.3 (4)		4.5 ± 0.1 (2)	5.4 ± 0.7 (4)	
Florentine Valley	2.5 ± 0.7 (14)	3.7 ± 0.5 (8)	4.9 ± 0.5 (15)	5.6 ± 0.7 (23)	6.0 ± 0.7 (13)
Styx	2.4 ± 0.5 (4)			5.8 ± 0.3 (4)	7.0 ± 0.3 (5)
Granville Harbour	2.8 ± 0.6 (19)	3.8 ± 0.5 (17)	4.5 ± 0.5 (9)	5.2 ± 0.3 (5)	5.7 ± 0.5 (9)
F-test	F (8,108) = 3.0	F (6,88) = 2.3	F (8,66) = 6.6	F (9,71) = 7.6	F (8,72) = 14.9
Significance	p < 0.01	p < 0.05	p < 0.001	p < 0.001	p < 0.001

No correlations were found between hunting pressure and mean body weight of the oldest age class of either species (Table 4.14).

The relationships between mean annual rainfall and mean body weight of the oldest age class are given in Figures 4.6 and 4.7. With the exception of male pademelons, there was evidence of a correlation between these two variables (Table 4.15). In relation to rainfall the mean body weight of wallabies from Rushy Lagoon were higher than those of other study areas (Figures 4.6 and 4.7). Removal of this study area from the data set results in significant correlations between rainfall and mean body weight for all four comparisons (Table 4.16).

Table 4.14 Correlation between annual harvest pressure and mean body weight of oldest wallabies (6+ years for Bennett's wallabies and 30+ months for Tasmanian pademelons) using Kendall's Rank Correlation Coefficient (Tau).

Species	Sex	Tau	z	Probability
Bennett's wallaby	Male	0.161	0.558	0.2709
	Female	0.322	1.117	0.1314
Tasmanian pademelon	Male	0.327	1.227	0.3745
	Female	0.033	0.124	0.4880

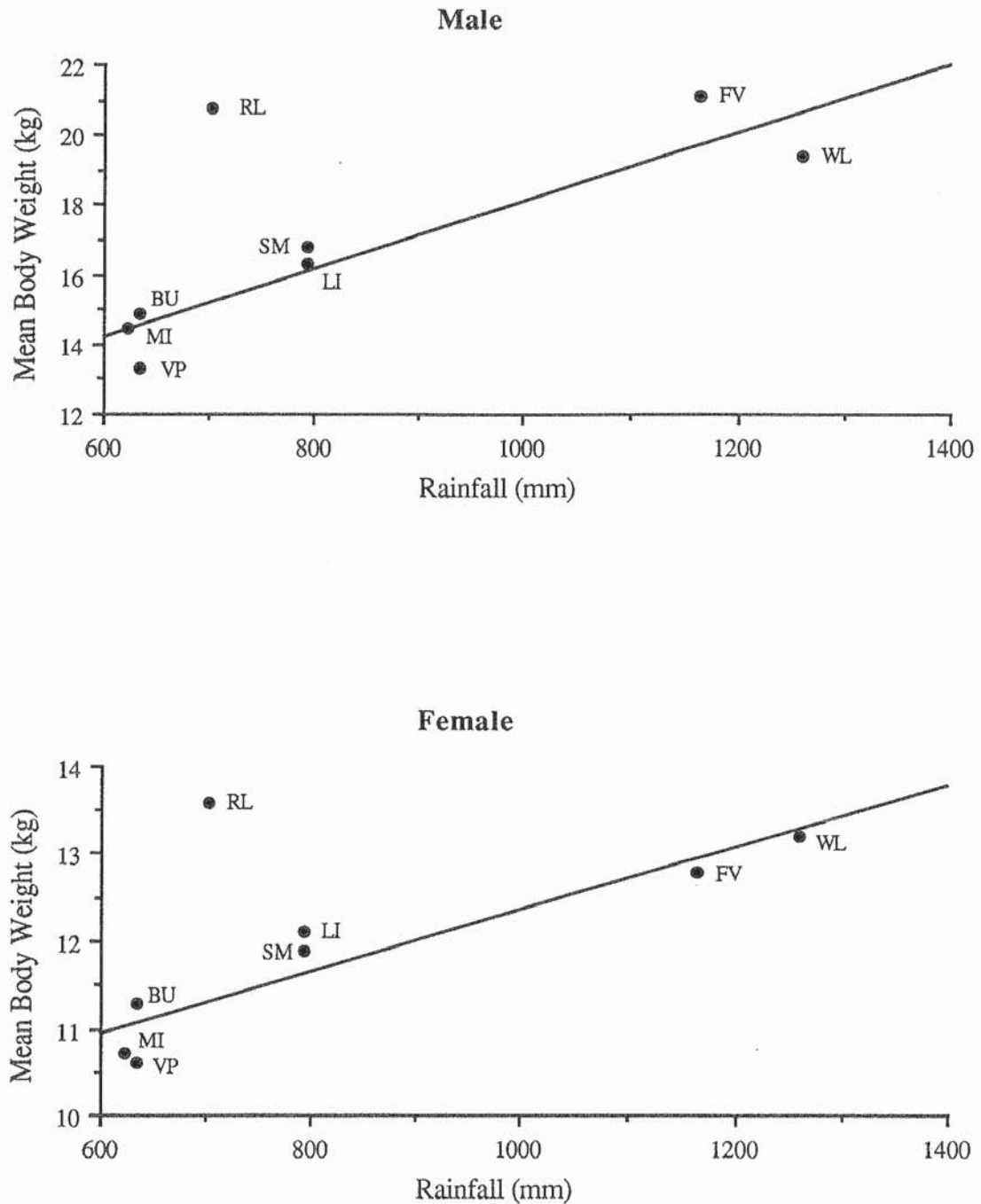


Figure 4.6 Correlation between mean body weight (standard deviations given in Table 4.12) of Bennett's wallabies in the oldest age class and mean annual rainfall (1977-86). For males $r=0.70$, $p=0.05$ and for females $r=0.65$, $p=0.08$. Note position of Rushy Lagoon.

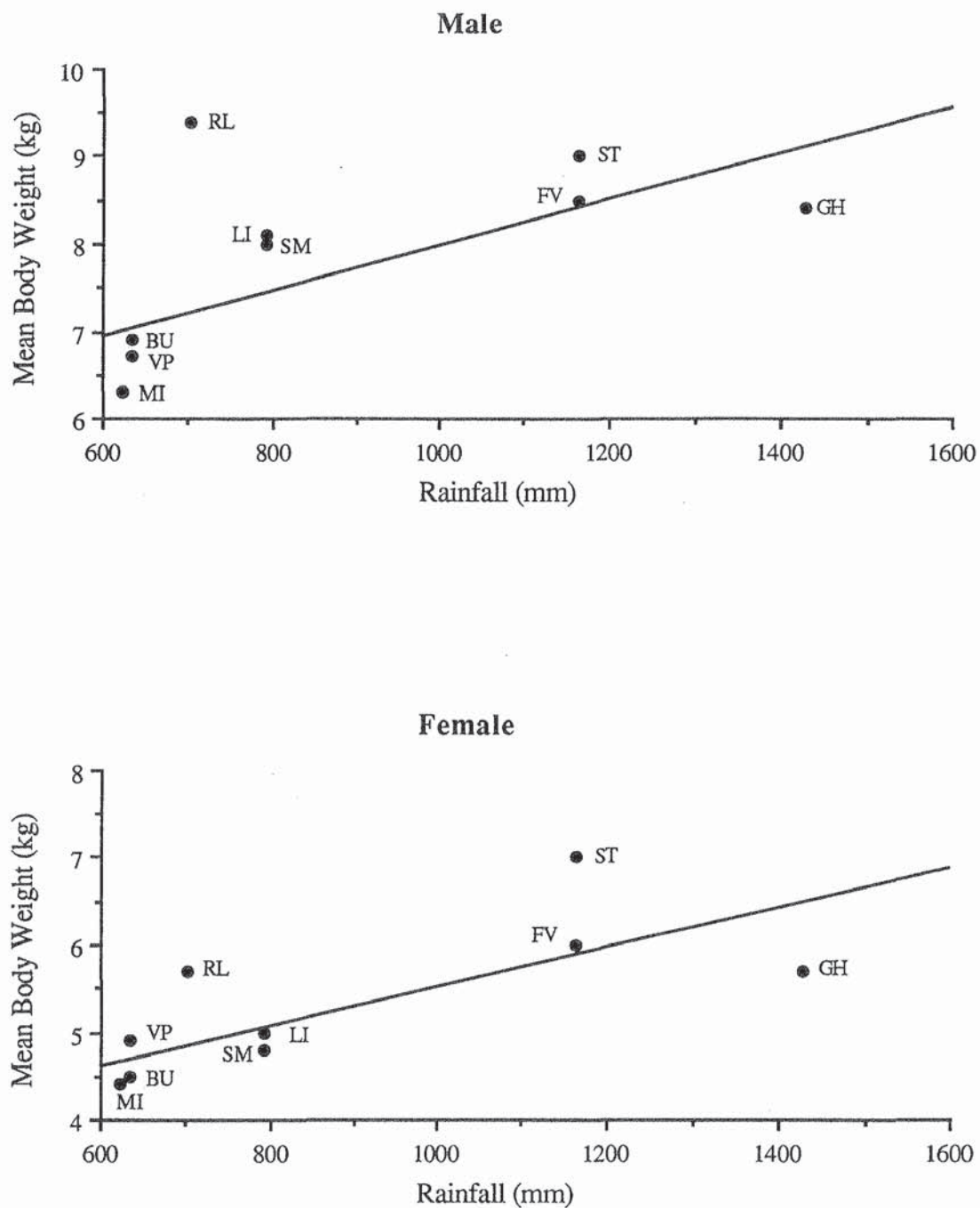


Figure 4.7 Correlation between mean body weight (standard deviations given in Table 4.13) of Tasmanian pademelons in the oldest age class and mean annual rainfall (1977-86). For males $r=0.56$, $p=0.10$ and for females $r=0.72$ $p=0.03$. Note position of Rushy Lagoon.

Table 4.15 Correlation between mean annual rainfall (1977-86) and mean body weight of oldest wallabies (6+ years for Bennett's wallabies and 30+ months for Tasmanian pademelons) for all study areas.

Species	Sex	r	F-test	Probability
Bennett's wallaby	Male	0.70	$F_{(1,6)} = 5.7$	0.05
	Female	0.65	$F_{(1,6)} = 4.2$	0.08
Tasmanian pademelon	Male	0.56	$F_{(1,7)} = 3.3$	0.10
	Female	0.72	$F_{(1,7)} = 7.6$	0.03

Table 4.16 Correlation between mean annual rainfall (1977-86) and mean body weight of oldest wallabies (6+ years for Bennett's wallabies and 30+ months for Tasmanian pademelons) for all study areas excluding Rushy Lagoon.

Species	Sex	r	F-test	Probability
Bennett's wallaby	Male	0.94	$F_{(1,5)} = 36.4$	0.002
	Female	0.94	$F_{(1,5)} = 37.8$	0.002
Tasmanian pademelon	Male	0.82	$F_{(1,6)} = 12.3$	0.010
	Female	0.79	$F_{(1,6)} = 10.0$	0.020

4.4 DISCUSSION

4.4.1 Variation in Kidney Weight to Body Weight Ratio

According to Van Vuren and Coblenz (1985), the underlying assumption of KFI, that kidney weight is proportional to body weight, has been assumed but not substantiated in past studies. Although Van Vuren and Coblenz (1985) found a significant correlation between kidney weight and body weight for feral sheep, *Ovis aries*, they also found that this relationship differed slightly between juveniles and adults. This was because juveniles had proportionally larger kidneys than adults. The results for both the Tasmanian pademelon and Bennett's wallaby showed this same pattern. Hence, KFIs for juvenile wallabies will be underestimated relative to adult wallabies. However, in most cases, the differences between mean KFIs for adults and juveniles (refer to Table 4.3 and 4.6) were greater than 26% which is more than can be attributed to the variation in kidney weight alone. Kidney weights did not vary between adults and juveniles by more than 10% and 13% for Bennett's wallabies and Tasmanian pademelons respectively. Only the comparison between mean KFIs for adult female and juvenile Bennett's wallabies during summer may be affected by variation in kidney weight as the difference in mean KFI was only 11%.

The present study found that, for both wallaby species, there were small decreases in mean KW/BW ratios during late autumn of 1989 and early winter of 1988. This decrease was due to a decrease in kidney weight rather than an increase in body weight (refer to Appendix I). A number of authors (Batcheler and Clarke 1970; Flux 1971; Dauphine 1975; Mitchell *et al.* 1976; Havera 1977; Finger *et al.* 1981; Spinage 1984; Van Vuren and Coblenz 1985; Pepin 1987; Coblenz and Van Vuren 1988) have shown that kidney weights may fluctuate seasonally and not necessarily as a function of body weight. However, there are differences of opinion about the effect of seasonal variation of kidney weight on estimates of body condition based on KFI. Some authors (Batcheler and Clarke 1970; Dauphine 1975; Van Vuren and Coblenz 1985) argue that variation in kidney weight will substantially influence inter-seasonal comparisons of KFI. Dauphine (1975) found that KFIs

were distorted by a 70 to 80% increase in kidney weight during summer and early autumn for caribou, *Rangifer tarandus*. Other authors (Flux 1971; Finger *et al.* 1981; Mitchell *et al.* 1976; Spinage 1984; Pepin 1987) consider that the effect of seasonal variation in kidney weight in their studies was insignificant. Both Flux (1971) and Pepin (1987) reported variations in kidney weights of up to 10% in hares, *Lepus europaeus*, however, this was not considered to be large enough to cause any significant differences in seasonal patterns of KFI. Similarly, Havera (1977) found that KFI provided a satisfactory estimate of fox squirrel, *Sciurus niger*, body condition despite variations in kidney weights of up to 20% for males and 32% for females .

In the present study kidney weights did not vary by more than 12% for either wallaby species. This seasonal difference in kidney weight had little influence on seasonal trends in KFI because most seasonal differences between mean KFIs (Tables 4.3 and 4.7) were greater than 12%. In addition there was little sampling during that time when kidney weights were significantly low.

The cause of the decrease in kidney weight during late autumn is unclear but may be related to water stress at this time. In Tasmania effective rainfall is typically lowest during summer and early autumn (Section 2.2). In 1988 the low kidney weights continued into early winter, presumably due to the drought which ended in July of that year (Section 2.2). In the following year when rainfall had returned to more normal levels there were no significant decreases in kidney weight during early winter. Kidney weight has been shown to decrease during periods of water stress in shrews (Pucek 1970), feral sheep (Van Vuren and Coblentz 1985) and the Indian mongoose, *Herpestes auropunctatus*, (Coblentz and Van Vuren 1988).

For both wallaby species there were also small, but significant, differences in mean KW/BW ratios between study areas. This difference was also due to changes in kidney weight rather than body weight (refer to Appendix I). The maximum differences for kidney weights between study areas were 23% for Bennett's wallabies and 12% for Tasmanian

pademelons. However, maximum differences between mean KFIs (Table 4.4 and 4.7) were typically greater than can be attributed to variation in kidney weight alone. Only the comparisons between juveniles during summer 1988 and winter 1989 may be influenced by the variation in kidney weight and this is taken into account when discussing mean KFIs below.

The cause of variation in kidney weight between study areas is unclear. It is possible that water stress and/or food deprivation are involved, as the two study areas with the lowest kidney weights were subject to low rainfall. However, the remaining study areas which had similar kidney weights do not support this explanation. It is possible that the proportionally higher kidney weights at Western Lakes for Bennett's wallaby was due to the cold temperatures (refer to Section 2.3) at this high altitude study area. Chaffee and Roberts (1971) and Balcer and Chaffee (1984) have reported for several mammal species that cold acclimation leads to an increase in kidney weight.

According to Coblenz and Van Vuren (1988) body water kinetics, metabolic activity, and temperature stress may all influence kidney mass simultaneously. Further explanation of variation in kidney weights for both wallaby species was beyond the scope of the present study. However, the variations in kidney weights between age groups, seasons and study areas were not considered to be large enough to influence the general trends observed in KFI. These trends are discussed below.

4.4.2 Kidney Fat Index

KFIs for Bennett's wallaby and the Tasmanian pademelon were used to assess the short term response in body condition to recent environmental conditions. Although small sample sizes hampered comparisons, some general trends were apparent.

KFIs for both wallaby species were higher in winter than in summer. This trend has been reported for a number of other species such as; grey kangaroos (Caughley 1962), thar, *Hemitragus jemlahicus*, (Caughley 1970), red deer (Caughley 1971a), hares (Flux 1971), chamois (Henderson and Clarke 1986), white-tailed deer (Waid and Warren 1984; DeLiberto *et al.* 1989) and wild European rabbits, *Oryctolagus cuniculus*, (Boyd and Myhill 1987). Yearly variation in body condition is often linked to the reproductive cycle which, in turn, is linked to the availability of food resources at critical stages of reproduction. For adult female wallabies, the yearly trend in KFI also appeared to be linked to the reproductive cycle. KFIs for adult females were lowest in summer presumably as a result of lactational demands from young during spring and summer. It is also likely that the decrease in KFI is associated with food shortages at the end of winter and before there is effective spring growth. Once the young have been weaned over summer, adult females showed evidence of increasing their fat reserves presumably in preparation for winter food shortages and the energy demands of the next young.

The loss of condition between winter and summer shown by males is also likely to be a result of food shortages at the end of winter. However, other factors must be involved otherwise they would show an increase in KFI over spring when food resources increase substantially. It is suspected that time and energy spent on activities associated with mating in spring and summer may be associated with this loss of body condition. Several studies have shown that KFIs for some species of ungulates decrease during the rutting season (Attwell 1982; Clutton-Brock *et al.* 1982; Dunham and Murray 1982). Whilst macropods do not have a rutting season, males of most species show increased levels of aggression around females which are in oestrous (Russell 1974). Physiological changes associated with mating, such as increases in prostate weight (Appendix II), may also contribute to a reduction in KFI. It is also possible that the lower KFIs recorded in summer for male wallabies is a result of maximizing growth during spring when food resources are relatively stable. Seasonal periodicity in growth has been shown for several species of ungulate in temperate zones (Wood *et al.* 1962; Houston *et al.* 1989) and peak growth occurs spring and summer. Whether this occurs in wallabies will require investigation.

Juveniles of both species also had lower KFIs in summer than in winter. The majority of young of both species vacate the pouch in spring and early summer and, as a result, have not had time to deposit fat reserves. This period when KFIs were low is associated with high mortality of young which have recently left the pouch (Johnson 1989c; section 5.4.4).

In winter adult females had higher KFIs than adult males. This sex-related difference in KFI has also been found in other animals such as white-tailed deer (Johns *et al.* 1984), nyala, *Tragelaphus angasi*, (Anderson 1985) and wild European rabbits (Boyd and Myhill 1987) and is attributed to the requirement by females for better body condition to cope with the demands of pregnancy and lactation. In addition, the lower KFIs recorded for males may be a result of maximising their potential for growth. Clutton-Brock *et al.* (1982) showed that, in winter, female red deer will reduce their growth rate to a greater degree than males in favour of depositing fat. For male red deer, large body size is important for reproductive success and hence there are obvious advantages in maximizing growth. Similarly, for both wallaby species, body size of males is important in establishing dominance relationships (Clancy 1982; Johnson 1989a) and Johnson (1989a) was able to show that for the mainland subspecies, the red-necked wallaby, large males accounted for most matings.

In summer female Bennett's wallabies had lower KFIs than males which can be attributed to the high energy demands placed on females at this time of the year by large pouch young or suckling young which have left the pouch. By contrast, female Tasmanian pademelons still had higher KFIs than male Tasmanian pademelons. Thus male Tasmanian pademelons showed a greater decrease in KFI between winter and summer than did male Bennett's wallabies (refer to Tables 4.3 and 4.6). Why this difference between the species should occur is not clear but may be related to the difference in onset of reproductive activity between the two species. Increases in prostate weight prior to breeding (Appendix II) indicate that male Tasmanian pademelons commence mating activity earlier in spring than Bennett's wallabies and presumably begin to lose condition earlier. In addition, fighting scars were frequently seen on Tasmanian pademelon pelts but rarely on Bennett's wallaby pelts (unpublished observations). This suggests that the degree of fighting between

pademelons may be higher than that between Bennett's wallabies and this may also help to explain the differences in KFIs.

Juveniles of both species had lower KFIs than adults, although this difference was less apparent in summer than in winter. It should be noted that juveniles had proportionally larger kidneys than adults thereby decreasing their KFIs in comparison. However, for winter at least, this did not account for all of the observed difference in KFI. Such a difference is not unreasonable as younger animals have higher growth rates than adults (Tables 4.10 and 4.11) and have had less time to develop fat reserves. Similar results, using KFI, have been reported for other species such as red deer (Riney 1955), chamois (Henderson and Clarke 1986), red fox, *Vulpes vulpes*, (Lindstrom 1983), hares (Pepin 1987) and impala, *Aepyceros melampus*, (Dunham and Murray 1982).

Although sample sizes for unsuccessful breeders were small, there was evidence to suggest that a lack of breeding success was associated with low KFIs. Similar findings, using KFI, have been reported for fox squirrels (Havera 1977) and caribou (Thomas 1982). In addition, Newsome (1977b) found that, during drought, weights of non-breeding red kangaroos were lower than their reproductive counterparts of the same age. This lower breeding success of animals in poor condition is presumably a strategy to conserve energy.

Mean KFIs were higher for Tasmanian pademelons than for Bennett's wallabies (compare Tables 4.3 and 4.6). Whether this difference represents a real difference in body condition between the two species is not known as it is possible that the different KFIs represent differences in patterns of fat deposition. However, it is possible that body condition of Tasmanian pademelons is higher than that of Bennett's wallabies as evidenced by differences in the quality of their diets. Bennett's wallabies are grazers feeding primarily on grasses (Calaby 1983; Statham 1983; Southwell 1987; Jarman and Phillips 1989) which are generally low in nutrients (Taylor 1981; Dawson 1989; Freudemberger *et al.* 1989; Norbury *et al.* 1989). By comparison, Tasmanian pademelons have a more varied diet (Statham 1983; Johnson and Rose 1983) feeding on soft green grasses, browse, forbs and

shrubs which are generally high in nutrients (Dawson 1989). This difference in the quality of the diet consumed by each species was confirmed by analysing stomach samples for nitrogen content (Appendix III). Thus, it is possible that the differences in mean KFI between the two wallaby species may, in part, reflect differences in body condition.

Effect of hunting and rainfall on KFI

Both the 1987/88 drought and the variation in rainfall between study areas were found to influence KFIs for both species of wallaby.

Mean KFIs for Bennett's wallabies were significantly lower in 1988 than in 1989. As rainfall is a significant factor affecting vegetation quality and quantity (Sinclair 1977; Shepherd 1987), this result suggests that food resources for this species were poorer in 1988 as a result of the drought. The effect of the drought on Tasmanian pademelons was less apparent. Only mean KFIs for adult male pademelons were significantly lower in 1988 than in 1989. Although mean KFIs for adult females were 24% lower in 1988 than in 1989, this difference was not significant at the 0.05 level. Given the high variation in KFIs for adult female pademelons (Table 4.8) it's probable that greater sampling would have resulted in a significant difference in mean KFIs between years. This high coefficient of variation can be attributed to the fact that Tasmanian pademelon births occur over a period of 4 months (Section 5.4.1) and, hence, body condition will vary depending upon when a female gave birth. By comparison, Bennett's wallaby births occur over a much shorter period, hence, females are more likely to have similar body condition. These results suggest that the drought may have had a greater impact on the body condition of Bennett's wallabies than on Tasmanian pademelons. This difference between the two species is possibly due to differences in diet which has already been discussed. This difference in the quality of diet will be increased during periods of drought as it has been shown that, during times of low rainfall, grasses characteristically lose crude protein more rapidly and to a greater degree than do shrubs (De Vos and Mosby 1969).

In 1988 variation in rainfall between study areas was positively correlated with mean KFI for both species. This indicates that the drought affected low rainfall study areas to a greater extent than high rainfall study areas. This is supported by the variation in rainfall deficit between study areas during the drought (Section 2.2). In 1989 there was no evidence of a correlation between rainfall and mean KFIs for either species of wallaby. Presumably the higher rainfall in the latter half of 1988 and all of 1989 resulted in improved food resources at all study areas. In addition, density may have been reduced as a result of lower survival of young after the drought (Section 5.4.4).

Similar relationships between KFI, rainfall and food resources have been shown for other species of kangaroos (Shepherd 1987) as well as other non-macropod mammals (Sinclair 1977; Anderson 1985).

There was little evidence that hunting pressure influenced KFI during the present study. The high mean KFIs for both species at Rushy Lagoon, the most heavily hunted study area, suggest that hunting may have some influence on body condition. It is reasonable to assume that if the level of wallaby hunting is high, then wallaby density will be low resulting in more resources for the surviving population (Caughley 1977). Such a response, using KFI, was reported by Kie *et al.* (1983) for white-tailed deer and Storch (1989) for chamois. It is possible that in 1988 the effect of the drought was such that it obscured any effect of hunting on KFI. In 1989 there was still little evidence of hunting pressure affecting body condition as a combined result of 1) greater quantity and quality of food due to good rainfall in late 1988 and 1989 and 2) reduced density due to low breeding success in 1988 (Section 5.4.4).

Other Effects on KFI

In addition to hunting and rainfall, there was evidence to suggest that low temperatures may also have an effect on KFI. Mean KFIs for Bennett's wallabies at Western Lakes showed a greater decrease between winter and summer than other study areas (note, no samples of Tasmanian pademelons were obtained from this study area). Western Lakes

occurs at the highest altitude and is subjected to the coldest temperatures (Section 2.3). It is believed that this greater decrease in mean KFIs between winter and summer is due to the delay in spring growth caused by low temperatures (J. Yates, unpublished data). Hence the period of food shortage between the end of winter and the onset of spring growth is greater at this study area than at the other lower altitude study areas.

4.4.3 Growth

Growth in terms of mean body weight was used to assess variation in long-term body condition between study areas. When resources are abundant animals tend to grow larger and faster (Risenhoover and Bailey 1988).

The short-term response in KFIs to rainfall was also apparent in the growth of wallabies. Wallabies in high rainfall areas attained greater weights than wallabies in low rainfall areas. As high rainfall areas in Tasmania show less variability in rainfall than low rainfall areas (Langford 1965), growth rates are less likely to be reduced as a result of food and water shortages.

Although rainfall was found to influence the growth of wallabies, it is unlikely to be the only factor involved. This may be demonstrated by the fact that mean body weights at Rushy Lagoon were among the highest of all study areas despite the fact that this study area had a medium level of rainfall. The greater growth of wallabies at Rushy Lagoon may be due to the effect of high hunting pressure which maintained wallaby numbers at low densities. Hence, there will be greater resources for those wallabies which survive hunting. Challies (1973) reported such a response by red deer in New Zealand. In areas where harvesting pressure was high, the deer of similar age were larger than those in areas where harvesting pressure was low.

4.5 SUMMARY

The aim of this chapter was to assess the body condition of Bennett's wallabies and Tasmanian pademelons and to determine whether hunting and rainfall influences body condition. The Kidney Fat Index (KFI) was used to assess the short-term response of wallabies to the quality of their environment and growth in body weight was used to assess the longer term response.

The underlying assumption of KFI, that kidney weight is proportional to body weight, was tested. This relationship was found to vary among age groups, seasons and study areas and should be taken into consideration in future studies. In the present study, the variation in the kidney weight to body weight relationship was not large enough to influence general trends in KFI.

The trends in KFI and growth were generally similar for both species. Adults had higher KFIs than juveniles because juveniles put most of their energy into growth and because they have not had time to deposit fat reserves. Females had higher KFIs than males and this can be attributed to the requirement by females for better condition to cope with the demands of pregnancy and lactation and because there are reproductive advantages for males to convert food resources into growth rather than into fat.

KFIs were higher in winter than in summer. This was, in part, due to food shortages at the end of winter and before the onset of spring growth. KFIs for adult females continued to decrease over spring and early summer due to the increasing demands of dependent young over this time. It was proposed that the continued decrease in KFI by males over spring and summer was due to time and energy spent on mating activities and, perhaps, seasonal periodicity in growth. Juveniles had lower KFIs in summer than in winter simply because they have not had time to deposit fat reserves.

Females which failed to breed had lower KFIs than those females which succeeded. This presumably reflects a strategy to conserve energy.

KFIs for Tasmanian pademelons were higher than those for Bennett's wallabies. This difference may be due to different strategies of fat deposition between the two species. However, the higher quality of diet consumed by Tasmanian pademelons suggests that the difference in KFI may reflect, in part, a difference in body condition.

Both the 1987/88 drought and variation in rainfall between study areas were found to influence KFIs. KFIs were lower in 1988 than in 1989 as a result of the drought. The drought appeared to have a greater affect on Bennett's wallaby KFIs than on Tasmanian pademelon KFIs possibly because of differences in diet. The drought had greater effect on KFIs in low rainfall areas than in high rainfall areas, as evidenced by a positive correlation between mean KFI and annual rainfall. In year following the drought there was no such correlation due to improved conditions at all study areas. The effect of rainfall on KFI during the drought was also reflected in the different growth rates of wallabies between study areas. In general, wallabies in high rainfall areas attained greater body weights than those in low rainfall areas. This was attributed to less variability in rainfall in high rainfall areas than in low rainfall areas and, hence, less food shortages.

The effects of hunting on KFI were largely masked by the drought. However, high growth rates and high levels of body condition at the most heavily hunted study area suggested that an increase in hunting pressure can lead to an increase in body condition.

CHAPTER 5

BREEDING

5.1 INTRODUCTION

The reproductive biology of Bennett's wallaby and the Tasmanian pademelon has been the subject of more research than any other aspect of their biology. For Bennett's wallaby, most of this research has been conducted on captive populations on the Australian mainland and in England as well as wild populations introduced to New Zealand. Most information on Tasmanian pademelon reproduction is based on captive populations in Tasmania. The main features of their pattern of reproduction are outlined below.

Bennett's wallaby is a seasonal breeder with a well defined period of births between late January and July with most births occurring in February and March. This period of births has been recorded in captivity (Merchant and Calaby 1981) and in wild populations in Tasmania (Curlewis 1989) and in New Zealand (Catt 1977). A similar seasonal period of births was reported in Whipsnade Park, England, albeit transposed six months (Fleming *et al.* 1983). The well-defined season of births exhibited by Bennett's wallaby differs from the mainland subspecies, the red-necked wallaby, in which births occur in all months of the year with a slight increase during summer (McEvoy 1970; Merchant and Calaby 1981). However, within the breeding season the lengths of the oestrous cycle and gestation period are similar for the two subspecies (Merchant and Calaby 1981). The gestation period is about 30 days and the length of the oestrous cycle is approximately 33 days.

The pattern of reproduction in Bennett's wallaby is unusual among macropods, being found in only one other species, the Tammar wallaby, *M. eugenii*. Both Bennett's wallaby and the Tammar wallaby have a post-partum oestrus and conception. The blastocyst is maintained in embryonic diapause as a result of lactation controlled quiescence during the

months of shortening day length and, unlike other macropods, there is a seasonal quiescence during the months of increasing day length (Tyndale-Biscoe, 1989). This has been achieved as a result of the corpus luteum becoming sensitive to prolactin during the months of increasing day length (McConnel *et al.* 1986; Hinds 1989).

In both subspecies the young typically remain in the pouch for approximately nine months (Catt 1977; Calaby 1983; Fleming *et al.* 1983). Hence, young leave the pouch in spring when food conditions are most favourable. The length of time during which young are suckled after leaving the pouch varies from three to eight months (Calaby 1983).

In captivity females of both subspecies first mate at an age of about 14 months and males begin to produce mature spermatozoa by about 19 months (Merchant and Calaby 1981). From studies of wild populations of Bennett's wallabies in New Zealand, Catt (1977) recorded that all males were mature by 21-22 months of age and females by 14-17 months of age. Catt (1977) also reported that females breeding for the first time usually give birth later in the breeding season than experienced females.

Reproduction in the Tasmanian pademelon conforms to the pattern reported for many other macropods (McCartney 1978; Rose and McCartney 1982a). Parturition is followed by mating and the embryo produced remains dormant until either suckling becomes intermittent near the end of pouch life or the young is lost.

The Tasmanian pademelon is a seasonal breeder with most births occurring in April, May and June. There is also a small peak of births in October, November and December. The average gestation length of 30.2 days is just shorter than the average length of the oestrus cycle of 30.3 days (Rose and McCartney 1982a). Removal of the pouch young results in activation of the blastocyst and the birth of a new young about 29 days later (Rose and McCartney 1982a). Pouch life is approximately 200 days, thus young usually leave the pouch in spring when conditions are most favourable. Young are usually weaned about one

month after leaving the pouch (Johnson and Rose 1983) and mature at 14-15 months of age (Rose and McCartney 1982a).

In captivity vacuation of the pouch by young pademelons coincides with parturition and post-partum mating (Rose and McCartney 1982a). However, in the wild, Rose and McCartney (1982a) recorded few births in spring/summer when young leave the pouch and they suggested that the viability of the blastocyst is decreased outside of the main breeding season. This also implies that female pademelons enter seasonal anoestrus during summer as seen in some populations of the quokka, *Setonix brachyurus* (Sharman 1955).

Field studies of the biology of macropods have indicated significant relationships between environmental conditions and reproduction (Russell 1974). One environmental condition which is often implicated as influencing reproduction is rainfall due to its effect on food quantity and quality.

Studies on red kangaroos, grey kangaroos and wallaroos have shown that low rainfall, particularly during drought, will delay the onset of maturity (Frith and Sharman 1964; Newsome 1965; Kirkpatrick and McEvoy 1966; Poole 1973; Shepherd 1987) and reduce the proportion of adults in breeding condition (Newsome 1964, 1965, 1966, 1973; Shepherd 1987). Furthermore, Russell and Richardson (1971) found differences in the period of births in wallaroo populations from New South Wales compared to the Northern Territory and this was attributed to differences in rainfall between the two locations and hence, differences in food supply.

There are few if any studies which have investigated the effect of hunting pressure on the reproduction of macropods. Indeed, studies of this type on other mammals are also scarce. Wilson and Roth (1967) found that hunting of common duiker, *Sylvicapra grimmia*, in East Zambia led to a decrease in the age at which animals matured and an increase in breeding success. This increase in breeding performance was attributed to an increase in resources for the surviving animals as a result of a decrease in density.

The aim of this chapter is to describe aspects of reproduction in wild populations of Bennett's wallabies and Tasmanian pademelons and to determine whether hunting and rainfall influence the reproductive pattern.

5.2 METHODS

Season of Births

Dates of birth were calculated by extrapolating back from the estimated ages of pouch young. The method of aging pouch young was given in Section 3.2. Dates of birth calculated in this manner are subject to an error that increases with time since birth. Whilst this is not expected to bias the results it will affect the estimates of variance.

In order to examine variation in the timing of births only pouch young collected after the end of the main period of birth and prior to the first month of pouch vacation were used. Back-aging young taken before or after this time period would bias the mean birth date earlier or later respectively.

Age at Maturity

Females

The reproductive status of females was assessed from pouch examination. They were classified as immature if their pouches were undeveloped with teats inverted or rudimentary. They were classified as reproductively mature if they had fully formed, invaginated pouches and everted teats.

Males

The combined weight of each testis (without scrotal sac) was used to assess the stage at which males became sexually mature. Several studies have shown that testes weight in

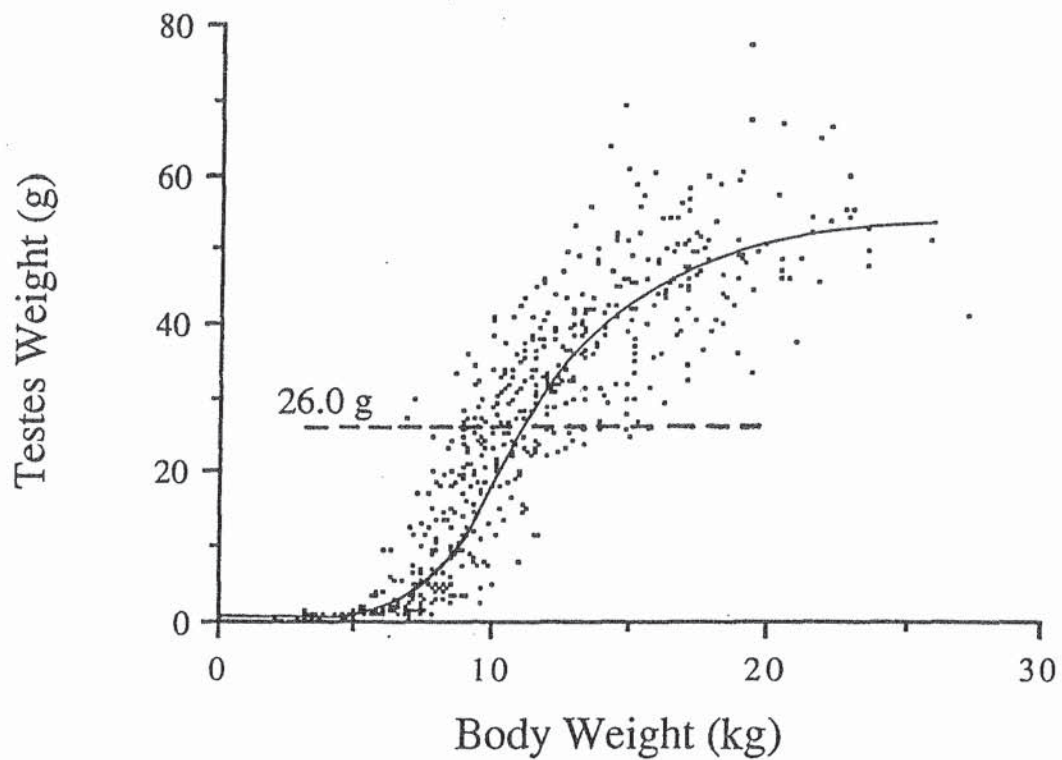
macropods increases rapidly just prior to the first occurrence of spermatozoa in the epididymis and with the onset of maturity (Frith and Sharman 1964; Sadlier 1965; Catt 1977). It should be noted that although testes weight can give an indication of when males are physiologically mature, it does not indicate when they are behaviourally mature. Nevertheless, the point at which testes weight rapidly increases provides a convenient measure for comparing age at maturity.

Testes weight was plotted against body weight for both species confirming the rapid increase in testes size relative to body weight observed by previous workers (Figure 5.1). Catt (1977) reported that 50% of male Bennett's wallabies were undergoing spermatogenesis at a testes weight of $23.8 \pm 3.23\text{g}$ and that this weight was approximately 50% of mature testes weight. On this basis 50% of mature testes weight for Bennett's wallaby was estimated from Figure 5.1 to be 26.0g. This falls within the range estimated by Catt (1977). Thus for the purposes of this study 26.0g was considered to be the testes weight at which male Bennett's wallabies mature. Those animals with a testes weight less than this threshold were classed as immature. Using these methods, a testes weight of 16.5g (Figure 5.1) was established as the weight at reproductive maturity for the Tasmanian pademelon.

Probit analysis

The median age at which 50% of animals matured was estimated using probit analysis (Finney 1952). Probit analysis is a method of regression analysis for estimating the amount of stimulus (in this case age or time) required to bring about a reaction (in this case reproductive maturity) in a given proportion of the population. This method has been most frequently used in toxicological studies where the aim is to determine the dose of chemical required to achieve a 50% mortality (LD50). However, this method is also widely used in fisheries research where it has been applied to determine maturity patterns (Fleming 1960). It has also been applied in mammal research to examine the season of births in ungulates (Caughley 1971b) and the age at maturity for the brushtail possum (Hocking 1981).

Bennett's Wallaby



Tasmanian Pademelon

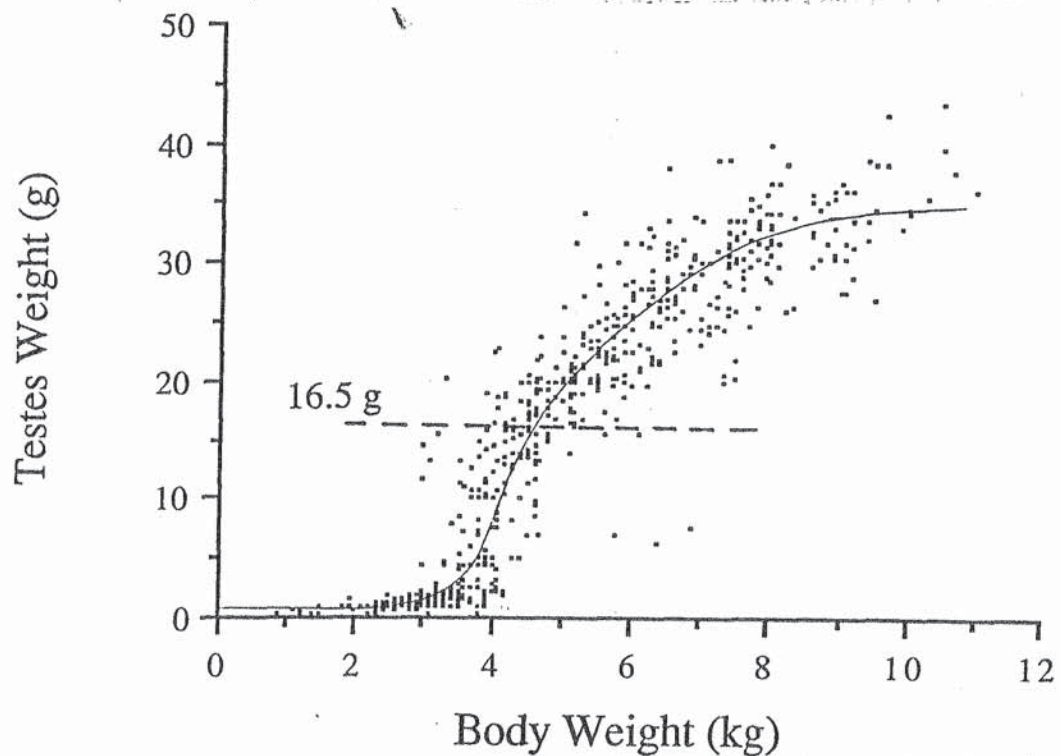


Figure 5.1 Estimation of mature testes weight for Bennett's wallaby (26.0g) and the Tasmanian pademelon (16.5g). The trend line was fitted by eye.

Probit analysis converts the sigmoidal form of a cumulative frequency distribution (in the present study the proportion of animals maturing in increasing age classes) to a straight line through a sequence of transformations which attempt to satisfy the assumptions of regression. A chi-squared test is then applied to ascertain how well the original observations fit the computed straight line. If there are no significant deviations it is then valid to compare the regression lines in the conventional manner.

It should be noted that the figures derived by this method for median age at maturity do not necessarily coincide with the actual ages at which any individuals matured. This is to be expected given the previously described seasonal nature of breeding. Nevertheless, the figures are useful as a means for allowing comparisons to be made.

Breeding Success

The proportion of mature females which reared a young to independence was used as a measure of breeding success. This measure of breeding success is a product of the proportion of mature females which gave birth and the survival of young to independence.

The following criteria were applied in determining whether female Bennett's wallabies had dependent young:

- (a) a young in the pouch from May to December, or
- (b) an enlarged lactating teat, from December to February indicating young which had left the pouch but were not weaned.

The following criteria were applied in determining whether female Tasmanian pademelons had dependent young:

- i) Autumn/Winter Born Young
 - (a) a young in the pouch during July and December or
 - (b) an enlarged lactating teat during December and January indicating young which had left the pouch but were not weaned.

ii) Spring/Summer Born Young

- (a) a young in the pouch during December and June.
- (b) an enlarged lactating teat during June and July indicating young which had left the pouch but were not weaned.

It should be noted that estimating the presence of pouch young this way will tend to over-estimate pouch young survival for two reasons. Firstly, young that are lost may be replaced after reactivation of blastocysts in diapause. This may occur at any time for Tasmanian pademelons but usually occurs only up until the winter solstice for Bennett's wallabies due to seasonal quiescence. Secondly, it cannot be determined from the lactating teat if the young were recently weaned or had recently died.

5.3 RESULTS

5.3.1 Season of Births

Between May 1988 and February 1990 a total of 234 Bennett's wallaby and 275 Tasmanian pademelon pouch young, which could be aged, were collected from all study areas. The season of births for each species is shown in Figure 5.2.

For Bennett's wallaby there was one season of births in late summer and autumn. The majority of births (80%) occurred in February and March. For the Tasmanian pademelon there were two distinct seasons of births; one from April to July (autumn/winter) and one from October to December (spring/summer). The number of births in each of these two periods is shown in Figure 5.2. The relative importance of each season of births can be obtained by comparing the proportion of mature females which gave birth in each season. A total of 95% of mature females gave birth in autumn/winter, compared to 61% in spring/summer (obtained from Section 5.3.4).

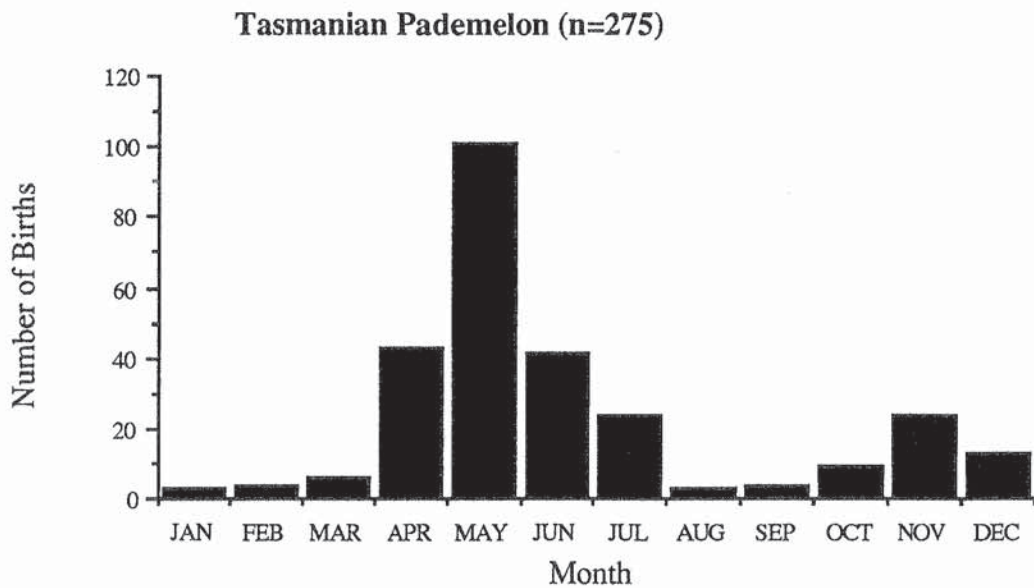
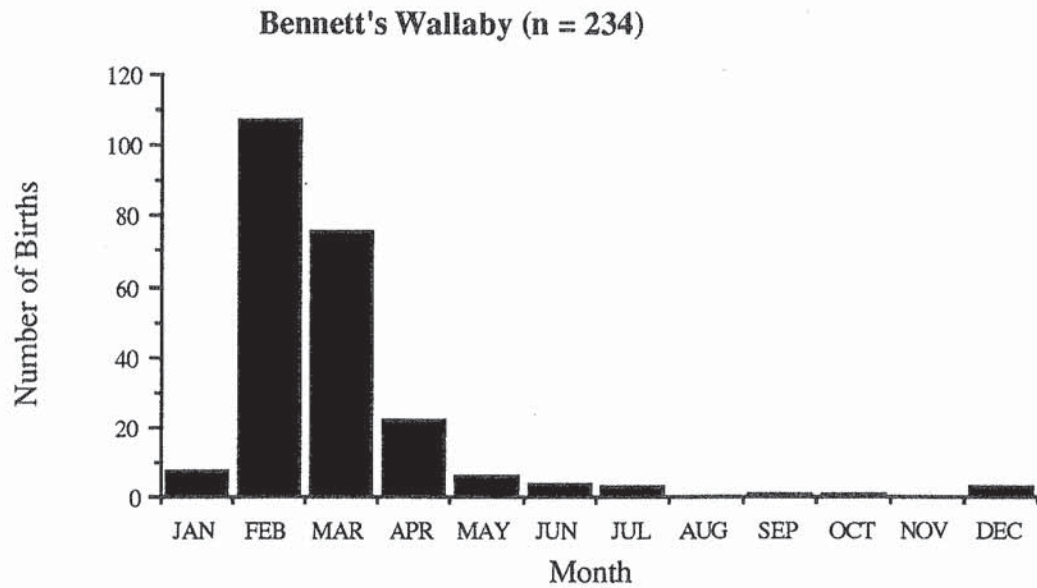


Figure 5.2 Total number of births recorded in each month for 1988 and 1989. The month of birth was determined by extrapolating back from the estimated age of pouch young. As sampling intensity was less in summer than in winter, the number of Tasmanian pademelon births in spring/summer was underestimated. 95% of mature females gave birth in autumn/winter compared with 61% in spring/summer.

Mean date of birth

The mean dates of birth for both species are given in Table 5.1. For the Tasmanian pademelon, the difference in mean date of birth between autumn/winter and spring/summer was approximately six months.

Table 5.1. Mean date of birth for Bennett's wallaby and the Tasmanian pademelon. Numbers in parentheses indicate sample size.

Species	Breeding Season	Mean Date of Birth
Bennett's wallaby	summer/autumn	27 February \pm 24 days (156)
Tasmanian pademelon	autumn/winter	26 May \pm 35 days (118)
	spring/summer	18 November \pm 28 days (49)

Variation in mean date of birth between years and study areas

For both species the mean dates of birth did not vary significantly between 1988 and 1989 (Table 5.2) or between study areas (Table 5.3).

The effect of hunting pressure and rainfall on mean date of birth was tested by grouping study areas into high (includes study areas with high and medium hunting pressure) and low hunting pressure, and low, medium and high rainfall. The levels of hunting pressure and rainfall at each study area are given in Chapter 2.

There was no evidence that hunting pressure or rainfall influenced mean date of birth for Bennett's wallaby (Hunting: $F_{(1,188)}=0.90$, $p>0.5$; Rainfall: $F_{(2,187)}=0.22$, $p>0.5$) or the Tasmanian pademelon in autumn/winter (Hunting: $F_{(1,106)}=1.65$, $p>0.5$; Rainfall: $F_{(2,105)}=2.28$, $p>0.2$) or spring/summer (Hunting: $F_{(1,46)}=0.40$, $p>0.5$; Rainfall: $F_{(2,45)}=3.36$, $p>0.1$).

Table 5.2 Comparison of mean date of birth in 1988 and 1989 for Bennett's wallaby and the Tasmanian pademelon. Numbers in rounded parentheses indicate sample size. ns=not significant.

	1988	1989
Bennett's wallaby	27 February \pm 22 days (79)	27 February \pm 25 days (77)
	$F_{[1,154]}=0.00^{ns}$	
Tasmanian pademelon		
Autumn/winter	3 June \pm 39 days (33)	23 May \pm 25 days (85)
	$F_{[1,116]}=2.29^{ns}$	
Spring/Summer (24)	24 November \pm 27 days (25)	16 November \pm 27 days
	$F_{[1,47]}=0.93^{ns}$	

Table 5.3: Results of One Way ANOVAs comparing mean date of births between study areas for Bennett's wallaby and the Tasmanian pademelon. ns=not significant.

Species	Season	Year	F-test	Significance
Bennett's wallaby	Feb-Mar	1988	$F_{[7,78]}=0.68$	ns
		1989	$F_{[7,96]}=0.69$	ns
Tasmanian pademelon	Apr-Jul	1988	$F_{[3,26]}=0.63$	ns
		1989	$F_{[7,70]}=1.29$	ns
	Oct-Dec	1988	$F_{[2,19]}=1.21$	ns
		1989	$F_{[4,21]}=1.37$	ns

Effect of Breeding History on Mean Date of Birth

In Table 5.4 the mean date of birth of Bennett's wallabies is compared between females which gave birth for the first time (first-time breeders) and females which have given birth more than once (experienced breeders). First-time breeders gave birth at a significantly later date than experienced breeders.

Table 5.4 Effect of breeding history on mean date of birth for Bennett's wallaby. Results for 1988 and 1989 are combined. Numbers in rounded parentheses indicate sample size.

Mother's Breeding Status	Mean Date of Giving Birth
Experienced breeder	22 February \pm 22 days (131)
First-time breeder	1 April \pm 37 days (31)
	$F_{[1,60]}=53.1, p<0.001$

Tasmanian pademelons were divided into 3 groups depending on their breeding history:

- Group 1 first-time breeders.
- Group 2 experienced breeders which showed no evidence of raising a young in the previous breeding season.
- Group 3 experienced breeders which showed evidence of raising a young in the previous breeding season.

The mean date of birth for each of these groups are compared in Table 5.5. The spring/summer data for 1988 and 1989 have been combined due to small sample sizes. In all comparisons, Group 3 females gave birth at a significantly later date than Group 2 females. In autumn/winter, Group 1 females gave birth at a significantly later date than Group 2 females but not Group 3 females. However, in spring/summer, Group 1 females gave birth

significantly earlier than Group 3 females but not Group 2 females. Furthermore, Group 1 females gave birth significantly later in 1988 than in 1989.

Table 5.5 Effect of breeding history on mean date of birth for Tasmanian pademelons. The data for spring/summer 1988 and 1989 were combined. Group 1: first-time breeders, Group 2: experienced breeders which showed no evidence of raising a young in the previous breeding season, Group 3: experienced breeders which showed evidence of raising a young in the previous breeding season. Numbers in rounded parentheses indicate sample size. ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Autumn/Winter 88	Autumn/Winter 89	
Group 1	3 July \pm 21 days (5)	26 May \pm 29 days (18)	F [1,21]=7.14*
Group 2	29 April \pm 14 days (14)	7 May \pm 24 days (41)	F [1,53]=1.09 ^{ns}
Group 3	29 June \pm 31 days (13)	14 June \pm 35 days (26)	F [1,37]=1.74 ^{ns}
	F [2,29]=23.26***	F [2,82]=14.05***	
Spring/Summer			
Group 1		31 Oct \pm 32 days (7)	
Group 2		1 Nov \pm 25 days (8)	
Group 3		29 Nov \pm 22 days (34)	
		F [2,46]=7.01**	

5.3.2 Sex Ratio of Pouch Young

A total of 234 Bennett's wallaby and 282 Tasmanian pademelon pouch young, which could be sexed, were collected from all study areas between May 1988 and February 1990.

The sex ratio of pouch young did not differ significantly from parity for Bennett's wallaby (M/F=0.83, $\chi^2=2.07$, $p=0.150$) or for the Tasmanian pademelon (M/F=1.04, $\chi^2=0.091$, $p=0.763$)

Comparison between years

Only study areas which were sampled in both years were used for this comparison. No significant differences in the sex ratio of pouch young were found between 1988 and 1989 for Bennett's wallaby ($\chi^2=0.02$, $df=1$, $p=0.887$) or the Tasmanian pademelon ($\chi^2=0.33$, $df=1$, $p=0.568$).

Comparison between study areas

No significant differences in sex ratio of pouch young were found between study areas for Bennett's wallaby ($\chi^2=10.02$, $df=12$, $p=0.614$) or the Tasmanian pademelon ($\chi^2=3.92$, $df=10$, $p=0.951$).

The effect of hunting and rainfall on the sex ratio of pouch young was tested by grouping study areas into areas of high (high+medium) and low hunting pressure, and low, medium and high rainfall. Only study areas sampled in both years were used for this comparison. There was no evidence of these factors influencing the sex ratio of pouch young for Bennett's wallaby (Hunting: $\chi^2=0.00$, $df=1$, $p=1$; Rainfall: $\chi^2=3.18$, $df=2$, $p=0.203$) or the Tasmanian pademelon (Hunting: $\chi^2=0.359$, $df=1$, $p=0.546$; Rainfall: $\chi^2=1.203$, $df=2$, $p=0.548$).

Comparison between different ages of pouch young

A comparison of sex ratios of Bennett's wallaby pouch young before and after 120 days of age is shown in Table 5.6. In 1988 the sex ratio of pouch young less than 120 days of age did not differ from parity ($\chi^2=0.35$, $df=1$, $p>0.5$). By comparison, the sex ratio of pouch

young greater than 120 days of age was biased towards females ($\chi^2=5.12$, $df=1$, $p<0.05$). This difference in sex ratio between the two age groups was statistically significant ($\chi^2=4.03$, $df=1$, $p<0.05$). In 1989 the sex ratios did not differ from parity for pouch young less than 120 days of age or greater than 120 days of age ($\chi^2=0.57$, $df=1$, $p>0.5$).

Table 5.6 Sex ratios of Bennett's wallaby pouch young less than and greater than 120 days of age.

Age (days)	M	1988 F	M/F	M	1989 F	M/F
0-120	25	21	1.19	17	24	0.71
120-280	17	33	0.52	47	50	0.94

The sex ratios of Tasmanian pademelons did not differ between those pouch young which were less than 120 days of age and those greater than 120 days of age in 1988 ($\chi^2=0.46$, $df=1$, $p>0.75$) or 1989 ($\chi^2=0.25$, $df=1$, $p>0.75$) (Table 5.7).

Table 5.7 Sex ratios of Tasmanian pademelon pouch young less than and greater than 120 days of age.

Age (days)	M	1988 F	M/F	M	1989 F	M/F
0-120	43	38	1.13	59	60	0.98
120-240	7	7	1.00	31	30	1.03

5.3.3 Age at Maturity

The proportion of male and female Bennett's wallabies which were mature in each age class is shown in Figure 5.4. For both species, females matured earlier than males. Median age at maturity for male Bennett's wallabies was 28 months (95% confidence limits (CL): 27, 29) which was significantly older than 21 months (95% CL: 20, 22) for females (slope: $F_{(1,11)}=3.220$, $p=0.100$; elevation: $F_{(1,11)}=9.564$, $p=0.010$).

Median age at maturity for Tasmanian pademelon males was 17 months (95% CL: 16.2, 17.3) which was significantly older than 13 months (95% CL: 12.8, 13.8) for females (slope: $F_{(1,7)}=0.880$, $p=0.613$; elevation: $F_{(1,7)}=13.923$, $p=0.007$).

Comparison between years

The median age at maturity for each species was calculated for the summer (Nov-Feb) and winter sampling periods (May-Aug) in 1988 and 1989. Only study areas which were sampled in each season were used in this analysis.

Significant differences in age at maturity were found between seasons for males of both species (Tables 5.8 and 5.9). Males matured at an older age during winter 1988 than during the other sampling periods. Although females of both species matured at an older age in winter 1988 this difference was not significant.

Comparison between study areas

Age at maturity varied significantly between study areas for both sexes of each species (Tables 5.10 and 5.11). The pattern of variation between study areas was similar for both species and both sexes. Wallabies occurring in study areas subjected to high hunting pressure matured earlier than those in study areas subjected to low hunting pressure.

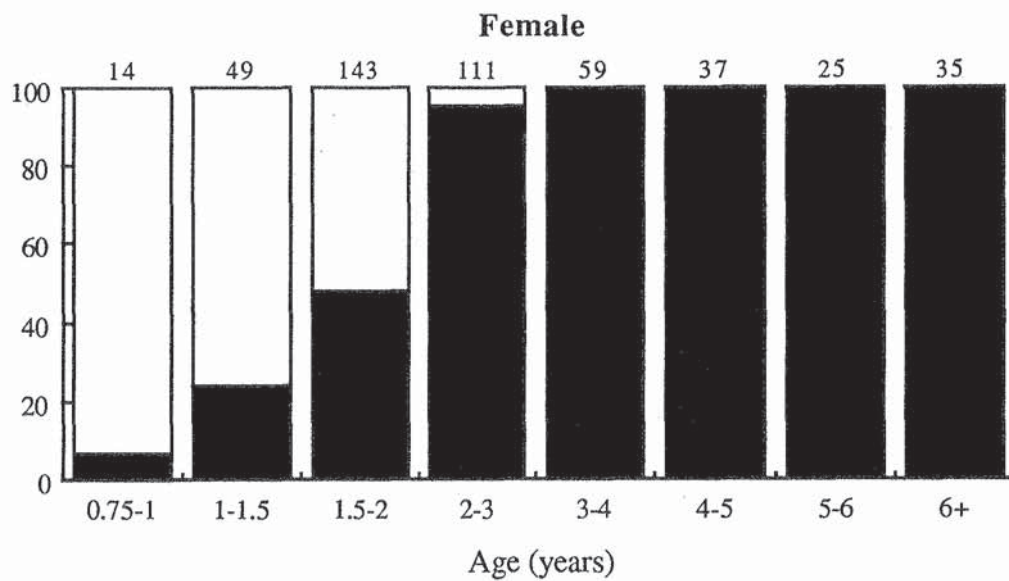
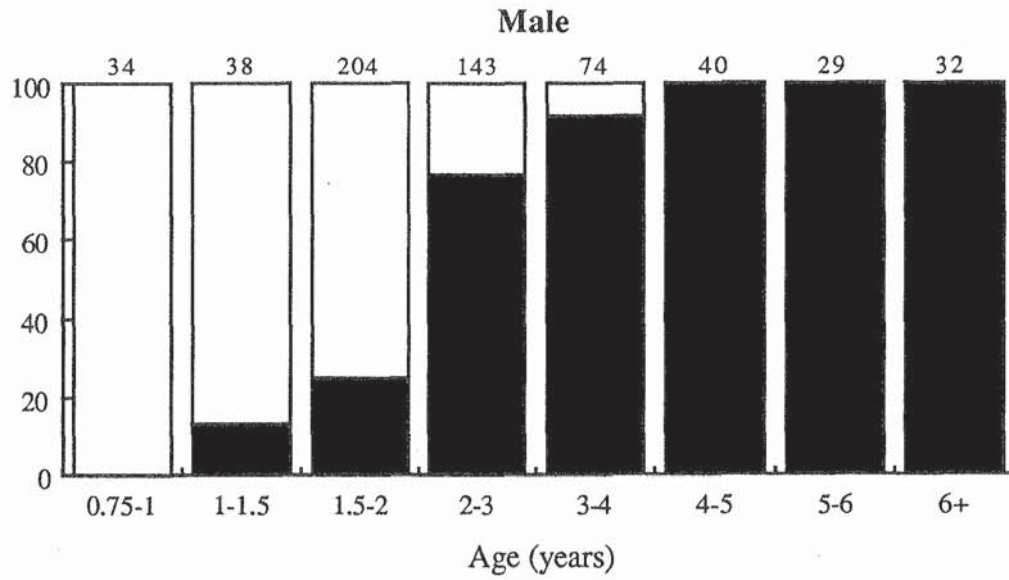


Figure 5.4 Proportion of mature Bennett's wallabies in each age class (shaded). Sample sizes are given at the top of each column.

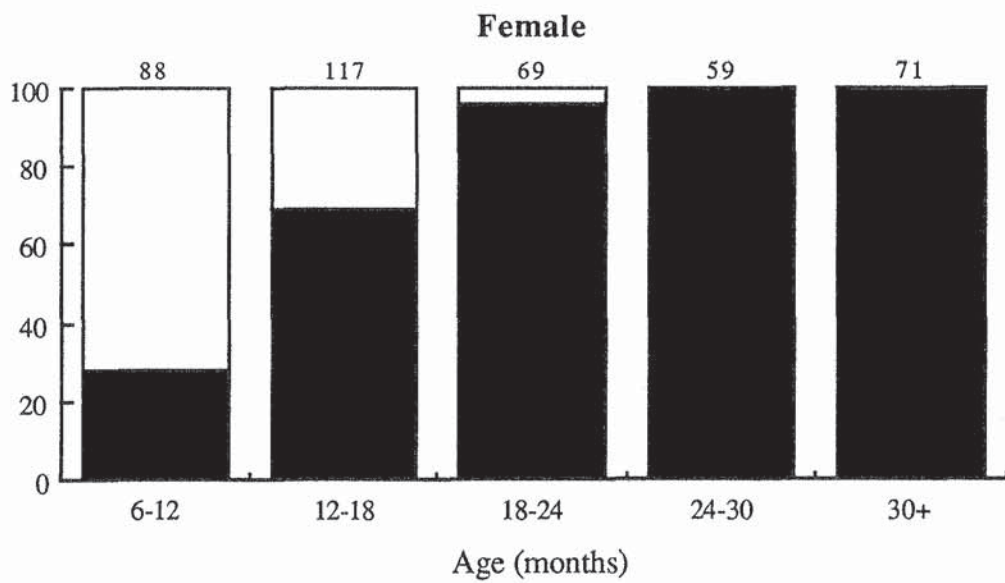
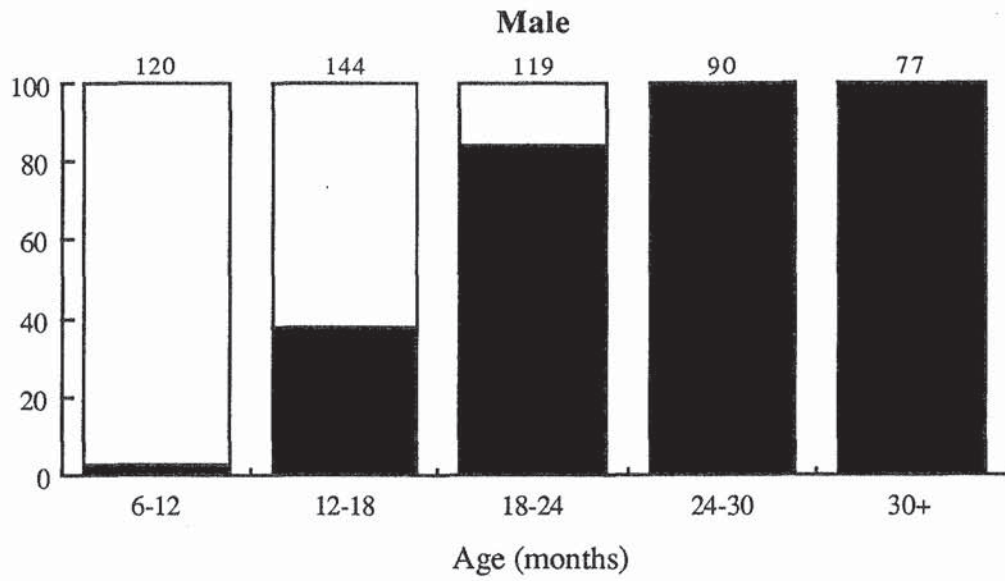


Figure 5.5 Proportion of mature Tasmanian pademelons in each age class (shaded). Sample sizes are given at the top of each column.

Table 5.8 Comparison of median age (months) at maturity between sampling seasons for Bennett's wallaby. Significant differences were found between sampling seasons for males (slope: $F_{(3,22)}=1.761$, $p=0.188$; elevation: $F_{(3,22)}=9.771$, $p=0.000$) but not for females (slope: $F_{(3,23)}=1.811$, $p=0.177$; elevation: $F_{(3,23)}=1.824$, $p=0.170$). n=sample size. 95% CL=95% confidence limits.

Season	Male				Female			
	n	Median	Age	95% CL	n	Median	Age	95% CL
Winter 1988	115	37	34	42	128	21	18	24
Summer 1988	94	24	21	27	70	18	15	21
Winter 1989	110	24	22	27	92	18	15	20
Summer 1989	92	22	21	24	60	20	16	23

Table 5.9 Comparison of median age (months) at maturity between sampling seasons for the Tasmanian pademelon. Significant differences were found between sampling seasons for males (slope: $F_{(3,15)}=1.243$, $p=0.338$; elevation: $F_{(3,15)}=4.960$, $p=0.014$) but not for females (slope: $F_{(3,15)}=1.092$, $p=0.391$; elevation: $F_{(3,15)}=1.243$, $p=0.330$). n=sample size. 95% CL=95% confidence limits.

Season	Male				Female			
	n	Median	Age	95% CL	n	Median	Age	95% CL
Winter 1988	87	19	18	21	88	14	13	15
Summer 1988	64	16	15	17	39	12	11	14
Winter 1989	111	16	14	17	85	12	8	14
Summer 1989	60	15	14	17	37	12	8	14

Table 5.10 Comparison of median age (months) at maturity between study areas for Bennett's wallaby. Significant differences occurred between study areas for males (slope: $F_{(7,47)}=1.80$, $p=0.113$; elevation: $F_{(7,47)}=5.350$, $p=0.000$) and females (slope: $F_{(7,47)}=1.398$, $p=0.236$; elevation: $F_{(7,47)}=6.832$, $p=0.000$). n=sample size. 95% CL=95% confidence limits.

Study Area	Hunting	Rainfall	n	Median Age	95% CL	
MALES						
Maria Island	Very Low	Low	26	36	24	46
Western Lakes	Low	High	72	28	25	30
Buckland	Low	Low	45	27	23	32
Florentine Valley	Low	High	87	26	23	29
Soldiers Marsh	Low	Medium	54	26	22	30
View Point	Medium	Low	39	23	20	29
Lagoon of Islands	High	Medium	68	24	21	27
Rushy Lagoon	Very High	Medium	70	18	14	20
FEMALES						
Maria Island	Very Low	Low	31	29	24	35
Western Lakes	Low	High	51	21	18	24
Buckland	Low	Low	37	24	20	31
Florentine Valley	Low	High	86	23	21	25
Soldiers Marsh	Low	Medium	70	23	21	26
View Point	Medium	Low	40	21	17	25
Lagoon of Islands	High	Medium	56	19	14	21
Rushy Lagoon	Very High	Medium	89	13	9	15

Table 5.11 Comparison of median age (months) at maturity between study areas for the Tasmanian pademelon. Significant differences occurred between study areas for males (slope: $F_{(6,27)}=9.150$, $p=0.000$) and females (slope: $F_{(5,27)}=0.668$, $p=0.655$; elevation: $F_{(7,47)}=8.817$, $p=0.000$). n=sample size. 95% CL=95% confidence limits.

Study Area	Hunting	Rainfall	n	Median Age	95% CL
MALES					
Granville Harbour	Low	High	99	18	16 19
Florentine Valley	Low	High	65	19	16 20
Buckland	Low	Low	32	16	13 19
Soldiers Marsh	Low	Medium	40	16	14 18
View Point	Medium	Low	45	17	15 19
Lagoon of Islands	High	Medium	96	15	14 16
Rushy Lagoon	Very High	Medium	73	14	13 16
FEMALES					
Granville Harbour	Low	High	59	16	14 18
Florentine Valley	Low	High	73	16	14 18
Buckland	Low	Low	30	14	12 19
Soldiers Marsh	Low	Medium	39	14	12 17
View Point	Medium	Low	48	12	6 14
Lagoon of Islands	High	Medium	77	11	9 13
Rushy Lagoon	Very High	Medium	74	11	6 12

The effect of hunting pressure on age at maturity was tested using Kendall's Rank Correlation Coefficient (Tau). For both sexes of both species there was a significant negative correlation (Table 5.12). Hence, as hunting pressure increased, the age at maturity decreased.

The effect of rainfall on age at maturity was tested using correlation analysis. There were no significant correlations between rainfall and age at maturity for either species (Table 5.13).

Table 5.12. Correlation between median age at maturity and hunting pressure for Bennett's wallaby and the Tasmanian pademelon. n=number of study areas

Species	Sex	n	Tau	z	Significance
Bennett's wallaby	male	8	-0.821	2.843	p=0.002
	female	8	-0.878	3.042	p=0.001
Tasmanian pademelon	male	7	-0.635	2.003	p=0.023
	female	7	-0.852	2.687	p=0.004

Table 5.13. Correlation between median age at maturity and rainfall for Bennett's wallaby and the Tasmanian pademelon. n=number of study areas. ns=not significant.

Species	Sex	n	R	F-test	Significance
Bennett's wallaby	male	8	-0.06	F (1,6) = 0.022	ns
	female	8	-0.16	F (1,6) = 0.170	ns
Tasmanian pademelon	male	7	-0.31	F (1,5) = 4.214	ns
	female	7	-0.48	F (1,5) = 4.715	ns

5.3.4 Breeding Success

Bennett's wallaby

The proportion of mature females with dependent young from May to February is shown in Table 5.14. The data from both years, all study areas and adjacent months have been pooled. The proportion of mature females with dependent young after the breeding period in February-April was 98%. This proportion dropped to 91% by the end of pouch life (Nov-Dec) and then dropped to 68% after the young left the pouch but were still dependent on the mother (Jan-Feb).

Table 5.14 The proportion of mature female Bennett's wallabies with dependent young from May to February. Data are pooled over both years and all study areas.

Month	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Jan-Feb
Number of mature females	84	111	60	85	47
Number of females with dependent young	82	101	53	77	32
% of females with dependent young	98	91	88	91	68

Comparison between years

The proportion of mature females with dependent young for each year of sampling is shown in Table 5.15. With the exception of the January-February period, no significant differences were found between sampling periods. This indicates that survival of dependent young until pouch vacation did not differ between years. However, the survival of dependent young between pouch vacation and weaning was significantly lower in 1988 than in 1989.

Table 5.15 The proportion of mature female Bennett's wallabies with dependent young in 1988 and 1989. The data from all study areas are pooled. Numbers in parentheses indicate number of mature females. ns=not significant

Months	Females with Dependent Young (%)		χ^2	Significance
	1988	1989		
May-Jun	97 (62)	100 (22)	0.002	ns
Jul-Aug	91 (47)	91 (64)	0.032	ns
Sep-Oct	86 (7)	89 (53)	0.157	ns
Nov-Dec	89 (38)	91 (47)	0.003	ns
Jan-Feb	45 (22)	88 (25)	4.980	p=0.026

Comparison between study areas

It was not possible to compare the proportion of mature females with dependent young between study areas using the two-monthly sampling periods because of small sample sizes. Hence, the proportion of mature females with dependent young was calculated over all months. Only study areas sampled during winter and summer of both years were compared.

The proportion of mature females with dependent young at each study area is given in Table 5.16. There was a significant difference in the proportion of mature females with dependent young between study areas ($\chi^2=18.83$, $df=8$, $p=0.016$). This difference was due to a lower proportion of mature females with dependent young at Western Lakes. There was no significant difference in the proportion of mature females with dependent young between the other study areas ($\chi^2=3.37$, $df=7$, $p=0.85$).

Table 5.16 The proportion of mature female Bennett's wallabies with dependent young at each study area. Western Lakes was significantly different from the other study areas ($\chi^2=18.83$, $df=8$, $p=0.016$).

Study Area	Females with Dependent Young (%)	Number of Mature Females
View Point	94	36
Buckland	93	28
Rushy Lagoon	95	93
Soldiers Marsh	90	42
Lagoon of Islands	89	54
Florentine Valley	89	53
Western Lakes	72	43

The effect of hunting and rainfall on the proportion of mature females with dependent young was tested by grouping study areas into areas subjected to high (high + medium) and low hunting pressure, and low, medium and high rainfall. Western Lakes was not included in the comparison as it was shown to be significantly different from the other study areas.

The proportion of mature females with dependent young was significantly higher in study areas subjected to high hunting pressure in 1988 but not in 1989 (Table 5.17). The proportion of females with dependent young did not vary between areas of different rainfall ($\chi^2=9.45$, $df=5$, $p=0.1$).

Table 5.17 Effect of hunting pressure on the proportion of mature female Bennett's wallabies with dependent young in 1988 and 1989 ($\chi^2=14.16$, $df=3$, $p=0.003$). Numbers in parentheses indicate number of mature females.

Hunting Pressure	Females with Dependent Young (%)	
	1988	1989
High	95 (110)	92 (73)
Low	78 (41)	96 (82)

Comparison between age groups

Significant differences in the proportion of mature females with dependent young were found between different age groups ($\chi^2=18.60$, $df=5$, $p=0.0023$) (Table 5.18). A total of 72% of all mature females which failed to raise a young to independence were first-time breeders. Females over 6 years of age accounted for 20% of all unsuccessful attempts to rear a young. Examination of tooth wear suggested that those animals over six years of age which failed to breed were amongst the oldest animals in this age class.

Table 5.18. Effect of age on the proportion of mature female Bennett's wallabies with dependent young ($\chi^2=18.60$, $df=5$, $p=0.002$). Numbers in parentheses indicate the number of mature females.

Age Class (years)	Females with Dependent Young (%)	
1-2	81	(84)
2-3	88	(106)
3-4	100	(61)
4-5	95	(60)
5-6	100	(16)
6+	87	(60)

Tasmanian pademelon

The proportion of mature females with dependent young from May to February for autumn/winter born young is given in Table 5.19. The data from both years, all study areas and adjacent months have been pooled. The proportion of mature females with dependent young in May-June was 95%. This proportion dropped to 88% by the end of pouch life (Nov-Dec) and then to 77% after the young left the pouch but were still dependent on the mother (Jan-Feb).

The proportion of mature females with dependent young for spring/summer born young is given in Table 5.20. The data from both years and all study areas have been pooled. Sample sizes for spring/summer born young were small, hence it was necessary to group samples taken over the periods of December-February and May-July. The proportion of mature females with dependent young dropped from 61% in the December-February period to 36% in the May-July period.

Comparison between years

For females which gave birth in autumn/winter, the proportion of mature females with dependent young for each year of sampling is shown in Table 5.21. The proportion of mature females with dependent young was significantly lower in 1988 than in 1989.

For females which gave birth in spring/summer, the proportion of mature females with dependent young for each year of sampling is shown in Table 5.22. The proportion of mature females with dependent young in May-July 1987/88 was significantly lower than in May-July 1988/89. The proportion of mature females with dependent young in December-February did not differ between 1988/89 and 1989/90.

Table 5.19 The proportion of mature female Tasmanian pademelons with dependent young from May to February. The data are for autumn/winter born young and are pooled over both years and all study areas.

Month	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Jan-Feb
Number of mature females	40	120	60	69	31
Number of females with dependent young	38	112	60	61	24
% of females with dependent young	95	93	100	88	77

Table 5.20 The proportion of mature female Tasmanian pademelons with dependent young from December-February to May-July. The data are for spring/summer born young and are pooled over both years and all study areas.

Month	Dec-Feb	May-Jul
No of mature females	72	138
Number of females with dependent young	44	50
% of females with dependent young	61	36

Table 5.21 The proportion of mature female Tasmanian pademelons with dependent young in 1988 and 1989. The data are for autumn/winter born young and are pooled over all study areas. Values in parentheses indicate the number of mature females. ns=not significant.

Months	Females with Dependent Young (%)		χ^2	Significance
	1988	1989		
May-Jun	100 (21)	89 (19)	2.33	ns
Jul-Aug	83 (30)	97 (90)	4.46	p=0.035
Sep-Oct	100 (10)	100 (50)	0.00	ns
Nov-Dec	87 (15)	96 (54)	0.62	ns
Jan-Feb	71 (17)	86 (14)	1.00	ns
Nov-Feb	78 (32)	94 (68)	5.69	p=0.017

Table 5.22 The proportion of mature female Tasmanian pademelons with dependent young in 1988 and 1989. The data are for spring/summer born young and are pooled over all study areas. Numbers in parentheses indicate the number of mature females. ns=not significant.

Months	Females with Dependent Young (%)		χ^2	Significance
	1988	1989		
Dec-Feb ^a	62 (27)	60 (45)	0.06	ns
May-Jul	12 (42)	47 (96)	15.47	p=0.0001

^a Years 1988 and 1989 refer to 1988/89 and 1989/90 respectively

Comparison between study areas

Because of the small sample size of spring/summer born young, comparison of the proportion of mature females with dependent young between study areas is only based on autumn/winter born young.

No differences in the proportion of mature females with dependent young were found between study areas ($\chi^2=12.12$, $df=9$, $p=0.21$).

The effect of hunting and rainfall on the proportion of mature females with dependent young was tested by grouping study areas into areas subjected to high (high + medium) and low hunting pressure, and low, medium and high rainfall. Only study areas sampled in both years were used. The proportion of mature females with dependent young was significantly higher in study areas subjected to high hunting pressure in 1988 but not in 1989 (Table 5.23). The proportion of females with dependent young did not vary between rainfall areas ($\chi^2=10.72$, $df=5$, $p=0.06$).

Table 5.23 Effect of hunting pressure on the proportion of mature female Tasmanian pademelons with dependent young in 1988 and 1989 ($\chi^2=8.48$, $df=3$, $p=0.04$). The data are for autumn/winter born young. Numbers in parentheses indicate the number of mature females.

Hunting Pressure	Females with Dependent Young (%)	
	1988	1989
High	94 (35)	99 (77)
Low	86 (50)	94 (49)

Comparison between age classes

Significant differences in the proportion of mature females with dependent young were found between different age groups (Table 5.24) ($\chi^2=10.50$, $df=4$, $p=0.0329$). A total of 50% of all mature females which failed to raise a young to independence were first-time breeders. Females over 30 months of age accounted for the remaining 50% of all unsuccessful attempts to rear a young. Examination of tooth wear suggested those animals over 30 months of age which failed to breed were amongst the oldest animals in this age class.

Table 5.24 Effect of age on the proportion of mature female Tasmanian pademelons with dependent young ($\chi^2=10.50$, $df=4$, $p=0.0329$). The data are for autumn/winter born young. Numbers in parentheses indicate the number of mature females.

Age Class (months)	Females with Dependent Young (%)	
6-12	88	(25)
12-18	94	(81)
18-24	97	(64)
24-30	100	(59)
30+	88	(86)

5.4 DISCUSSION

5.4.1 Season of Births

Bennett's wallabies were born in late summer and autumn with 80% of births occurring in February and March. This season of births conforms to that described by other authors for wild populations in Tasmania (Curlewis 1989), New Zealand (Catt 1977) and Britain (Fleming *et al.* 1983), and captive populations in Canberra (Merchant and Calaby 1981).

Females breeding for the first time gave birth later than experienced breeders. This can be attributed to the requirement of first-time breeders to come into oestrus, mate and give birth 30 days later. Experienced breeders usually carry a blastocyst in diapause from their previous post-partum mating and, hence, will give birth earlier. This difference in the timing of giving birth between first-time and experienced breeders has also been recorded for Bennett's wallabies in New Zealand (Catt 1977).

There was no variation in mean date of birth of Bennett's wallabies between years or between study areas, nor was there evidence that hunting pressure or rainfall influenced the timing of births. This result supports the conclusion by Tyndale-Biscoe (1989) that the highly seasonal pattern of reproduction in Bennett's wallaby is irreversible. This pattern of reproduction appears not to vary even when animals have been held for many years in captivity where nutritional conditions are likely to favour continuous breeding.

In contrast, Tasmanian pademelon births were recorded in all months, but with two distinct periods of birth. One was in autumn/winter with 95% of mature females giving birth and the other was in spring/summer with 61% of mature females giving birth. In the autumn/winter period 85% of births occurred in April, May and June. In spring/summer, 81% of births occurred in October, November and December.

Only one other study, Rose and McCartney (1982a), has described the breeding season of the Tasmanian pademelon. They found that the Tasmanian pademelon was a seasonal breeder with most births occurring in April, May and June. They also noted that some young were born in summer. No information was given on the timing of their sampling, but it is assumed that insufficient sampling over summer resulted in few births being recorded.

It was found that mean date of birth varied between female Tasmanian pademelons depending upon their previous breeding history. If an experienced breeder failed to raise a young to independence from the previous season, she would be ready to mate and give birth early in the next season. Experienced breeders which were successful in raising a young from the previous season must wait until the young vacate the pouch before they either mate or give birth after the reactivation of a blastocyst which was in diapause.

In autumn/winter, first-time breeders gave birth a month later than experienced breeders which failed to raise a young over the previous breeding season. This can be explained by the fact that female pademelons take 13 months to mature and hence cannot give birth until late in the breeding season. In spring/summer, the mean date of birth did not differ between these two groups of females. The cause of this lack of difference in spring/summer is unclear but may be due to the small number of females sampled with these two breeding histories ($n=7$ for the former and $n=8$ for the latter).

There was no evidence that hunting pressure or variation in rainfall between study areas influenced the timing of births in the Tasmanian pademelon. However, first-time breeders gave birth significantly later in 1988 than in 1989 and this corresponds with the finding that age at maturity was older in 1988 than in 1989 (see Section 5.4.3). This delay in attaining maturity and, hence, giving birth was probably a result of lower levels of body condition and slower growth during the drought of 1987/88. This is discussed further in Section 5.4.3.

5.4.2 Sex Ratio of Pouch Young

The sex ratio of Bennett's wallaby pouch young was biased towards females but it was not significantly different from parity ($M/F=0.83$, $n=234$). Although most previous studies of the sex ratios in Bennett's wallaby have not shown significant variation from parity, virtually all have shown a bias towards males (Table 5.24). Indeed, combining the results of these previous studies resulted in a sex ratio significantly biased towards males. In contrast, the sex ratio reported in the present study was significantly different from the combined sex ratio of previous studies ($\chi^2=6.2$, $df=1$, $p=0.013$).

In a preliminary review of sex ratios in macropods, Johnson (1989d) found that several species, including Bennett's wallaby, had sex ratios biased towards males and suggested that this was associated with male-biased dispersal. Johnson (1989d) argued that in producing more male offspring, mothers can reduce competition from their philopatric daughters. In contrast, Stuart-Dick and Higginbottom (1989) reported that male red-necked wallabies, as well as male eastern grey kangaroos, were more likely to be conceived when the climate was favourable, or had been favourable for several months prior to conception. This finding supports the Trivers-Willard Hypothesis (Trivers and Willard 1973) that males are produced to take advantage of good environmental conditions since males' expected lifetime reproductive success is likely to be more strongly influenced by early growth rate and physical condition than is that of females.

The results of the present study tend to support Stuart-Dick and Higginbottom (1989) as more females were produced during poor environmental conditions, and this was linked with poor body condition of the mothers (Chapter 4). However, unlike the results of Stuart-Dick and Higginbottom (1989), the sex ratio reported in the present study did not differ from parity at birth. The proportion of males decreased after an age of 120 days and, therefore, cannot be construed to support the Trivers-Willard hypothesis as the male-biased mortality may be due to the greater demands of males for growth (Clutton-Brock *et al.* 1985).

Table 5.24. Previously published sex ratios for Bennett's and red-necked wallabies.
n=sample size. ns=not significant.

Source	Location	M/F (n)	χ^2	Signif.
Bennett's wallaby				
Present Study	Tasmania	0.83 (234)	2.07	ns
Catt (1977)	New Zealand	1.33 (56)	1.14	ns
Fleming <i>et al.</i> (1983)	Britain	1.60 (104)	5.54	p=0.020
Merchant and Calaby (1981)	Canberra	1.17 (39)	0.23	ns
Red-necked wallaby				
Merchant and Calaby (1981)	Canberra	0.79 (34)	0.47	ns
Johnson (1986)*	New South Wales	1.00 (82)	0.00	ns
Stuart-Dick and Higginbottom (1989)*	New South Wales	1.35 (134)	2.99	ns
Subspecies Combined				
Johnson (1989d)**		1.22 (615)	6.05	p=0.010
All the above data except present study		1.19 (904) [†]	7.08	p=0.008

* these sex ratios are based on observations of young just prior to permanent emergence from pouch. ** includes data from Catt (1977), Fleming *et al.* (1983) as well as data from unpublished sources.

Lower survival of male pouch young relative to females has only been shown in two other marsupial species, the quokka (Shield 1962) and the brushtail possum (Hope 1972). However, lower survival of male embryos and juveniles has been demonstrated in many eutherians and birds (Clutton-Brock *et al.* 1985).

The sex ratio of Tasmanian pademelon pouch young did not differ from parity (M/F=1.04, n=282). Similarly the only previous study (Rose and McCartney 1982a) on this species did not find a significant deviation from parity (M/F=0.98, n=170).

There was no evidence of mortality biased towards males for the Tasmanian pademelon despite the poor environmental conditions in 1988. This suggests that, with regard to pouch young sex ratios, the drought had less effect on Tasmanian pademelons than on Bennett's wallabies. Evidence from Chapter 4 suggests that the drought influenced body condition of Tasmanian pademelons to a lesser extent than Bennett's wallabies.

5.4.3 Age at Maturity

In the present study it was found that the median ages at maturity for male and female Bennett's wallabies were 28 and 21 months respectively. Approximately 7% of females had matured within 12 months of age and 13% of males had matured between 12 and 18 months of age.

These median ages at maturity for Bennett's wallabies are older than those reported by Catt (1977) for Bennett's wallabies in the Hunter Hills of New Zealand. Catt found that 50% of males matured between 19 and 20 months of age and most females had matured between 14 and 17 months of age. These ages at maturity are comparable to the high hunted areas of Tasmania and it is significant that Bennett's wallabies in the Hunter Hills were subjected to regular culling operations (Tustin 1971; Catt 1977).

From studies on captive Bennett's wallabies in Canberra, Merchant and Calaby (1981) found that males and females first mated at 19 and 14 months respectively. These younger ages at maturity may reflect the better condition of wallabies in captivity. Similar differences in age at maturity between captive and wild populations have been demonstrated for red kangaroos (Frith and Sharman 1964).

In the present study it was found that the median ages at maturity for male and female Tasmanian pademelons were 17 and 13 months respectively. Approximately 30% of females and 3% of males had matured within 12 months of age. The only previous estimate of age at maturity in this species was that of Rose and McCartney (1982a) who estimated that young first mature at 14-15 months from 4 captive males and one captive female.

For males of both species age at maturity occurred at an older age in 1988 than in 1989. Although females showed this same pattern the difference was not statistically significant. The older age at maturity in 1988 is likely to be due to inadequate food resources as a result of the drought. This is supported by the low levels of body condition recorded in wallabies in 1988 (Chapter 4).

Among marsupials, studies on variation in age at maturity have concentrated on females. Several studies have shown that poor body condition in female macropods, particularly as a result of drought, leads to a delayed onset of maturity (Frith and Sharman 1964; Newsome 1965; Kirkpatrick and McEvoy 1966; Shepherd 1987). Variation in age at maturity for male macropods has received much less attention. Newsome (1973) reported that high temperatures associated with drought impaired spermatogenesis in red kangaroos. Because of Tasmania's climate, impairment of spermatogenesis as a result of high temperatures is less likely to cause a delay in maturity in male wallabies than in arid areas of Australia.

The results of the present study indicate that drought had a greater impact on age at maturity of males than females. This is consistent with males being in poorer condition than females (Chapter 4).

Age at maturity was also found to be influenced by hunting pressure. An increase in hunting pressure led to a decrease in age at maturity. The most likely explanation for this would be that hunting pressure reduces competition for food resources between the surviving wallabies. As a result their body condition will improve and, hence, they mature at an earlier age. A similar explanation was given by Wilson and Roth (1967) who found that hunting of the common duiker in East Zambia led to a decrease in the age at which animals matured. However, the index of body condition, KFI, presented in Chapter 4 does not totally support this explanation. Although wallabies at the study area with the highest level of hunting, Rushy Lagoon, had high levels of KFI, wallabies at other study areas also had high KFIs yet matured at an older age. Why this inconsistency should occur is unclear and is considered further in Chapter 7.

5.4.4 Breeding Success

The proportion of mature females which reared a young to independence was used as a measure of breeding success. This measure of breeding success is a product of the proportion of mature females which gave birth and the survival of young to independence.

It was found that 98% of mature female Bennett's wallabies gave birth in late summer/autumn and 95% of mature female Tasmanian pademelons gave birth in autumn/winter. This reflects the fact that both species are seasonal breeders. This breeding strategy is common in macropods which occur in areas of Australia where the quality and quantity of food resources are predictably good in spring and early summer, and poor in autumn and winter (Lee and Cockburn 1985). Hence, the greatest demands of lactation and vacation of the pouch by young occurs when conditions are optimum. In Bennett's wallabies, seasonal breeding has been achieved as a result of combining lactational and seasonal quiescence (Tyndale-Biscoe 1989). However, in the Tasmanian pademelon seasonal quiescence is absent and seasonal breeding occurs as a result of mature females

entering anoestrus in spring/summer. It was found that only 61% of mature females gave birth in the spring/summer breeding season compared with 95% in autumn/winter. Those females which failed to breed entered anoestrus probably as a result of low body condition at this time of the year (refer to Chapter 4). This seasonal pattern of breeding in the Tasmanian pademelon is reinforced by low survival of spring/summer born young. The number of females with pouch young at comparable times of the year (Dec-Jan and Jun-Jul) indicates that the survival of autumn/winter born young may be up to 3.5 times higher than for spring/summer born young. This can also be directly related to poorer condition of mothers over summer than over winter (Chapter 4).

As 98% of mature female Bennett's wallabies gave birth during the late summer/autumn breeding season, variation in the estimates of breeding success can be attributed to the mortality of dependent young. This is also the case for Tasmanian pademelons which gave birth in autumn/winter as 95% of mature females gave birth during this period. For both species, survival of young from birth to weaning conforms to the pattern recorded in most macropods, with high survival of young up until pouch vacation followed by a relatively large decrease in survival once young begin to permanently leave the pouch. This decrease in survival at pouch vacation coincides with peak energetic costs of lactation (Green 1984), low fat reserves (Caughley 1962; present study) and the change from the relatively secure environment inside the pouch to the more stressful environment outside the pouch.

For both species, pouch young survival was significantly lower in 1988 than in 1989. This difference in survival between years can be attributed to the drought in 1988 as the poorer condition of female wallabies in 1988 (Chapter 4) would have reduced their chances of successfully raising a young to independence. Similarly, survival of Tasmanian pademelon pouch young born in spring/summer 1987 and weaned during the drought was lower than for those born in spring/summer 1988. Studies on other macropods have also shown that drought can cause reduced survival of pouch young (Frith and Sharman 1964; Newsome 1965), however, in these studies, survival was much lower due to the greater severity of the drought where the studies were conducted.

There was evidence to suggest that pouch young survival during the drought was lower for Bennett's wallabies than for Tasmanian pademelons. During the year of the drought Tasmanian pademelon pouch young survival was 58% higher than that for Bennett's wallabies. By comparison, there was no significant difference in pouch young survival in the year after the drought. The lower survival of Bennett's wallaby pouch young relative to Tasmanian pademelon pouch young is linked with the finding that the body condition of mothers was higher in the Tasmanian pademelon than in Bennett's wallaby and that the body condition of the Tasmanian pademelon appeared to be less affected by the drought. (Chapter 4). This difference in pouch young survival between the two species of wallaby may also reflect differences in their ability to replace young from blastocysts in diapause. There was evidence that Tasmanian pademelon pouch young died during July-August of 1988 (Table 5.21) and these could have been replaced from blastocysts in diapause, as all females in September-October had pouch young. As Bennett's wallabies have seasonal as well as lactational quiescence (Tyndale-Biscoe 1989), any young lost after the winter solstice are unlikely to be replaced.

In 1988, survival of pouch young for both species of wallaby was higher at study areas with high hunting pressure than at study areas with low hunting pressure. High hunting pressure can reduce the density of animals and hence reduce competition for resources. In 1989, when conditions improved for the surviving wallabies, due to good rainfall and poor recruitment of young, there was no significant difference in pouch young survival between study areas.

In addition to hunting and rainfall there was evidence to suggest that temperature may also influence breeding success. Survival of Bennett's wallaby pouch young at Western Lakes was lower than at all other study areas and is linked with significantly lower body condition during summer when young leave the pouch (Chapter 4). The cause of this lower body condition and hence, breeding success, is believed to be due to the delay in the onset of

spring growth as a result of cold temperatures at this high altitude study area (Chapter 2, Chapter 4).

Comparison of breeding success among age groups indicated that it was the youngest and, to a lesser extent, oldest members of the population which were most likely to be unsuccessful breeders. Results from Chapter 4 revealed that these animals had lower body condition levels. This variation in breeding success with age is typical of vertebrates (Clutton-Brock *et al.* 1982).

In a study in northern New South Wales, Johnson (1989c) estimated that 50% of red-necked wallabies survived until they were weaned. This survival rate is slightly higher than that reported in this study for 1988 but substantially lower than in 1989. These results highlight the different reproductive strategies exhibited by these two subspecies. Bennett's wallaby is a strict seasonal breeder as a result of adaptation to a highly predictable annual climate (Tyndale-Biscoe 1989). Hence, under normal conditions the majority of young leave the pouch at the time of year when conditions are best and hence, survival to independence is high. In contrast, red-necked wallabies leave the pouch all year round. Some young will leave the pouch when conditions are unfavourable and hence, overall survival may be lower than that for Bennett's wallabies. However, on the rare occasions when Bennett's wallabies leave the pouch during drought, competition for limited resources will be high and hence mortality will be high. The lower survival rate in red-necked wallabies during good years is partially offset by the gains of continual breeding. In theory red-necked wallabies could produce an average of 1.3 young a year, compared to an average of 1.0 young a year for Bennett's wallabies.

5.5 SUMMARY

This chapter described aspects of reproduction in wild populations of Bennett's wallabies and Tasmanian pademelons and investigated the effects of hunting and rainfall on the reproductive pattern.

Bennett's wallabies were born in late summer and autumn with 80% of births occurring in February and March. Mean date of birth was the 27th February \pm 24 days.

Tasmanian pademelon births were recorded in all months, but there were two distinct periods of birth, one in autumn/winter with 95% of mature females giving birth and one in spring/summer with 61% of mature females giving birth. In the autumn/winter period, 85% of births occurred in April, May and June with the mean date of birth being 22nd May \pm 34 days. In the spring/summer period, 81% of births occurred in October, November and December with the mean date of birth being 18th November \pm 28 days.

For Bennett's wallabies, first-time breeders gave birth later than experienced breeders. For Tasmanian pademelons, experienced breeders which showed evidence of raising young from the previous breeding season gave birth later than first-time breeders which, in turn, gave birth later than experienced breeders which showed no evidence of raising a young from the previous breeding season.

There was no evidence that variation in hunting pressure or rainfall between study areas influenced the mean date of birth. However, pademelons which were first-time breeders gave birth later in 1988 than in 1989 and this was attributed to the effects of the drought on age at maturity.

The sex ratio of Bennett's wallaby pouch young was biased towards females, M/F = 0.83, but did not differ significantly from parity. There was a higher mortality of male pouch young than females in 1988 but not in 1989 and this was attributed to the effects of the

drought. The sex ratio of Tasmanian pademelon pouch young did not differ from parity, $M/F = 1.04$. There was no evidence that variation in hunting pressure or rainfall among study areas influenced the sex ratio of pouch young for either species.

The median age at maturity for male and female Bennett's wallabies was 28 and 21 months respectively. For male and female Tasmanian pademelons it was 17 and 13 months respectively. There was evidence to suggest that the drought caused a delay in attainment of maturity for both species. Age at maturity was negatively correlated with hunting pressure. This was due to increased resources for surviving wallabies in high hunted areas.

For Bennett's wallabies and Tasmanian pademelons, survival of young to independence conforms to the pattern recorded in most macropods. The youngest, and to a lesser extent, oldest wallabies were most likely to be unsuccessful breeders and this was associated with lower body condition levels.

For the Tasmanian pademelon, survival of dependent young which were born in autumn/winter was higher than those which were born in spring/summer. This can be directly related to poorer condition of mothers over summer than over winter.

For both species, survival of dependent young was lower in 1988 than in 1989 as a result of the drought in 1988. The effect of this drought was less in high hunted areas as a result of reduced competition for resources. Survival of dependent young during the drought was higher for Tasmanian pademelons than for Bennett's wallabies and this was linked to lower body condition levels and different reproductive strategies.

Survival of dependent young at the highest altitude study area was significantly lower than at other study areas. This was associated with lower levels of body condition and is believed to be a result of low temperatures delaying the onset of spring growth in high altitude areas.

CHAPTER 6

POPULATION STRUCTURE

6.1 INTRODUCTION

The investigation of sex ratio and age structure can provide valuable information on the relative survival and recruitment rates of animal populations (Caughley 1977). Changes in population structure are invariably associated with changes in population size (Eberhardt 1969).

The direct effect of hunting pressure on populations is to reduce density. If all sex and age groups are shot equally there would be no change in population structure (Caughley 1974). However, unbiased hunting is uncommon due to preferences by the hunter, and/or differences in size or behaviour within a species making some members of a population more vulnerable to hunting. Thus, Russell and Richardson (1971) were able to show that age structures of wallaroos in areas subjected to high hunting were younger than those in areas subjected to low hunting. This was due to hunting which was biased towards larger and hence older animals. Newsome (1977a) found that hunting pressure on red kangaroos resulted in a sex ratio biased towards females in age classes greater than three years old. As this was the age when sexual dimorphism becomes apparent, it was suggested that this difference in sex ratio was due to hunters selecting larger animals to shoot.

Bias has also been identified in the hunting of different species of macropods. Wilson (1975) compared the age structures of grey kangaroos, red kangaroos and wallaroos taken by professional shooters and found that red kangaroos had the highest survival rate while grey kangaroos had the lowest. Wilson suggested that red kangaroos were shot less intensively than grey kangaroos due to a greater tolerance to this species by farmers.

Rainfall is a significant factor influencing food quality and quantity which, in turn, will influence body condition and breeding success of macropod populations (Frith and Sharman 1964; Newsome 1965; Shepherd 1987; present study). Thus rainfall will ultimately affect population structure. Several studies have shown that severe drought can cause direct mortality of kangaroos through starvation (Newsome *et al.* 1967; Robertson 1986; Norbury *et al.* 1988). Both Robertson (1986) and Norbury *et al.* (1988) found that drought resulted in higher mortality of male eastern and western grey kangaroos than females. Norbury *et al.* (1988) believed this bias was a consequence of the disparate energy costs imposed by differences in body size and mobility between the sexes. Robertson (1986) also reported that subadult and old kangaroos were more vulnerable to the effects of drought. Although no explanation was given, it is presumed that these groups of animals were in poor condition relative to other members of the population. The present study has shown that subadults and some very old wallabies have significantly lower body condition than other age groups (Chapter 4).

The structure of Bennett's wallaby and Tasmanian pademelon populations has not been previously studied. The aim of this chapter is to determine the population structure of these two species and to investigate the effect of hunting and rainfall on population structure.

6.2 METHODS

Sampling and aging of wallabies has previously been described in Chapter 2. The present chapter only deals with wallabies which were shot without regard for sex or size.

The data were pooled over seasons and years. However, for Bennett's wallabies, data collected over summer were omitted because (a) adult females with young were less vulnerable to shooting during this time (see Appendix IV) and (b) there was a greater proportion of young animals in the samples during this time compared with winter. There

was no significant change in the proportion of young animals between winter and summer for the Tasmanian pademelon as a result of two breeding periods.

The population structure for both species on Maria Island National Park was considered separately from other study areas in this chapter. This is due to the small sample obtained from this study area and because the population processes which occur on this island are markedly different from the other study areas. Bennett's wallabies were collected from pasture areas around Darlington and native forest areas south of Darlington (Chapter 2). Tasmanian pademelons were only collected from pasture areas.

The Chi-squared test was used to compare sex ratios and age structures of both species.

6.3 RESULTS

6.3.1 Sex Ratios

The sex ratios for Bennett's wallabies at each study area are shown in Table 6.1. The sex ratio at Soldiers Marsh was significantly biased towards males. At all other study areas the sex ratio did not differ from parity. The sex ratios of Bennett's wallabies did not differ significantly between study areas ($\chi^2=6.96$, $df=7$, $p=0.433$), thereby allowing the data set to be pooled. The sex ratio for all 858 animals sampled did not differ from parity.

The sex ratios for Tasmanian pademelons at each study area are shown in Table 6.2. All study areas had a sex ratio which was biased towards males, and in most cases this was significant. The sex ratio for Tasmanian pademelons did not differ between study areas ($\chi^2=1.45$, $df=7$, $p=0.984$), thereby allowing the data set to be pooled. The sex ratio for all 1146 pademelons sampled showed a significant bias towards males.

Table 6.1 Sex ratios of Bennett's wallabies at each study area. Data obtained from shot samples. ns=not significant.

Study Area	M	F	M/F	χ^2	Significance
Lemont	9	9	1.00	0.00	ns
View Point	31	39	0.79	0.91	ns
Buckland	37	38	0.97	0.01	ns
Rushy Lagoon	114	107	1.07	0.22	ns
Soldiers Marsh	75	51	1.47	4.57	p=0.030
Lagoon of Islands	24	27	0.89	0.18	ns
Florentine Valley	87	85	1.02	0.02	ns
Western Lakes	72	53	1.36	2.89	ns
Total	449	409	1.10	1.87	ns

Table 6.2 Sex ratios of Tasmanian pademelons at each study area. Data obtained from shot samples. ns=not significant.

Study Area	M	F	M/F	χ^2	Significance
View Point	153	97	1.58	12.54	p=0.0004
Buckland	40	29	1.38	1.75	ns
Rushy Lagoon	84	58	1.45	4.76	p=0.029
Soldiers Marsh	56	38	1.47	3.45	ns
Lagoon of Islands	127	87	1.46	7.48	p=0.006
Florentine Valley	101	74	1.36	4.17	p=0.041
Styx	26	16	1.62	2.38	ns
Granville Harbour	101	59	1.71	11.02	p=0.0009
Total	688	458	1.50	46.16	p=0.0001

Effect of hunting pressure on sex ratio

The effect of hunting pressure on sex ratios was tested by grouping the study areas into areas subjected to low and high (medium-very high) hunting pressure. The level of hunting pressure at each study area was given in Chapter 2.

The sex ratio for Bennett's wallabies in areas subjected to low hunting pressure was significantly biased towards males whereas the sex ratio in areas subjected to high hunting pressure did not differ significantly from parity (Table 6.3).

There was no evidence that hunting pressure influenced the sex ratio of Tasmanian pademelons (Table 6.4).

Table 6.3 Effect of hunting pressure on Bennett's wallaby sex ratio. Data based on shot samples. ns=not significant.

Hunting Pressure	M	F	M/F	χ^2	Significance
Low	271	227	1.19	3.89	p=0.048
High	178	182	0.98	0.04	ns

Table 6.4 Effect of hunting pressure on Tasmanian pademelon sex ratio. Data based on shot samples.

Hunting Pressure	M	F	M/F	χ^2	Significance
Low	364	242	1.50	24.56	p=0.0001
High	324	216	1.50	21.60	p=0.0001

Effect of rainfall on sex ratio

The effect of rainfall on sex ratio was tested by grouping the study areas into areas of low and high rainfall (medium-high). Rainfall levels at each study area were given in Chapter 2.

The sex ratio of Bennett's wallabies at study areas with low rainfall did not differ significantly from parity (Table 6.5). The sex ratio at study areas with high rainfall showed a strong bias towards males but was not statistically significant at the 0.05 level. There was no evidence that rainfall influenced the sex ratio of Tasmanian pademelons (Table 6.6).

Table 6.5 Effect of rainfall on Bennett's wallaby sex ratio. Data based on shot samples. ns=not significant.

Rainfall	M	F	M/F	χ^2	Significance
Low	83	86	0.97	0.05	ns
High	372	323	1.15	3.46	p=0.063

Table 6.6 Effect of rainfall on Tasmanian pademelon sex ratio. Data based on shot samples.

Rainfall	M	F	M/F	χ^2	Significance
Low	193	126	1.53	14.07	p=0.0002
High	495	332	1.49	32.12	p=0.0001

6.3.2 Age Structure

The age structure for male and female Bennett's wallabies at each study area are shown in Figure 6.1. Although there were less males than females in the older age classes, there were no significant differences in age structure between the two sexes (lowest probability value for the χ^2 comparisons was 0.17 for Rushy Lagoon).

The age structure of male Bennett's wallabies differed between study areas ($\chi^2=31.70$, $df=18$, $p=0.02$). This appeared to be related to hunting pressure as there was a greater proportion of young wallabies (<2 years old) at study areas subjected to high hunting pressure compared to study areas subjected to low hunting pressure (Table 6.7). Although female Bennett's wallabies showed the same trend the differences in age structure were not significant ($\chi^2=11.76$, $df=18$, $p=0.86$).

The age structures for male and female Tasmanian pademelons at each study area are shown in Figure 6.2. There were no significant differences in age structures between sexes (lowest probability value for the χ^2 comparisons was 0.212 for Rushy Lagoon).

Age structures differed between study areas for male ($\chi^2=65.22$, $df=14$, $p=0.001$) and female ($\chi^2=36.91$, $df=14$, $p=0.008$) Tasmanian pademelons. This appeared to be related to hunting pressure, with a greater proportion of young pademelons (<18 months old) occurring in study areas subjected to high hunting pressure (Table 6.7).

The exception to this trend for the Tasmanian pademelon was Granville Harbour. Although hunting pressure at this study area was low, the age structure was similar to that of high hunted areas. This discrepancy is believed to be due to the removal of stock animals from the study area in 1987 (see study area description, Section 2.4). This resulted in increased resources for wallabies in 1988 and 1989 which led to a higher survival of young.

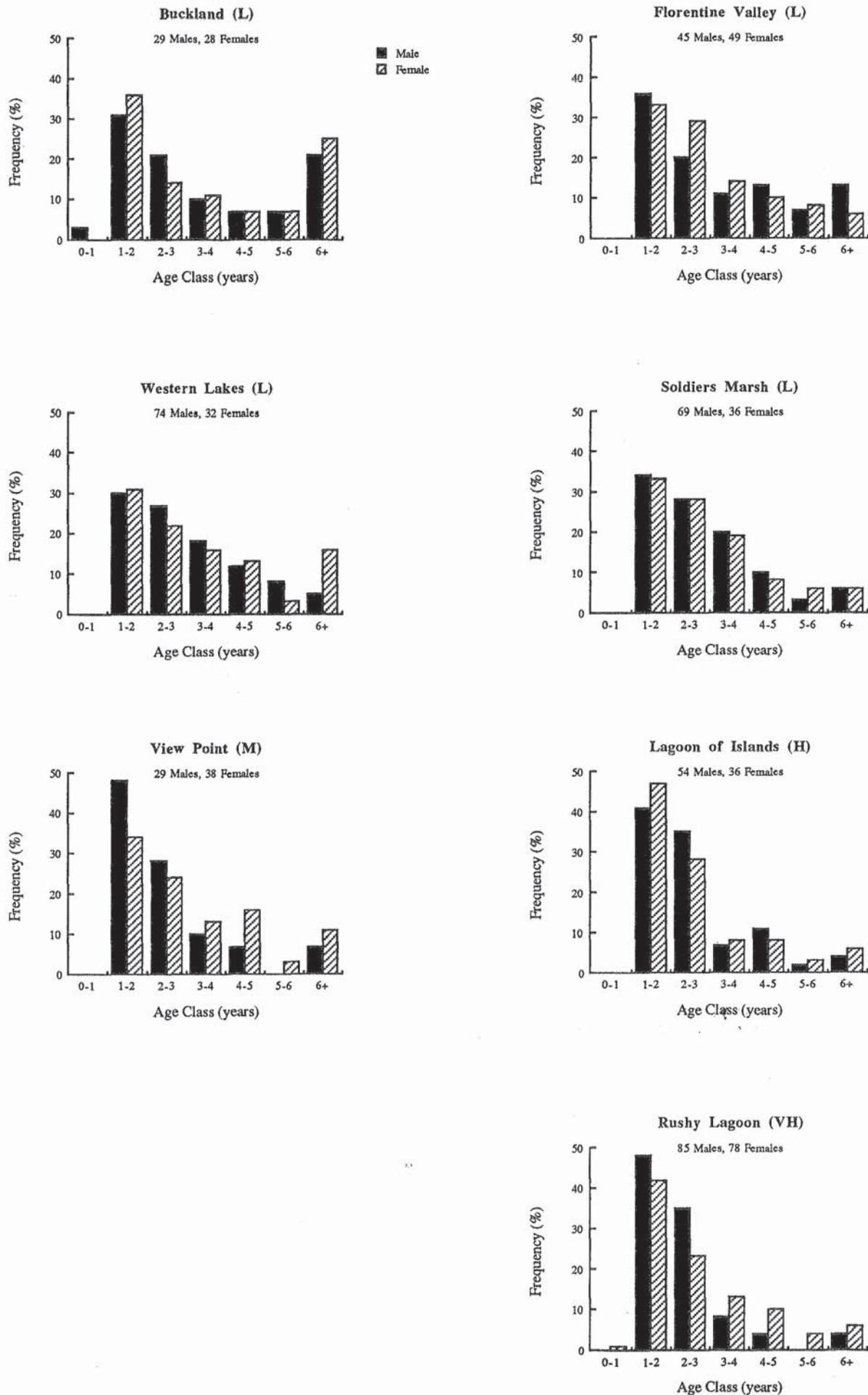


Figure 6.1 Age structure for Bennett's wallaby populations. Data obtained from shot samples. Study areas are ordered down the page in relation to (L)ow, (M)edium, (H)igh and (V)ery (H)igh hunting pressure.

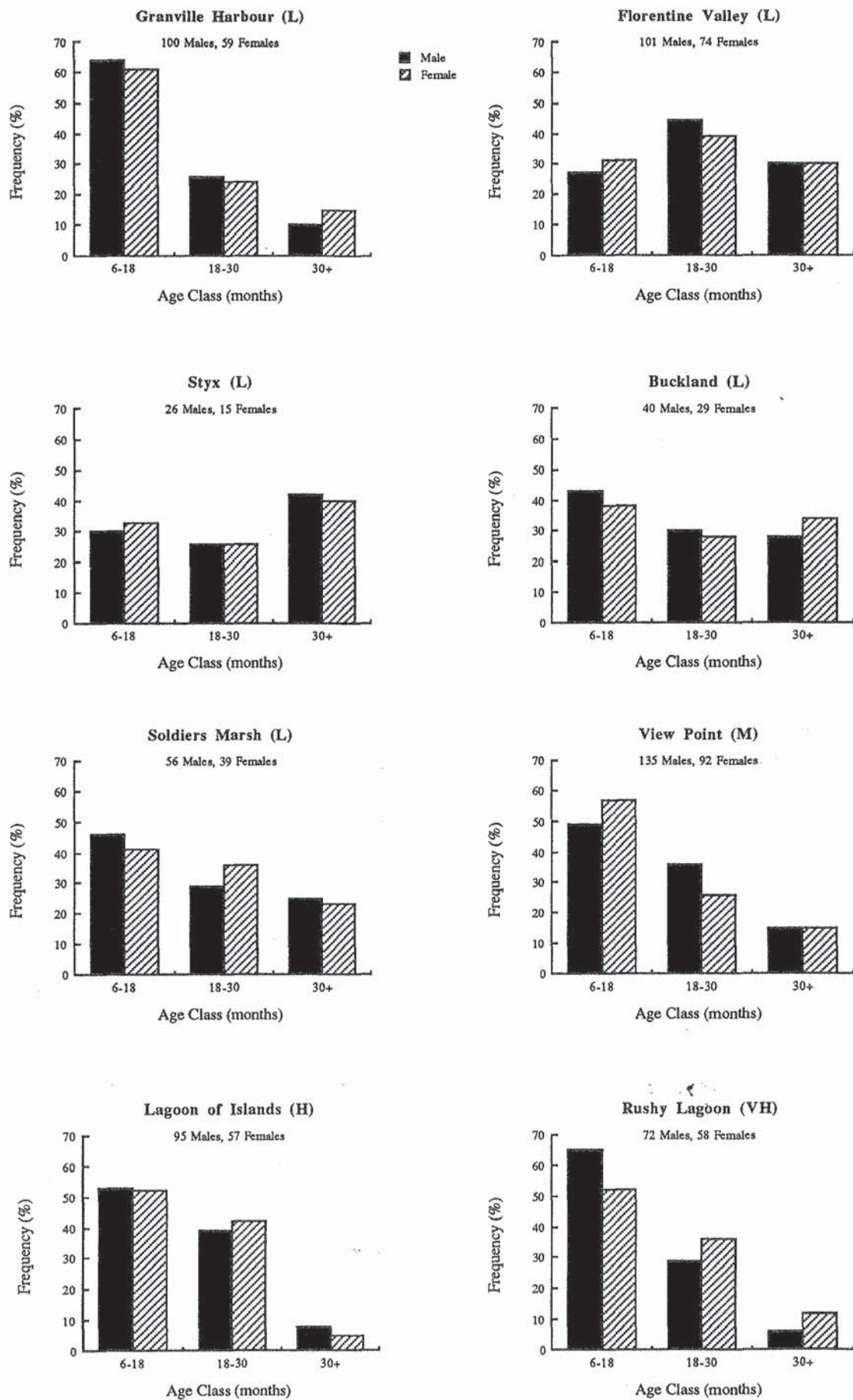


Figure 6.2 Age structure for Tasmanian pademelon populations. Data obtained from shot samples. Study areas are ordered down the page in relation to (L)ow, (M)edium, (H)igh and (V)ery (H)igh hunting pressure.

Table 6.7 The percentage of young Bennett's wallabies (<2 years) and Tasmanian pademelons (<18 months) at each study area in relation to hunting and rainfall.

Study Area	Hunting	Rainfall	Ben. wallaby		Tas. pademelon	
	Level		M	F	M	F
Florentine Valley	Low	High	36	33	26	31
Buckland	Low	Low	32	36	43	38
Soldiers Marsh	Low	Medium	35	33	46	41
Western Lakes	Low	High	29	31	-	-
Granville Harbour	Low	High	-	-	64	61
View Point	Medium	Low	48	34	49	59
Lagoon of Islands	High	Medium	41	47	53	53
Rushy Lagoon	Very High	Medium	48	42	65	52

The proportion of young pademelons at the Florentine Valley study area was lower than all other study areas. It can be seen from Figure 6.2 that Florentine Valley had the only age structure where the number of pademelons increased between the 6-18 month and 18-20 month age classes. This is believed to be a result of a 1080 poisoning operation which occurred after the winter 1988 sampling period (see study area description in Section 2.4).

The effect of hunting on age structure

The effect of hunting pressure on age structure was tested by grouping the study areas into areas subjected to high (medium-very high) and low hunting pressure. Tasmanian pademelon data from the Granville Harbour and Florentine Valley study areas were omitted from the comparison for reasons previously given. The results are shown in Figures 6.3 and 6.4.

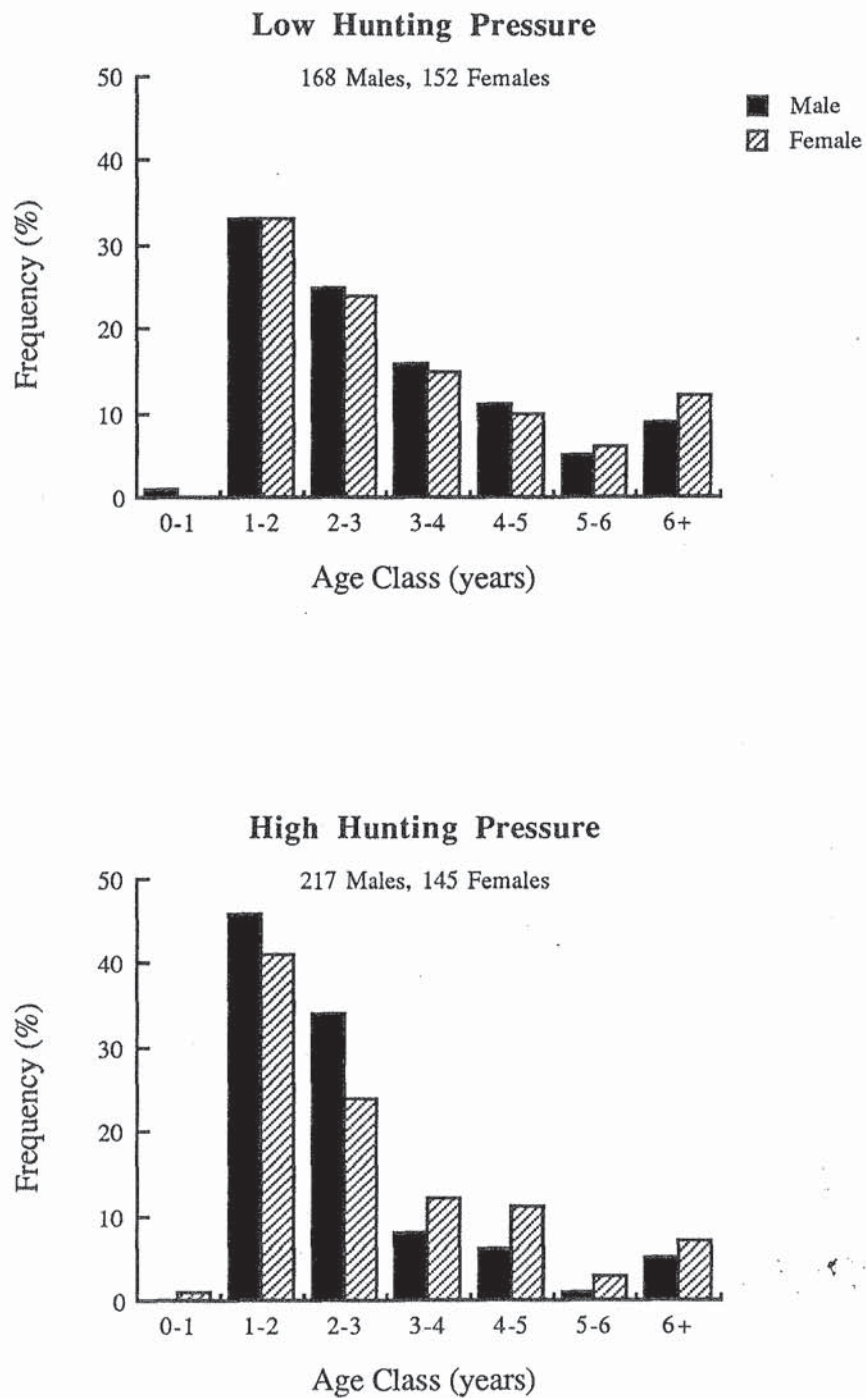


Figure 6.3 Comparison of Bennett's wallaby age structures between areas subject to low and high hunting pressure. Data were obtained from shot samples.

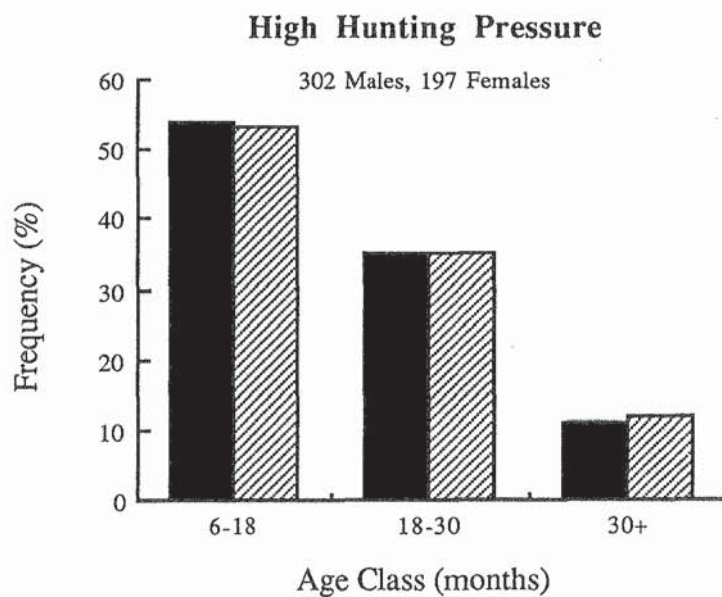
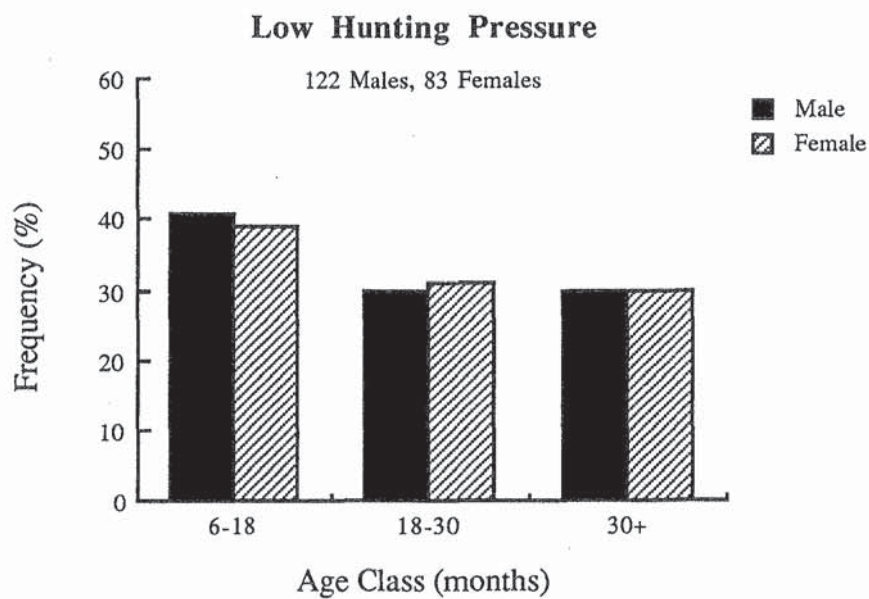


Figure 6.4 Comparison of Tasmanian pademelon age structures between areas subject to low and high hunting pressure. Data obtained from shot samples.

The age structure of male Bennett's wallaby populations in areas subjected to high hunting pressure was younger than in areas subjected to low hunting pressure ($\chi^2=20.22$, $df=4$, $p=0.0005$). The proportion of males less than 2 years of age was 46% in areas subjected to high hunting pressure compared with 33% in areas subjected to low hunting pressure. Although the age structure of female Bennett's wallaby populations was younger in areas subjected to high hunting pressure (41% were less than 2 years of age) than in areas subjected to low hunting pressure (33% were less than 2 years of age), the difference was not significant ($\chi^2=5.25$, $df=4$, $p=0.2625$).

In study areas with high levels of hunting pressure there were more male Bennett's wallabies in proportion to females up until 3 years of age, after which there was a bias towards females (Figure 6.3). The difference between the proportion of males and females was significant ($\chi^2=8.36$, $df=3$, $p=0.039$). There was no difference in the proportion of male Bennett's wallabies to females at study areas with low levels of hunting pressure ($\chi^2=0.999$, $df=4$, $p=0.91$).

The age structure of Tasmanian pademelon populations in areas subjected to high hunting pressure was significantly younger than the age structure in areas subjected to low hunting pressure for males ($\chi^2=23.20$, $df=2$, $p=0.0001$) and females ($\chi^2=13.41$, $df=2$, $p=0.0012$). The proportion of males less than 18 months of age in areas subjected to high and low hunting pressure was 54% and 41% respectively. For females the proportions were 53% and 39% respectively.

There was no difference in the proportion of male and female Tasmanian pademelons in study areas subjected to high hunting pressure ($\chi^2=0.30$, $df=2$, $p=0.86$) or low hunting pressure ($\chi^2=0.133$, $df=2$, $p=0.936$).

Effect of rainfall on age structure

The results shown in Table 6.7 indicate that variation in rainfall between study areas did not influence age structure in either Bennett's wallaby or the Tasmanian pademelon.

6.3.3 Maria Island

Sex ratio

The sex ratios of both species on Maria Island are given in Table 6.8. The sex ratio of Bennett's wallabies taken from pasture areas around Darlington was significantly biased towards females, whereas the sex ratio of Bennett's wallabies taken from native bush south of Darlington did not differ from parity. The sex ratio from Darlington differed from the combined sex ratio of all other study areas ($\chi^2=5.97$, $df=1$, $p=0.015$). The sex ratio of Bennett's wallabies taken from south of Darlington did not differ from the combined sex ratio of all other areas ($\chi^2=0.182$, $df=1$, $p=0.670$).

Although the sex ratio of the Tasmanian pademelon showed a bias towards females it was not significantly different from parity. Nevertheless it was the only study area where the sex ratio of this species showed a bias towards females. A comparison of this sex ratio with the combined sex ratio of all other study areas tended to show evidence of a difference ($\chi^2=3.35$, $df=1$, $p=0.062$).

Table 6.8 Bennett's wallaby and Tasmanian pademelon sex ratios at Maria Island. Data obtained from shot samples. ns=not significant.

Location	M	F	M/F	χ^2	Significance
Darlington (Pasture)					
Bennett's Wallaby	16	31	0.52	4.79	$p=0.029$
Tasmanian pademelon	12	16	0.75	0.57	ns
South of Darlington (Native Forest)					
Bennett's wallaby	11	12	0.92	0.04	ns

Age structure

The age structures for both species on Maria Island are given in Figures 6.5 and 6.6. At Darlington the age structure of males was younger than that of females for Bennett's wallabies ($\chi^2=10.36$, $df=2$, $p=0.006$) and the Tasmanian pademelon ($\chi^2=7.42$, $df=2$, $p=0.025$).

South of Darlington, the age structure of male and female Bennett's wallabies did not differ significantly ($\chi^2=0.03$, $df=1$, $p=0.8548$).

The age structure of male Bennett's wallabies at Darlington was significantly younger than the age structure of males south of Darlington ($\chi^2=6.061$, $df=1$, $p=0.014$). Although female Bennett's wallabies tended to be younger at Darlington compared with south of Darlington, this difference was not significant ($\chi^2=5.23$, $df=1$, $p=0.073$).

The age structures obtained from Maria Island were compared with the combined age structures of other low hunted areas in Table 6.9. The age structure of male Bennett's wallabies from Darlington differed from the age structure of males from low hunted areas. This was due to the lack of animals greater than 5 years old at Darlington and the relatively high number of 4-5 year old animals. The age structure of female Tasmanian pademelons at Darlington also differed from the age structure of females from low hunted areas. This was due to the high proportion of old females compared to young females at Darlington.

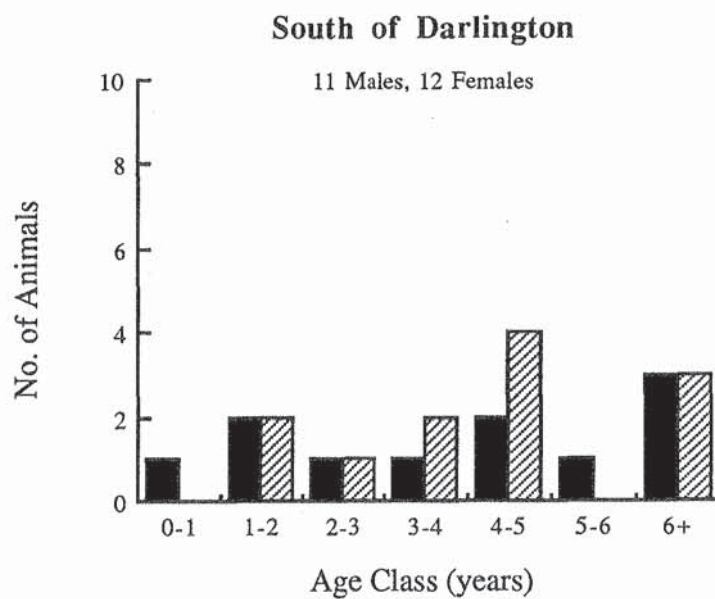


Figure 6.5 Age structures of Bennett's wallaby from two locations on Maria Island. Data obtained from shot samples.

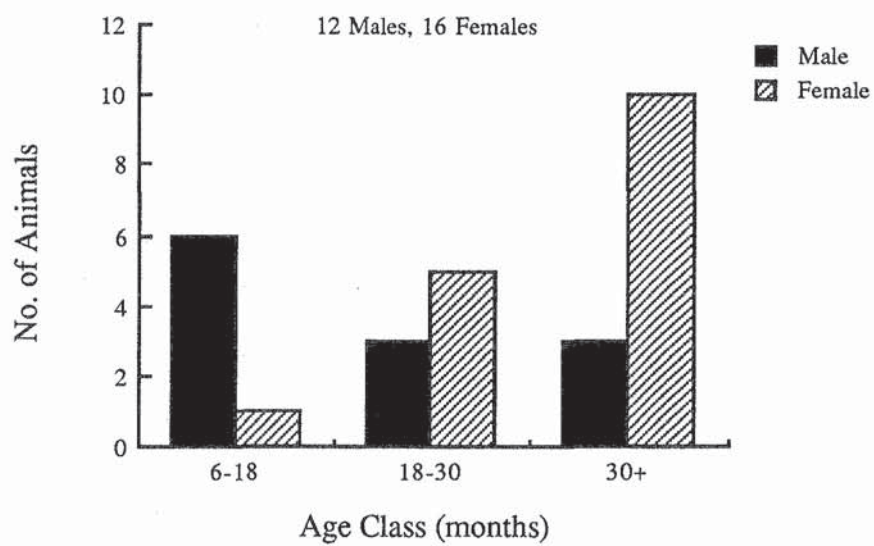


Figure 6.6 Age structure of Tasmanian pademelons from Darlington on Maria Island. Data obtained from shot samples.

Table 6.9 Comparison of wallaby age structures obtained from Maria Island with the combined age structure of wallabies obtained from low hunted study areas. ns=not significant.

Comparison	χ^2	df	Significance
Darlington vs Low Hunted Areas			
Bennett's wallaby			
Male	14.942	2	p = 0.0006
Female	1.838	3	ns
Tasmanian pademelon			
Male	0.365	2	ns
Female	8.178	2	p = 0.0168
South of Darlington vs Low Hunted Areas			
Bennett's wallaby			
Male	5.009	3	ns
Female	7.254	3	ns

6.4 DISCUSSION

6.4.1 Shooting Bias

Before discussing the results of sex ratio and age structure, it is necessary to consider the implications of shooting bias. The use of shot samples to assess population structure can be influenced by two types of bias which can be referred to as 'active' and 'passive' hunting selection.

Active Hunting Selection

Active hunting selection occurs when hunters choose to shoot a certain species, sex or size of an animal. From observations in the field and discussions with hunters, it was apparent that, in general, most wallaby hunters, whether commercial or recreational will shoot larger individuals in preference to smaller individuals. This preference occurs both within and between the two wallaby species.

Commercial hunters shoot larger wallabies in preference to smaller wallabies because of the obvious higher financial reward and this has been observed in studies by Newsome (1977a) and Wilson (1975). Hunters who shoot wallabies for crop protection will cull larger animals as they are considered to be a greater threat to their crops. Recreational hunters also show this bias which is due to the desire to shoot the biggest prey. On a number of occasions during the present study, the hunting practices of recreational shooters were observed and where there was a choice between large and small animals the largest was invariably shot first.

Because of their larger size Bennett's wallabies were shot in preference to Tasmanian pademelons. This was particularly true of commercial hunters. The commercial hunter at Rushy Lagoon shot 5000 wallabies a year of which about 200 were Tasmanian pademelons.

When shooting for personal consumption some hunters prefer to shoot young wallabies, however, the numbers shot on this basis are insignificant in comparison to the numbers of large wallabies shot.

Some hunters actively avoid shooting females with large young in the pouch due to compassion for the joey. However, one commercial hunter avoided females with large pouch young in order to ensure availability of animals in future years.

The net result of active hunting selection is that males are shot in greater proportion to females and Bennett's wallabies are shot in preference to Tasmanian pademelons.

Passive hunting selection

Although a hunter may not be actively selecting for a particular size or sex, some members of the population will remain more vulnerable to being shot than others. This is termed passive hunting selection. Factors which may cause passive selection are prey size, prey behaviour or the habitat in which hunting occurs.

Large wallabies are more likely to be seen before small wallabies, particularly in habitats with dense cover, and therefore they are more likely to be shot first.

Greater activity by male wallabies will make them more vulnerable to hunting than females. Male Bennett's wallabies are typically more active than females and have larger home ranges and disperse over greater distances (Johnson 1987a). No information on home range and dispersion is available for male and female Tasmanian pademelons, however, results from the red-legged pademelon, *Thylogale thetis*, (Johnson 1977b) suggest that male pademelons are more active than females.

Female Bennett's wallabies spend large periods of time adjacent to or in cover, particularly around the time of pouch vacation by their young (Catt 1977; Johnson 1987a;

Appendix IV). Hence females, as well as very young wallabies will be less vulnerable to shooting at particular times of the year.

The net effect of passive shooting selection is the same as for active shooting selection in that more male wallabies will be shot than females and more Bennett's wallabies will be shot than Tasmanian pademelons.

The bias due to active selection of wallabies was minimised in the present study by asking hunters to shoot without regard for sex or size, however the potential for passive selection to influence results still remains.

6.4.2 Sex Ratio

Because of the effects of passive shooting selection for males, the sex ratios obtained from shot samples for both Bennett's wallaby and the Tasmanian pademelon do not accurately reflect the sex ratio of these species in the field. Evidence presented in Chapter 5 and in this chapter indicates that mortality of male wallabies is likely to be higher than that of females as a result of active hunting selection and drought stress. Hence, it is reasonable to expect that the sex ratio of both species in the field will be biased towards females. However, the sex ratio of Bennett's wallabies and Tasmanian pademelons obtained from randomly shot samples were biased towards males. This discrepancy is believed to be due to the effects of passive shooting selection.

Results from Johnson (1986) also support the belief that the sex ratios of Bennett's wallabies obtained by shooting do not reflect the true field sex ratio. Johnson determined the sex ratio of a red-necked wallaby population by direct observation of animals which he had learnt to recognise over a period of three years. Using this more reliable method, Johnson found that the sex ratio was significantly biased towards females as a result of male biased mortality.

Although the sex ratios reported in this study were biased by passive shooting selection, it was still possible to investigate the effects of hunting and rainfall on the sex ratio of each species.

High hunting pressure was found to reduce the proportion of male Bennett's wallabies relative to females. This supports the observation that, under normal hunting conditions, male Bennett's wallabies are shot more frequently than females. Previous studies on other species such as red kangaroos (Newsome 1977a), elephants, *Loxodonta africana*, (Jachmann 1980), red foxes, *Vulpes vulpes*, (Yoneda 1982), bobcats, *Felis rufa*, (Rolley 1985) and bison, *Bison bison*, (Van Vuren and Bray 1986) have reported similar results. The study on bobcats is particularly comparable in that male bobcats are more vulnerable to harvesting than females because they have larger home ranges and daily movements. Thus, as was found for Bennett's wallabies, the sex ratio of bobcats in lightly harvested areas is biased towards males, however in heavily harvested areas the sex ratio is more even.

In contrast to Bennett's wallabies, there was no evidence that hunting influenced the sex ratio of Tasmanian pademelons. This result appears to contradict the finding presented above that more male pademelons are shot than females due to passive selection. This suggests that active selection for male Tasmanian pademelons at the study areas was not as great as for Bennett's wallabies and hence the combined effect of active and passive hunting selection did not influence the sex ratio enough to be detected in this study. This also reflects the fact that there is less hunting pressure on Tasmanian pademelons than on Bennett's wallabies at the high hunted study areas (see Chapter 2).

The greater hunting pressure on Bennett's wallabies may also help to explain the difference in sex ratio obtained between the two species. It has already been established that the shot samples of both species obtained during the present study are likely to be biased towards males due to passive shooting selection. The sex ratio of the Tasmanian pademelon showed a greater bias towards males than did Bennett's wallaby. This is consistent with

greater hunting pressure on Bennett's wallabies and in particular on male Bennett's wallabies.

There was evidence to suggest that low rainfall is associated with a reduction in the proportion of male Bennett's wallabies relative to females. This was particularly supported by the sex ratio at Darlington, Maria Island which was significantly biased towards females. The density of wallabies in this low rainfall study area is very high (Appendix IV) and wallabies were known to have died from starvation during the droughts of 1982/83 and 1987/88 (G. Hocking unpublished data). The sex ratio of Tasmanian pademelons appeared to be influenced less by rainfall than Bennett's wallabies. Only on Maria Island, where the lack of rainfall is likely to have the most significant effect, was there evidence to suggest that rainfall can reduce the proportion of male pademelons relative to females. This difference between the two species is supported by the results for pouch young mortality (Section 5.4.2). It was shown for Bennett's wallaby pouch young that more males than females died during 1988 as a result of drought. For Tasmanian pademelon pouch young, there was no evidence of mortality biased towards males.

Other studies have also shown that male macropods are more vulnerable to drought stress than females (Robertson 1986; Norbury *et al.* 1988). Norbury *et al.* (1988) suggested this male-biased mortality was a consequence of the disparate energy costs imposed by differences in body size and mobility between the sexes.

6.4.3 Age Structure

The age structure for both species of wallaby conformed to a pyramidal structure of declining frequency with increasing age similar to those reported for various species of wallaroo (Russell and Richardson 1971), eastern and western grey kangaroos (Wilson 1975, Norbury *et al.* 1988, Quin 1989) and red kangaroos (Wilson 1975). There were, however, significant variations in age structures between populations in the present study which were

largely a result of differences in hunting pressure. Age structures of both species were younger in high hunted areas than in low hunted areas. Similar results have been found in species such as wallaroos (Russell and Richardson 1971), red foxes (Phillips 1970), bobcats (Lembeck and Gould 1979, Rolley 1985), grizzly bears, *Ursus arctos*, (McLellan and Shackleton 1988) and feral cats, *Felis catus* (Bloomer and Bester 1991).

The young age structure of wallabies in high hunted areas was the combined result of (a) active and passive selection of large, and hence old individuals and (b) fewer animals surviving to old age. However, Frith and Sharman (1964) found that large male red kangaroos react to spotlight shooting earlier than other conspecifics suggesting that they were less likely to be shot. Similarly, Wilson (1975) postulated that older animals may develop some skill in avoidance of hunters where heavy shooting occurs. In contrast to these studies, Newsome (1977a) and Norbury *et al.* (1988) found no evidence that older male red and grey kangaroos avoided being shot to a greater extent than other conspecifics. There was no direct evidence in the present study that old males avoided being shot in heavily hunted areas. Even if this were to occur to some extent, high levels of hunting must reduce the number of older animals provided there is no significant immigration.

At study areas with high hunting pressure, the sex ratio of Bennett's wallabies varied with age indicating sex related differences in mortality. Fewer male Bennett's wallabies survived to old age than females. There was no significant difference in sex ratio of Bennett's wallabies in the study areas with low hunting pressure. This reflects the general preference of hunters to shoot larger and hence older animals. Similarly, Newsome (1977a) found that the main cause of females outnumbering males in red kangaroo populations was selective shooting by hunters.

Newsome (1977a) found an excess of female red kangaroos developed after they reached three years of age. This was the age of sexual maturity in red kangaroos and when sexual dimorphism becomes apparent. For Bennett's wallabies an excess of females also occurs after three years of age when males are 22% heavier than females. At this age all females and

most males have matured. McLellan and Shackleton (1988) demonstrated that for grizzly bears a change in sex ratio occurs when the sexes first become differentially vulnerable to hunting. This also appears to be the case for Bennett's wallabies.

There was no evidence that the sex ratio of Tasmanian pademelons varied with age in areas of either low or high hunting pressure. Hence, there was no evidence of sex related mortality due to hunting. This further suggests that, in general, pademelons are shot by hunters without regard to sex and that passive hunting selection has had little effect on the sex ratio of this species.

The only evidence that rainfall influenced the age structure of wallabies was on Maria Island where the effects of rainfall can be extreme due to high densities of wallabies. The age structure of male Bennett's wallabies at Darlington on Maria Island differed from age structures at other low hunted areas. There was a lack of animals over 5 years of age and there was a high proportion of males in the 4-5 year age class. This suggests a high mortality of males occurred over 5 years ago. This corresponds with an extended period of low rainfall in southeast Tasmania between 1979 and 1984. In particular, the period between February 1982 and April 1983 was one of the most severe droughts in the State's history (Shepherd 1991). During this period of drought, high mortalities of Bennett's wallabies were recorded by the Department of Parks, Wildlife and Heritage with mortality of males being three times higher than females (G. Hocking, unpublished data).

The age structures of male Bennett's wallabies also differed between pasture and native bush areas on Maria Island. This result suggests that the effects of the drought were less severe in the native forest.

The age structure of male Tasmanian pademelons on Maria Island did not differ from other low hunted study areas. This indicates that the drought of 1987/88 had little effect on the age structure of this high density island population. In comparison with Bennett's wallabies, the shorter life span of the Tasmanian pademelon would have obscured any

effects of the 1979-84 period of low rainfall. The age structure of female Tasmanian pademelons differed from other low hunted areas as well as from male pademelons on the island. There was a high proportion of old females to young females on Maria Island. The cause of this high proportion of old females is not known and may be an artifact of a small sample size.

Other Effects on Age Structure

Whilst hunting pressure and, to a lesser extent, rainfall were shown to influence the age structure of wallaby populations in this study, other factors also affected age structure.

At the Granville Harbour study area, the age structure of Tasmanian pademelons was comparable to that of high hunted areas, however, the hunting pressure was low. It is believed that this young age structure was caused by population expansion following the removal of stock prior to commencement of sampling (see study area description in Chapter 2). The removal of stock increased the amount of food available and presumably the survival of young increased. This population expansion is similar to that described for parma wallabies, *Macropus parma* on Kawau Island, New Zealand (Maynes 1977). An excess of 1 and 2 year old parmas was attributed to continuous breeding as a result of the development of pasture on the island. In other areas, the parma wallaby normally has a well defined breeding season.

At the Florentine Valley, the age structure of Tasmanian pademelons was older than at other study areas. Indeed, it was the only study area which had an age structure showing the proportion of pademelons increasing between the 6-18 month and 18-20 month age classes. This is believed to be a result of a 1080 poisoning operation which occurred after the winter 1988 sampling period (see study area description Chapter 2). This 1080 poison operation significantly reduced the numbers of Tasmanian pademelons at this study area (Appendix IV). McIlroy (1981) reported that young animals are generally more susceptible to 1080 poisoning than older animals. The use of 1080 poison did not affect the age structure of

Bennett's wallabies at this study area presumably because of their larger size (McIlroy 1986) and their lack of acceptability of the bait (Gregory 1988).

6.5 SUMMARY

The aim of this chapter was to determine the population structure of Bennett's wallaby and Tasmanian pademelon populations and to investigate the effect of hunting and rainfall on their population structure.

Hunting and rainfall were found to influence the population structure of Bennett's wallaby and the Tasmanian pademelon. Hunting pressure had a greater impact on population structure than did rainfall. Both hunting and rainfall had a greater impact on Bennett's wallabies than on Tasmanian pademelons.

The sex ratio of randomly shot samples of wallabies were biased as a result of passive shooting selection. Hence, males, because of their larger size and greater mobility, were more likely to be seen before females and therefore shot first.

High hunting pressure reduced the proportion of Bennett's wallaby males to females due to the combined effect of active and passive shooting selection of males. No influence of high hunting pressure on the sex ratio of Tasmanian pademelons could be detected. This was a result of less preference for male pademelons to females by hunters and lower hunting pressure on Tasmanian pademelons than on Bennett's wallabies.

In low rainfall areas the proportion of male Bennett's wallabies to females was lower than in high rainfall areas as males are believed to be more vulnerable during periods of food shortages. Only on Maria Island, where densities are very high, did low rainfall influence the sex ratio of Tasmanian pademelons.

The age structure for both species conformed to a pyramidal structure of declining frequency with increasing age similar to those reported for other macropods. For both species high hunting pressure resulted in a younger age structure as a result of (a) active and passive selection of larger and hence older animals and (b) fewer animals surviving to old age. In areas subjected to high hunting pressure the proportion of male Bennett's wallabies was greater than females up to 3 years of age, after which there was increased mortality of males. This corresponds to the age when sexual dimorphism becomes most visually apparent. There was no evidence of the proportion of male and female Tasmanian pademelons varying with age in areas subjected to high hunting pressure. This further suggests that there was no active selection for male pademelons over female pademelons.

On Maria Island, where densities of wallabies were high, rainfall was found to have influenced age structure. The period of low rainfall from 1979 to 1984 reduced the proportion of male to female Bennett's wallabies above 5 years of age. Because of the shorter life-span of Tasmanian pademelons the effect of this period of low rainfall could not be detected on this species.

Two other factors also influenced the age structure of Tasmanian pademelons. Removal of stock from a study area resulted in an increase of young animals as a result of increased resources. The use of 1080 poison at another study area caused a reduction in young Tasmanian pademelons as these animals were most vulnerable to the poison.

CHAPTER 7

CONCLUSIONS

This study investigated the effects of hunting and rainfall on populations of Bennett's wallabies and Tasmanian pademelons and represents the first major field based study on the biology of these species in their native environment.

Despite widespread culling of macropods across Australia there have been few studies investigating the effects of hunting on their biology. By comparison, the influence of rainfall on macropod populations has received greater attention. However, most of these studies on rainfall were conducted on larger macropods in areas of the Australian mainland where the pattern of rainfall is characterised by high variability. The present study differs from these previous studies in that the rainfall of Tasmania is characterised by low variability.

7.1 Effects of Hunting

It was found that hunting had a direct effect on the population structure of the two wallaby species. High levels of hunting reduced the average age of their populations, initially as a result of selective shooting for larger and hence, older individuals. However, with continued hunting pressure fewer wallabies will survive to old age.

The effect of selective shooting of large animals was greater on male than on female Bennett's wallabies and this caused a reduction in the proportion of males in the population. This disproportionate loss of males is unlikely to substantially influence the reproductive performance of the population, as only a small number of males are required to mate with all females (Johnson 1989d).

By comparison, for the Tasmanian pademelon, there was no evidence that selective shooting produced a difference in population structure between males and females. This suggests that discrimination between male and female pademelons by hunters was minimal. It may also reflect the fact that the difference in hunting pressure between study areas was less for Tasmanian pademelons than for Bennett's wallabies. Hence, the difference in hunting pressure was not sufficient to result in a detectable difference in age structure between male and female pademelons.

Russell and Richardson (1971) also found that hunting pressure reduced the average age in macropod populations and they suggested that this increase in the proportion of young animals would reduce the reproductive potential of the population. The present study has shown that the loss of reproductively mature animals was largely compensated for by increases in breeding performance. Wallabies in areas subjected to high hunting pressure reproduced at a younger age than wallabies in areas subjected to low hunting pressure. Moreover, areas subjected to high hunting pressure showed higher breeding success during the 1987/88 drought than areas subjected to low hunting pressure. This can be attributed to a decrease in density and subsequently an increase in the quantity of resources available for the surviving individuals (Caughley 1977). In the year following the drought there was no evidence of improved breeding success in areas subjected to high hunting pressure. Presumably, the improved rainfall and lower recruitment following the drought year resulted in improved resources at all study areas.

The biological responses to hunting shown by both species of wallaby are similar to those observed in previous studies on other mammals (e.g. Russell and Richardson 1971; Newsome 1977a; Rolley 1985). However, in the present study it was not clearly demonstrated that the improved breeding performance of wallabies in areas subjected to high hunting pressure was associated with higher levels of body condition, as measured by the Kidney Fat Index (KFI). Although KFIs at the most heavily hunted study area were very high, this was not the case in other hunted study areas. This is difficult to explain, especially as KFI was shown to be a good indicator of the effects of rainfall on breeding performance

(as is discussed below). These results suggest that other, as yet, unidentified factors must be causing this lack of agreement between KFI and breeding performance in hunted areas. It is possible that the effect of hunting on KFI has been confounded by the effects of rainfall on KFI.

The results of this study indicate that hunting had a greater influence on Bennett's wallabies than on Tasmanian pademelons. This reflects the greater hunting pressure on Bennett's wallabies both in this study (refer to Chapter 2) and across Tasmania (Anon 1984). This has important implications for the management of this species in Tasmania as both species of wallaby are essentially managed, by the Department of Parks, Wildlife and Heritage, as a single species (Anon 1984). This greater vulnerability of Bennett's wallaby to hunting is increased by the fact that the reproductive rate of Bennett's wallabies was shown to be lower than that of Tasmanian pademelons (Chapter 5). These results support the findings of Driessen and Hocking (1992) who demonstrated that the increase in Bennett's wallaby numbers following record levels of hunting in the late 1970s was significantly slower than the increase in Tasmanian pademelon numbers. Although current exploitation of wallabies is at an all-time low level (Driessen and Hocking 1992), this greater vulnerability of Bennett's wallaby to hunting should be taken into consideration if the commercial market for wallabies expands.

7.2 Effects of Rainfall

Although rainfall may influence populations directly through flooding or extreme drought, the most common effect is through plant growth and hence, food supply. Caughley (1987) concluded that population fluctuations in kangaroos is determined by pasture biomass and that this is largely determined by rainfall.

In the present study it was possible to investigate the effect of rainfall on wallaby populations in two ways. Firstly, it was possible to compare study areas with markedly

different levels of rainfall and, secondly, it was possible to compare a year influenced by drought with a year of average rainfall. The drought was shown to have greater influence on the biology of both species than did variation in rainfall between study areas.

As rainfall usually affects food supply it therefore follows that a decrease in rainfall will usually influence body condition. It was shown that the body condition (as measured by KFI) of wallabies was lower in 1988 than in 1989. This difference can be attributed to the drought which occurred in 1988.

In 1988 variation in rainfall between study areas was positively correlated with body condition for both species. This was attributed to the greater effect of the drought on study areas with low rainfall than on study areas with high rainfall. This effect was not repeated in 1989 as a result of improved rainfall and lower recruitment and hence, more resources per wallaby. The effect of rainfall on body condition was also reflected in their rates of growth. In general, wallabies from study areas with high rainfall grew faster and attained greater weights than wallabies in low rainfall areas. This reflects the fact that variability in rainfall is less in high rainfall areas of Tasmania than low rainfall areas (Langford 1965) and hence, wallabies in high rainfall areas are less likely to suffer from food shortages.

The effect of the drought on body condition was apparent in the breeding performance of both species. Age at maturity was older and breeding success was lower in 1988 than in 1989. Indeed, this delay in attaining maturity resulted in a delay in giving birth in 1988 by pademelons which were first-time breeders. There was also evidence to suggest that experienced breeders gave birth later in 1988 than in 1989.

In terms of condition and breeding, the effects of drought on Bennett's wallabies and Tasmanian pademelons were, in general, similar to those reported for other species of macropod (Russell 1974). Although this drought was severe by Tasmanian standards (Shepherd 1991), it did not produce the same level of response seen in kangaroos as a result of severe drought in arid and semi-arid areas of Australia. For example, Frith and Sharman

(1964) found that only 27% of red kangaroos reached maturity during a drought in inland New South Wales and Queensland. Newsome (1965) found that only 29% of red kangaroo pouch young survived in the pouch during a drought in central Australia and 50% of females entered anoestrus after 3-5 months of drought. Robertson (1986) reported many deaths of large adult red and grey kangaroos as a result of a severe drought in western New South Wales. Such a severe response to drought has not been observed in Tasmania.

The results of this study indicate that the 1987/88 drought caused a greater reduction in breeding success for Bennett's wallabies than for Tasmanian pademelons. It was shown that kidney fat indices were higher for Tasmanian pademelons than for Bennett's wallabies and it was suggested that this probably reflected differences in body condition as a result of differences in the quality of their diets. Bennett's wallabies feed primarily on grasses which are generally low in nutrients. By comparison, Tasmanian pademelons have a more varied diet containing dietary items such as short green grass, browse, forbs and shrubs which generally have high nutrient levels. Analysis of stomach samples of both species for nitrogen content also indicated that Tasmanian pademelons select a higher quality diet than do Bennett's wallabies. This difference in the quality of diet is probably increased during times of low rainfall as studies have shown that grasses characteristically lose crude protein more rapidly and to a greater degree than do shrubs (De Vos and Mosby 1969). This was supported by the fact that body condition of Tasmanian pademelons appeared to be less affected by the drought than the body condition of Bennett's wallabies.

The difference in breeding success between the two species of wallaby may also reflect differences in their ability to replace young from blastocysts in diapause. There was evidence of mortality of Tasmanian pademelon pouch young in July-August of 1988 which may have been replaced from blastocysts held in diapause, as all females in September-October had pouch young. As Bennett's wallabies have seasonal as well as lactational quiescence (Tyndale-Biscoe 1989), any young lost after winter solstice are unlikely to be replaced.

The results of this study indicate that droughts in Tasmania have a significant effect on body condition, breeding success and hence, recruitment of young into wallaby populations and therefore should be taken into account when managing these species.

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APPENDIX I

VARIATION IN MEAN KIDNEY WEIGHT AND MEAN BODY WEIGHT

Table 1 Variation in mean kidney weight and mean body weight between months of low KW/BW ratios (Bennett's wallaby: June 88 and May 89, Tasmanian pademelon: June and July 1988) and months of high KW/BW ratios (the remaining months sampled, see Figure 4.2, Chapter 4).

	Mean KW/BW Ratio (g/kg)	Mean Body Weight (kg)	Mean Kidney Weight (g)	Sample Size
Bennett's Wallaby				
High KW/BW ratio	2.08 ± 0.24	13.09 ± 3.78	27.12 ± 8.05	123
Low KW/BW ratio	1.84 ± 0.26	10.58 ± 2.24	19.58 ± 5.22	46
Variation (%)	12	19	28	
Tasmanian pademelon				
High KW/BW ratio	1.98 ± 0.23	6.03 ± 1.55	11.83 ± 3.16	237
Low KW/BW ratio	1.76 ± 0.27	5.51 ± 2.10	9.45 ± 3.50	45
Variation (%)	11	9	20	

Table 2 Variation in mean kidney weight and mean body weight relative to variation in KW/BW ratio among study areas. Only study areas with the greatest difference in KW/BW ratios are compared.

	Mean KW/BW Ratio (g/kg)	Mean Body Weight (kg)	Mean Kidney Weight (g)	Sample Size
Bennett's Wallaby				
Western Lakes	2.17 ± 0.27	13.32 ± 3.20	28.62 ± 6.67	113
Buckland	1.66 ± 0.17	10.75 ± 2.27	17.79 ± 3.57	61
Variation (%)	23	19	38	
Tasmanian pademelon				
Soldiers Marsh	2.09 ± 0.24	5.63 ± 1.61	11.60 ± 2.97	47
View Point	1.83 ± 0.21	5.48 ± 1.29	10.02 ± 2.60	76
Variation (%)	12	3	14	

APPENDIX II

VARIATION IN PROSTATE WEIGHT

Horak (1980) demonstrated that prostate weights of Tasmanian pademelons increased in March/April just prior to the major period of births in autumn/winter. Horak suggested it was possible that prostate weights may increase again during the spring/summer period of births but had no data on prostate weights to test this. To this end prostate weights were collected during the period which was not sampled by Horak to test his claim. The results shown in Figure 1 indicate that prostate weight increased significantly between October and November ($F_{(1,28)}=31.05$, $p<0.0001$) and decreased again between December and February ($F_{(1,26)}=9.15$, $p<0.005$).

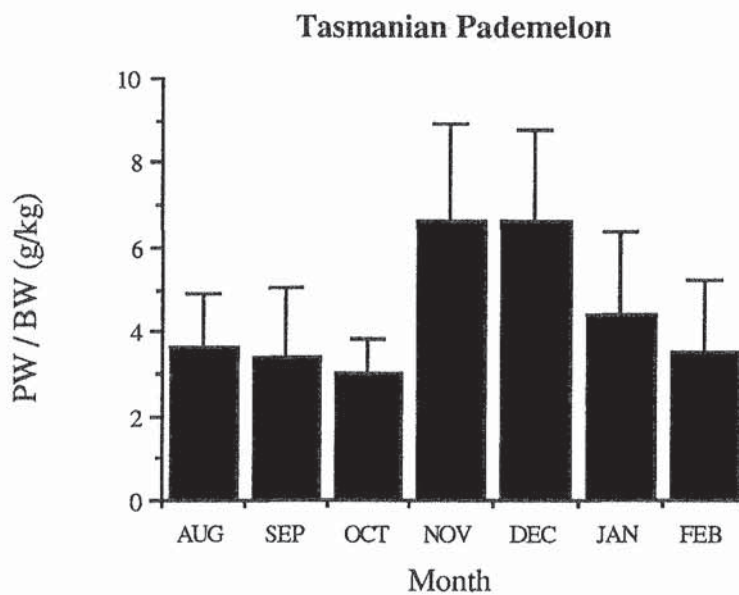


Figure 1 Variation in Tasmanian pademelon prostate weight between August 1989 and February 1990.

The spring/summer variation in prostate weight for Bennett's wallaby is shown in Figure 2. Prostate weights increased significantly between December and February ($F_{(1,20)}=62.78$, $p<0.0001$).

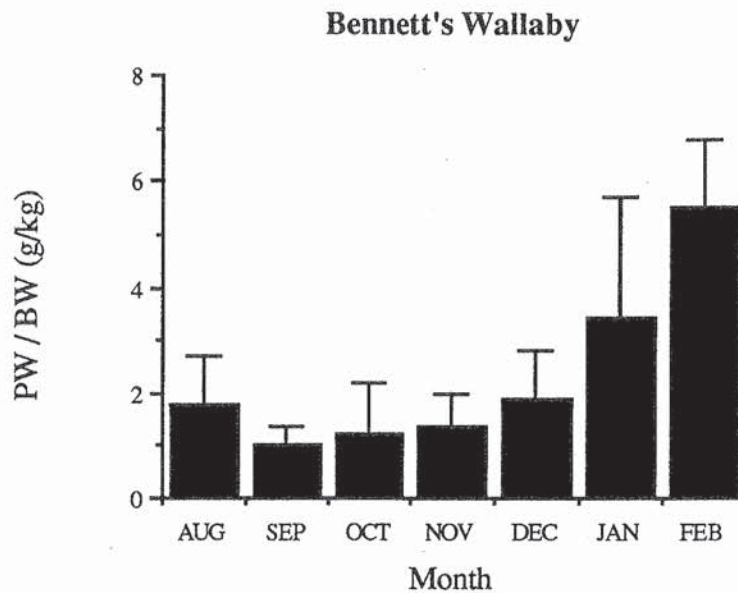


Figure 2 Variation in Bennett's wallaby prostate weight between August 1989 and February 1990.

Reference

Horak, J.A.A. (1980). Delayed gestation in the red-bellied pademelon (*Thylogale billardierii*). Hons Thesis, University of Tasmania.

APPENDIX III

QUALITY OF DIET

1. INTRODUCTION

The aim of this section is to assess the quality of diet for Bennett's wallaby and the Tasmanian pademelon by measuring the protein content of gut samples. A similar approach has been used for other macropods (Main 1970; Bakker and Main 1980; Shepherd 1987) and ungulates (Corn and Warren 1985). This information would prove useful in assessing patterns in growth and condition. However, the quality of food available says nothing about the quantity of food available. This will depend on factors such as vegetation present, stocking levels, harvesting rates and weather.

Like all macropods Tasmanian pademelons and Bennett's wallabies are foregut fermenters, which means that ingested food is subjected to microbial attack before exposure to gastric and intestinal enzyme action (Hume 1982). A deficiency in nitrogen supply results in poor microbial growth and consequently reduced fibre digestion and intake (Van Soest 1982). This, in turn, would lead to a reduction in available nutrients and possibly malnutrition. However, it has been shown that where diet is deficient in protein, some macropods can recycle urea to the forestomach where the microbes can utilise it for protein synthesis (Hume 1982). Nitrogen is not likely to be in short supply in areas with high rainfall and longer growing seasons (Hume 1982; Freudenberg *et al.* 1989).

2 METHODS

Stomach samples were collected from the anterior portion of the forestomach and frozen until analysis. Protein content was measured by the Kjeldahl method in 2.0 grams of undried

stomach sample. The constant relationship between nitrogen and protein content for most plant species ($\% \text{ nitrogen} \times 6.25\% = \% \text{ protein}$) was assumed.

All analyses were undertaken by the Tasmanian Government Analyst.

3 RESULTS

Comparison between sexes and age groups

Protein content in the diet of both species for each sex and age group is shown in Table 1. There were no significant differences in protein content in the diet between these groups. Thus the data were combined to compare protein levels in each species between seasons and between years

Comparison between seasons and years

Protein content in the diet of both species for each year is shown in Table 2. For the Tasmanian pademelon at Rushy Lagoon the protein content in the diet was significantly higher in summer 1989 than in winter 1989. There were no other significant differences in protein content in the diet for either species. With the exception of Tasmanian pademelons at Rushy Lagoon, the data were further combined to compare differences between species and study areas.

Comparison between study areas

Protein content in the diet of each species at each study area are given in Table 3. The habitat type has also been included as an indication of food sources and land management practices. Protein content in the diet varied between study areas for Bennett's wallabies ($F_{(6,144)}=11.72$, $p<0.001$) and Tasmanian pademelons ($F_{(8,155)}=17.57$, $p<0.001$). In general protein levels in the diet were higher in areas of pasture (Rushy Lagoon, Lagoon of Islands and Maria Island) than in areas of native vegetation (Styx, Buckland and Western Lakes).

Table 1 Comparison of protein content (%N x 6.25%) in stomach samples between males and females and adults and juveniles. Values in parentheses refer to sample sizes.

Bennett's Wallaby

Study Area	Adult Male	Adult Female	Juvenile Male	Juvenile Female	F-test	Significance
Florentine Valley 1988	31.2 ± 3.0 (4)	31.2 ± 3.0 (8)	37.2 ± 2.6 (3)	33.9 ± 5.5 (6)	F (3,17) = 2.11	ns
Florentine Valley 1989	32.8 ± 0.8 (4)	33.8 ± 2.2 (6)	32.1 ± 2.3 (2)	31.7 ± 3.0 (6)	F (3,14) = 0.83	ns
Maria Island	29.1 ± 2.4 (7)	33.4 ± 4.0 (9)	32.8 ± 4.9 (3)	28.9 ± 3.9 (5)	F (3,20) = 2.70	ns
Western Lakes	28.2 ± 4.3 (5)	27.8 ± 3.2 (7)	31.0 (1)	29.4 ± 3.1 (3)	F (2,12) = 0.21	ns

Tasmanian Pademelon

Study Area	Adult Male	Adult Female	Juvenile Male	Juvenile Female	F-test	Significance
Florentine Valley	35.4 ± 4.0 (11)	36.0 ± 4.5 (5)	35.0 ± 4.9 (4)	34.9 (1)	F (2,17) = 0.06	ns
The Styx	26.2 ± 5.2 (10)	30.4 ± 6.2 (5)	28.7 ± 2.7 (3)	30.7 (1)	F (2,15) = 1.15	ns
Buckland	31.5 ± 4.5 (4)	31.6 ± 2.6 (6)	36.0 ± 7.1 (3)	-	F (2,10) = 1.15	ns
Granville Harbour	30.6 ± 2.7 (6)	32.6 ± 3.5 (6)	34.0 ± 2.0 (4)	31.8 ± 1.1 (4)	F (3,16) = 1.46	ns

Table 2 Comparison of protein content (%N x 6.25%) in stomach samples between sampling periods. Values in parentheses refer to sample sizes.

Bennett's Wallaby

Site	Winter 88	Winter 89	Summer 89	F-test	Significance
Florentine Valley	32.8 ± 4.2 (21)	32.7 ± 2.3 (18)	30.7 ± 6.0 (12)	F (2,48) = 1.11	ns
Buckland	28.1 ± 4.0 (16)	-	30.1 ± 4.0 (10)	F (1,24) = 1.53	ns
Rushy Lagoon	-	35.5 ± 2.5 (4)	38.1 ± 3.9 (10)	F (1,12) = 1.41	ns

Tasmanian Pademelon

Site	Winter 88	Winter 89	Summer 89	F-test	Significance
Florentine Valley	35.5 ± 4.0 (21)	33.8 ± 3.5 (11)	36.5 ± 4.7 (10)	F (2,39) = 1.28	ns
Buckland	32.6 ± 4.5 (13)	-	30.7 ± 3.0 (11)	F (1,22) = 1.34	ns
Soldiers Marsh	-	32.1 ± 5.8 (6)	36.2 ± 3.5 (8)	F (1,12) = 2.74	ns
Rushy Lagoon	-	35.7 ± 4.8 (15)	52.6 ± 6.2 (5)	F (1,18) = 73.54	p < 0.001
Granville Harbour	-	32.1 ± 2.8 (20)	32.7 ± 4.2 (10)	F (1,18) = 0.20	ns

Table 3 Comparison of protein content (%N x 6.25%) between study areas. Two Rushy Lagoon values are presented for the Tasmanian pademelon because a significant difference was found between seasons. Solid lines indicate study areas which were not significantly different from each other at the 0.05 level. IP=improved pasture, UP=unimproved pasture, NV=native vegetation, PP=pine plantation. Numbers in parentheses indicate sample sizes.

Bennett's wallaby

Study Area	Habitat Type	Mean \pm s.d.(n)	No Significant Differences
Lagoon of Islands	IP	38.4 \pm 4.6 (7)	
Rushy Lagoon	IP	37.3 \pm 3.6 (14)	
Soldiers Marsh	NV	33.7 \pm 5.4 (13)	
Florentine Valley	NV/PP	32.3 \pm 4.2 (51)	
Maria Island	UP	31.2 \pm 4.1 (24)	
Buckland	NV	28.9 \pm 4.0 (26)	
Western Lakes	NV	28.4 \pm 3.3 (16)	

Tasmanian pademelon

Study Area	Habitat Type	Mean \pm s.d.(n)	No Significant Differences
Rushy Lagoon (Summer 1989)	IP	52.6 \pm 6.1 (5)	
Maria Island	UP	36.4 \pm 4.5 (7)	
Rushy Lagoon (Winter 1989)	IP	35.7 \pm 5.3 (15)	
Florentine Valley	NV/PP	35.3 \pm 4.1 (42)	
Lagoon of Islands	IP	34.5 \pm 4.1 (7)	
Soldiers Marsh	NV	34.5 \pm 4.5 (14)	
Granville Harbour	UP	32.3 \pm 3.3 (30)	
Buckland	NV	31.7 \pm 3.9 (24)	
Styx	NV	27.93 \pm 5.2 (19)	

Table 4 Comparison of protein levels between species. Two Rushy Lagoon values are presented for the Tasmanian pademelon because a significant difference was found between seasons (*=winter 1989, **=summer 1989). Numbers in rounded parentheses indicate sample sizes.

Study Area	Bennett's wallaby	Tas. Pademelon	F-test	Significance
Buckland	28.9 ± 4.0 (26)	31.7 ± 3.9 (24)	F _(1,48) = 6.50	p<0.025
Soldiers Marsh	33.7 ± 5.4 (13)	34.5 ± 4.9 (14)	F _(1,27) = 0.13	ns
Maria Island	31.2 ± 4.1 (24)	36.4 ± 4.5 (7)	F _(1,29) = 8.62	p<0.01
Florentine Valley	32.3 ± 4.2 (51)	35.3 ± 4.1 (42)	F _(1,91) = 12.1	p<0.001
Lagoon of Islands	38.4 ± 4.6 (7)	34.5 ± 4.1 (7)	F _(1,12) = 3.99	ns
Rushy Lagoon*	35.5 ± 2.5 (4)	35.7 ± 5.3 (15)	F _(1,17) = 0.01	ns
Rushy Lagoon**	38.1 ± 3.9 (10)	52.6 ± 6.1 (5)	F _(1,13) = 32.0	p<0.001

Comparison between species

The protein levels in the diet of each species are compared in Table 4. The protein levels in the diet of Tasmanian pademelons were generally higher than those in the diet of Bennett's wallabies and in half of these comparisons the differences were statistically significant. The exception to this trend was the Lagoon of Islands study area where the protein measurement was higher in Bennett's wallabies, although not significant.

4 DISCUSSION

Bennett's wallabies feed primarily on grasses (Calaby 1983; Statham 1983; Southwell 1987; Jarman and Phillips 1989). Although the diet of the Tasmanian pademelon also includes grasses, it is more varied containing forbs, shrubs and browse (Statham 1983; Johnson and Rose 1983). This difference in diet is reflected in the tooth morphology of both

species. Sanson (1978) believes that there are two basic types of masticatory organisation; (i) an ancestral browsing grade and (ii) a derived grazing grade. The pademelons are considered to have a browsing grade dentition whereas the larger wallabies such as Bennett's wallaby are grazers or intermediate browser/grazers (Sanson 1989). Dawson (1989) considered that size was important in determining diet choice in macropods for two reasons:

- i) Smaller animals have a proportionally greater metabolic intensity than larger animals and thus need to process more food relative to their size.
- ii) Fermentative digestion of plant fibre is a relatively slow process and Dellow *et al.* (1983) reported that the microbial activity in the forestomach of macropods is similar in animals of different body size and similar to that of ruminants.

Although smaller wallabies have a faster through-put of food than larger wallabies (Short 1985), the digestibility of a fibrous diet decreases as rate of passage increases (McIntosh 1966; Prince 1976). This led Dawson (1989) to consider that the only option for smaller mammals is to select plant material that is low in cell wall constituents (fibre) and high in cell wall contents (largely proteins, soluble carbohydrates and fats). With the exception of young grass, grasses are high in fibre and low in cell contents such as protein (Taylor 1981; Dawson 1989; Freudemberger *et al.* 1989; Norbury *et al.* 1989). Thus, although grasses are more abundant, special tooth morphology and more energy is required to break these food items into small fragments (Sanson 1989). By comparison, the soft growing tips of forbs, shrubs, and browse are low in fibre and have generally high nutrient levels (Dawson 1989). These plants or parts thereof require less energy to breakdown and digest.

Thus in general smaller to medium sized macropods such as the Tasmanian pademelon tend to be more generalist feeders, feeding on diets low in fibre and higher in nutrients (Dawson 1989). The larger wallabies such as the Bennett's wallaby and in particular the kangaroos have become specialist grass eaters feeding on diets high in fibre and generally low in nutrients. These two different nutritional strategies appear to be reflected in the results

of this present study. The level of protein recorded in the diet of Tasmanian pademelons was generally higher than the levels recorded in the Bennett's wallaby.

Sexual dimorphism is common among the larger macropods with mature males doubling (or more) the size of mature females. Both Bennett's wallaby and the Tasmanian pademelon exhibit sexual dimorphism with mature males attaining weights 50% greater than females (Chapter 4). Dawson (1989) considered that larger animals should be able to process high fibre feed better and this has been demonstrated in grey kangaroos, *Macropus giganteus*, (Forbes and Tribe 1970). Similarly, the ability of juveniles to digest high fibre foods would be limited given the size of their digestive tracts and would therefore require low fibre diets. In the present study there was no evidence of variation in protein levels in the diet between sexes or age groups for either species. This suggests that, although the sex and age groups may differ in foods consumed, they were able to maintain similar levels of nitrogen, at least for the periods sampled in this study.

The nitrogen content in plants can also vary between seasons and years. Nitrogen levels may be low during summer or during droughts (Kinnear and Main 1975; Wake 1980; Hume 1982). However, nitrogen is less likely to be limiting where higher rainfall and longer growing seasons result in abundant green foliage (Hume 1982; Freudenberger *et al.* 1989). As stomach samples were obtained during periods of average rainfall it is not surprising that no differences in protein levels in the diet were recorded between years and seasons during this present study. It is also possible that selective grazing by the wallabies may be maintaining protein content in the diet during periods of nitrogen shortage.

Significant differences in the amount of protein in the diet were found between study areas. The occurrence of protein in the diet was higher in study areas which were actively managed for agricultural or forestry purposes than in study areas with natural vegetation. This probably reflects; 1) the fact that fertile areas of land are generally chosen for agricultural purposes and 2) the active management of these areas, particularly in the use of fertilisers.

5 SUMMARY

Quality of diet, as measured in terms of protein content in stomach samples, did not vary significantly between sex, age groups or seasons.

Quality of diet was generally higher in areas which were actively managed for agricultural or forestry purposes than in areas of natural vegetation.

The quality of diet was generally higher for the Tasmanian pademelon than for Bennett's wallaby which reflected differences in feeding strategies.

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APPENDIX IV

INDEX OF ABUNDANCE

1 INTRODUCTION

An index of abundance of each species was obtained by counting all wallabies seen while culling occurred and expressing this figure as the number of wallabies seen per kilometre. This method allows for:

- (i) a comparison of the abundance of Tasmanian pademelons and Bennett's wallabies within a study area, assuming they are equally visible. As the Tasmanian pademelon is the smaller species, it is possible that its numbers may be underestimated in areas where there is dense undergrowth,
- (ii) a comparison of the abundance of each individual species between sampling periods provided that a similar transect is traversed each time and that conditions such as weather and vegetation have not changed significantly.

Comparisons of the abundance of each species between habitats are less robust due to differences in sightability of animals as a result of differences in cover. However, some general comments can be made.

2 METHODS

Spotlight counts were always made by myself whilst hunters were shooting wallabies from a vehicle. The spotlight contained a 100 watt halogen globe. Vehicle speeds were usually less than 5 km/h and never more than 10 km/h. Two hand held counters were used to

record the number of each species seen and the results were expressed as the number of wallabies seen per kilometre.

3 RESULTS AND DISCUSSION

3.1 Trends in Abundance Between Sampling Periods

The average spotlight count at each study area for each of the four sampling periods is shown in Table 1. Certain spotlight counts for Bennett's wallabies taken in November and early December have been deleted from the analyses because females were less visible at this time of the year resulting in lower counts (Figures 1 and 2). At this time of year females had retreated to areas of cover as they were carrying large young or had young just leaving the pouch. A similar response was reported by Catt (1977) who found a low proportion of females in an October-February sample. Johnson (1987) also found that female red-necked wallabies tended to shift their home ranges towards edges of large beds of cover as their young left the pouch.

No significant differences were recorded between sampling periods at each study area for Bennett's wallaby.

Significant differences in counts between sampling periods were recorded for the Tasmanian pademelon at Florentine Valley, Western Lakes and at Lagoon of Islands. Although not tested, because of insufficient data, there appeared to be a decrease in spotlight counts between winter and summer of 1989 at Granville Harbour.

The change in abundance at the Florentine Valley study area is believed to be a direct result of a 1080 poison operation between winter and summer of 1989. Thus, there was a decline in abundance of the Tasmanian pademelons in summer 1988 followed by a general increase in winter and summer of 1989. Interestingly, Bennett's wallaby did not appear to be

affected. In his wallaby control study, Gregory (1988) found that Bennett's wallabies were not as readily controlled by 1080 poison as Tasmanian pademelons and he attributed this to a lack of acceptability of the bait by Bennett's wallabies. Body size may also be involved as McIlroy (1986) found that smaller macropods are generally more susceptible to 1080 poison than larger macropods. Mooney and Johnson (1979) reported that only large individuals of both wallaby species were seen after poisoning which indicated to them that small and young individuals were selectively poisoned. Johnson (1978) also found that the number of pademelons spotlighted in two areas after poisoning decreased significantly whereas the numbers of Bennett's wallaby did not change significantly.

The significant difference in abundance recorded at Western Lakes was due to a general increase in numbers of Tasmanian pademelons from 1988 to 1989. This confirms observations by the local ranger that the numbers of this species have been slowly increasing in this area in recent years. The data may also reflect the general increase in pademelon numbers throughout the State as indicated by spotlight surveys by the Department of Parks, Wildlife and Heritage (Driessen and Hocking 1982).

The change in abundance at Lagoon of Islands appeared to be related to season. Fewer Tasmanian pademelons were observed during summer counts than during winter counts. This was believed to be due to reduced sightability during summer as a result of tall grass. The change in abundance which appeared to occur at Granville Harbour was also likely to be due to an increase in vegetation height. In summer of 1989 the height of the bracken which covered large areas of pasture at this study area was noticeably higher than in winter of 1989.

Table 1 Average spotlight counts (number/km) for Bennetts Wallabies and Tasmanian Pademelons at each study area for winter and summer of 1988 and 1989. Numbers in rounded parentheses indicate number of counts. ns=not significant

Bennetts Wallaby

Study Area	Winter 1988	Summer 1988	Winter 1989	Summer 1989	F-test	Significance
Florentine Valley	2.5 ± 1.3 (2)	5.5 ± 2.9 (3)	3.8 ± 0.1 (3)	7.9 ± 1.6 (2)	F [3,6] = 3.17	ns
Buckland	2.5 ± 0.7 (2)	-	2.5 ± 0.6 (4)	2.0 (1)	F [1,4] = 0.00	ns
Rushy Lagoon	3.9 ± 0.3 (2)	4.5 ± 1.5 (2)	3.2 ± 1.3 (2)	5.6 (1)	F [2,3] = 0.62	ns
View Point	1.3 ± 0.9 (5)	1.4 (1)	1.4 ± 0.3 (2)	3.1 ± 1.3 (2)	F [2,6] = 2.97	ns
Lagoon of Islands	3.8 ± 2.4 (2)	3.7 ± 1.5 (3)	2.3 (1)	4.2 ± 2.6 (2)	F [2,4] = 0.04	ns
Soldiers Marsh	6.7 ± 0.7 (4)	-	4.9 ± 2.2 (5)	3.7 (1)	F [1,7] = 2.32	ns
Western Lakes	2.7 ± 0.8 (4)	3.0 ± 0.2 (2)	3.6 ± 0.9 (3)	4.4 (1)	F [2,6] = 1.33	ns
Granville Harbour	-	-	0.9 ± 0.9 (2)	0.7 (1)	-	-

Tasmanian Pademelon

Study Area	Winter 1988	Summer 1988	Winter 1989	Summer 1989	F-test	Significance
Florentine Valley	3.2 ± 1.4 (2)	0.5 ± 0.4 (3)	1.5 ± 0.4 (3)	2.0 ± 0.6 (2)	F [3,6] = 5.94	p<0.05
Buckland	2.1 ± 1.1 (2)	-	2.5 ± 0.8 (4)	2.1 ± 0.2 (2)	F [2,4] = 0.37	ns
Rushy Lagoon	8.3 ± 2.1 (2)	2.9 ± 1.0 (2)	7.5 ± 0.4 (2)	7.6 (1)	F [2,3] = 9.00	ns
View Point	3.9 ± 2.1 (5)	3.0 (1)	4.8 ± 0.1 (2)	5.6 ± 2.2 (2)	F [2,6] = 0.55	ns
Lagoon of Islands	16.1 ± 0.8 (2)	5.6 ± 1.4 (3)	14 (1)	6.1 ± 1.5 (2)	F [2,4] = 44.5	p<0.005
Soldiers Marsh	2.4 ± 1.1 (4)	-	2.4 ± 1.3 (5)	1.7 ± 1.0 (4)	F [1,7] = 0.61	ns
Western Lakes	0.1 ± 0.1 (4)	0.1 ± 0.1 (2)	0.8 ± 0.1 (3)	0.5 ± 0.4 (3)	F [2,6] = 6.89	p<0.05
Granville Harbour	-	-	30.1 ± 1.6 (2)	15.0 (1)	-	-

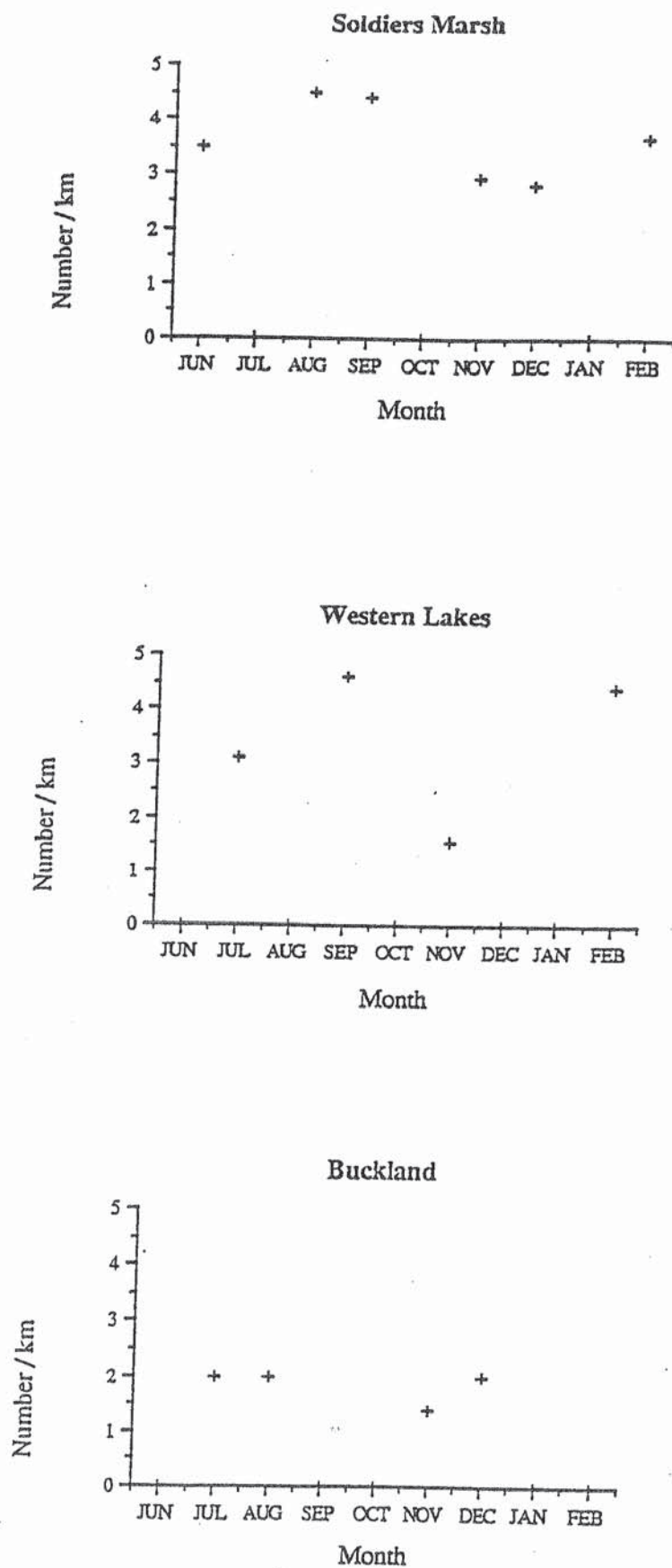


Figure 1 Spotlight counts for Bennett's wallaby between June and February. Note the decrease during November due to females with large young occurring in areas of cover.

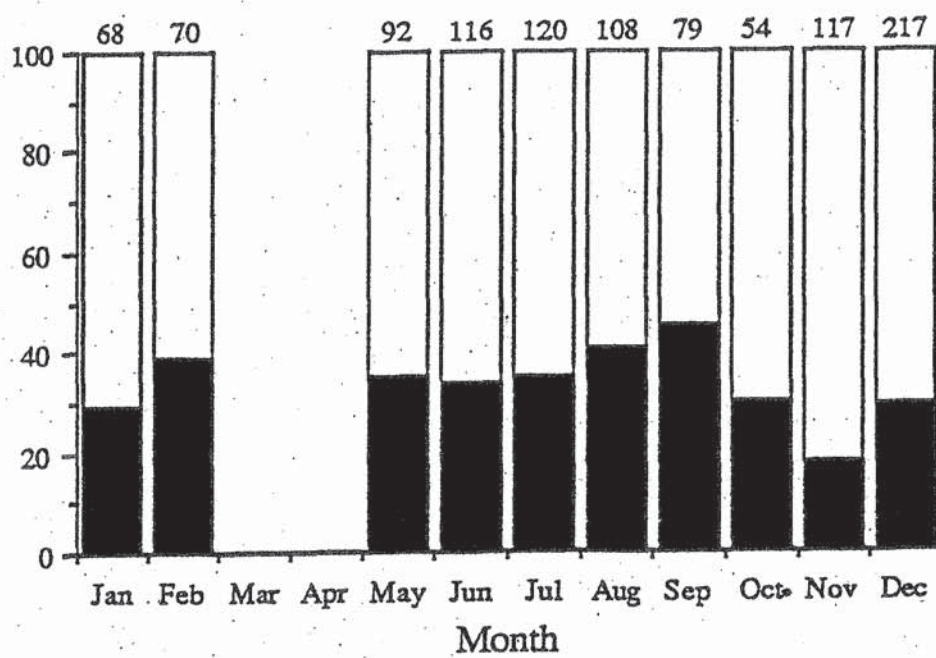


Figure 2 Monthly variation in the proportion of adult female Bennett's Wallabies recorded in shot samples. The data were pooled over 1988 and 1989 and all study areas. Sample sizes are given at the top of each column. No samples were obtained in March and April.

3.2 Comparisons between species and study areas

To compare the abundance of each species at each study area, the values in Table 1 were pooled where it was statistically valid to do so. The results, shown in Table 2, also include spotlight counts from the Styx, Maria Island and Lemont study areas which were sampled in only one time period. As has been mentioned, comparisons between study areas are not robust and only general comments can be made.

At most study areas the abundance of each species differed significantly. The exceptions were Buckland and the Florentine Valley prior to poisoning. The spotlight counts from Maria Island also indicated that both species are in similar abundance, although further spotlight counts are required.

Bennett's wallabies occurred in low abundance in relation to Tasmanian pademelons at the Styx and Granville Harbour study areas. It can also be confidently said that the abundance of Bennett's wallaby at these two study areas was low in relation to their abundance at other study areas. The native vegetation in these areas was dense mixed forest which is not considered to be ideal habitat for this species (Hocking and Guiler 1983; Taylor *et al* 1985). Two possible reasons for their absence relate to their diet and/or their large size. Bennett's wallaby are predominantly grazers (Calaby 1983; Statham 1983; Southwell 1987; Jarman and Phillips 1989), thus there is typically a lack of grass in this habitat for this species. By comparison, Tasmanian pademelons consume a wider variety of food types (Statham 1983; Johnson and Rose 1983). The dense nature of the vegetation in this habitat would also restrict movement of the larger Bennett's wallaby. The Tasmanian pademelon, which is considerably smaller (less than 50% of the size of Bennett's wallaby) and has a more 'crouched' gait would have no trouble moving through such habitat.

Table 2 Comparison of average spotlight counts (number/km) for Bennett's wallaby and the Tasmanian pademelon at each study area. Numbers in rounded parentheses indicate number of counts. ns=not significant.

Study Area	Bennett's Wallaby	Tasmanian Pademelon	F-test	Significance
Florentine Valley	4.9 ± 2.5 (10)	3.2 ± 1.4 (2) ^a 1.2 ± 0.7 (8) ^b	F [1,10] = 0.8 F [1,16] = 15.4	ns p<0.005
The Styx	0.03 ± 0.05 (4)	1.8 ± 0.6 (4)	F [1,6] = 35.1	p<0.005
Granville Harbour	0.8 ± 0.6 (2)	30.1 ± 1.6 (2)	F [1,3] = 973.8	p<0.0001
Buckland	2.4 ± 0.5 (7)	2.3 ± 0.7 (8)	F [1,13] = 0.2	ns
Soldiers Marsh	5.5 ± 1.8 (10)	2.2 ± 1.1 (13)	F [1,21] = 28.8	p<0.0001
Western Lakes	3.2 ± 0.9 (10)	0.7 ± 0.3 (6) ^c	F [1,14] = 46.7	p<0.0001
View Point	1.7 ± 1.0 (10)	4.3 ± 1.8 (10)	F [1,18] = 16.6	p<0.001
Lagoon of Islands	3.7 ± 1.7 (8)	15.4 ± 1.3 (3) ^d 5.8 ± 1.3 (5) ^e	F [1,9] = 119.4 F [1,11] = 5.9	p<0.0001 p<0.05
Rushy Lagoon	4.1 ± 1.2 (7)	7.8 ± 1.2 (5)	F [1,10] = 29.7	p<0.001
Lemont	2.4 (1)	4.1 (1)	-	-
Maria Island				
Darlington	52.4 (1)	63.5 (1)	-	-
Sth of Darlington	5.5 (1)	4.9 (1)	-	-

^a pre-poison count, ^b post-poison count, ^c 1989 count only, ^d winter count, ^e summer count.

The relatively high abundance of Bennett's wallabies in the Florentine Valley study area is unusual considering the dominance of dense mixed forest. However, this study area contained grassland originally created by aborigines through burning. In recent times pine trees have been planted over most of the area but grasses and small grasslands remain. Continual poisoning has probably had a greater impact on pademelon numbers than on Bennett's wallabies because of the smaller size of the former (as discussed above).

The abundance of Tasmanian pademelons was lower than that of Bennett's wallabies at Soldiers Marsh and Western Lakes. This is probably due to a lack of suitable cover at these two study areas. The vegetation of Soldiers Marsh consisted of large open marshes and open dry sclerophyll forests which are typical of Bennett's wallaby habitat. Tasmanian pademelons were only observed in association with dense vegetation which had a patchy distribution. Similarly the low alpine heath at Western Lakes provided little cover for Tasmanian pademelons and they were observed only where there were pockets of higher and more dense shrubs.

The abundance of Tasmanian pademelons at View Point, Lagoon of Islands and Rushy Lagoon was significantly higher than the abundance of Bennett's Wallaby. All three study areas contain a mosaic of pasture and native forest, are heavily shot, and have not been poisoned in recent years. Lemont could also be included in this group, although no information on poisoning is available. There appeared to be adequate habitat for both of these species at all four study areas. In fact with the exception of View Point the habitat of these study areas was more typical of Bennett's wallaby yet Tasmanian pademelons were significantly more abundant. According to the land owner and the local ranger, Bennett's wallabies were more abundant than Tasmanian pademelons prior to the commencement of shooting at Lagoon of Islands 15 years ago. It is possible that selective shooting for Bennett's wallabies at these study areas may have resulted in a low abundance of this species in relation to Tasmanian pademelons. Further support for this argument comes from Soldiers Marsh which was similar to these four study areas in terms of suitable habitat for Bennett's wallaby and sightability but with a lower hunting pressure. The abundance of Bennett's

wallaby at this study area appeared to be higher than the four more heavily hunted study areas even though they contained improved pasture.

The abundance of Tasmanian pademelons at Granville Harbour was considerably higher than at all other study areas except Maria Island. This can be attributed to the removal of stock from the study area in 1987.

The counts from Darlington (Maria Island) indicate that both species occur in high abundance at this study area in comparison to other areas. The counts are likely to be slightly exaggerated due to the tame nature of the wallabies in this National Park, but the high abundance is real resulting in starvation problems during times of drought. The counts made south of Darlington in native forest indicate that the abundance of wallabies is much lower than at Darlington itself (taking into account the lower sightability in forest compared with pasture). This difference is believed to be a result of less food resources available in the forest habitat.

In general the abundance of the Tasmanian pademelon is highest in areas adjacent to pasture or plantations, although at the Florentine Valley study area their numbers are kept in check by 1080 poisoning. A similar trend in abundance is not present for Bennett's wallaby possibly due to selective hunting of this species in areas adjacent to pasture. The exception to this is Maria Island where there is no hunting.

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APPENDIX V

ADDITIONAL INFORMATION

(not directly related to thesis)

1. Mean Body Weights

The Tables over the page give the mean body weights for Bennett's wallabies and Tasmanian pademelons shot during the field study. All animals were weighed using a Salter 25 kg spring balance. Mean body weights are given for adults and juveniles for each sex. The method of differentiating adults and juveniles is given in Chapter 5.

It should be noted that mean body weights of both species vary throughout Tasmania (see Chapter 4).

KEY: S.D. = standard deviation, n = sample size, CV = coefficient of variation, 95%L and 95%U = 95% confidence limits.

Bennett's Wallaby Body Weights

Females

	Mean (kg)	S.D.	Σx	Σx^2	n	CV	95%L	95%U	Range
All	9.42	2.82	4739	48639.72	503	29.9	9.17	9.67	2.6 - 15.8
Adults	10.60	2.16	3920.8	43264.94	370	20.357	10.38	10.82	5.6 - 15.8
Juveniles	6.15	1.61	818.2	5374.78	133	26.14	5.88	6.43	2.6 - 10.8

Males

	Mean (kg)	S.D.	Σx	Σx^2	n	CV	95%L	95%U	Range
All	11.36	4.31	6869.9	89231.99	605	38.0	11.01	11.70	2.0 - 27.2
Adults	14.40	3.53	4450.5	67944.31	309	24.5	14.01	14.80	6.9 - 27.2
Juveniles	8.17	2.26	2419.4	21287.68	296	27.7	7.92	8.43	2.0 - 15.0

Tasmanian Pademelon Body Weights

Females

	Mean (kg)	S.D.	Σx	Σx^2	n	CV	95%L	95%U	Range
All	4.03	1.23	1896.0	8359.06	470	30.5	3.92	4.15	1.0 - 7.4
Adults	4.56	0.96	1540.4	7333.10	338	21.1	4.45	4.66	2.2 - 7.4
Juveniles	2.69	0.72	355.6	1025.96	132	26.7	2.57	2.82	1.0 - 4.5

Males

	Mean (kg)	S.D.	Σx	Σx^2	n	CV	95%L	95%U	Range
All	5.18	1.99	3211.8	19076.74	620	38.3	5.02	5.34	0.9 - 11.0
Adults	6.53	1.52	2260.9	15566.19	346	23.2	6.37	6.70	3.3 - 11.0
Juveniles	3.47	0.88	950.9	3510.55	274	25.3	3.37	3.58	0.9 - 6.9

2 . Boned, Dressed and Gutted Weights

In recent years a small trade in wallaby meat has developed in Tasmania. While most meat is used for pet food the proportion of meat used for human consumption is steadily increasing. Bennett's wallaby is the main species used due to its larger size which brings a greater return per effort. Most wallaby meat enters the trade in a boned-out form in which the animals have been gutted, quartered and skinned above the line of the kidneys and below the rib cage. All bones are then removed from the hindquarters. Some wallaby meat also enters the trade in the quartered form which is generally referred to as a dressed carcass.

This section determines the relationship between boned-out weight, and size and age class. Some information is also presented for dressed carcass weight and gutted weight.

Wallabies were shot by commercial shooters from the back of a four wheel drive vehicle. All animals were sexed and total body weight was measured with a Salter 25 kg spring balance. The wallabies were again weighed after they had been (i) gutted, (ii) quartered or (iii) boned by the commercial shooters.

Boned out weights of Bennett's wallaby were obtained from the Western Lakes, Lemont and Lagoon of Islands study areas. Boned out weights for the Tasmanian pademelon were obtained from the Lagoon of Islands study area. Dressed carcass weights for Bennett's wallaby were obtained from the Western Lakes and Rushy Lagoon study areas. Dressed carcass weights for the Tasmanian pademelon were obtained from the Rushy Lagoon study area. Gutted weights for both species were obtained from the View Point study area.

Regressions of boned, dressed and gutted weights against age and body weight are shown in Figures 1-16. Only large, old males were shot when obtaining dressed carcass

weights for the Tasmanian pademelon, hence only the regression between dressed weight and body weight is shown.

All regression equations were statistically significant. Boned, dressed and gutted weights were more highly correlated against body weight than against age. Where sexes were treated separately the correlations against age improved.

Although reasonable correlations were obtained between wallaby age and the various carcass weights, their use would appear to be of limited value for determining age structure as its accuracy is confounded by the fact that it is impossible to sex boned-out carcasses and it is virtually impossible to sex dressed carcasses. Thus it would be necessary to group the sexes which introduces large errors as there are significant differences in body weights of male and females for both species after an early age (see Chapter 4). In addition further errors are introduced due to significant differences in weights attained by both species between different areas of the State (see Chapter 4).

Good correlations were obtained between carcass weights and total body weight. One possible use of this relationship would be to use the mean wallaby weights given part 1 of this appendix to estimate the number of wallabies shot from gross meat weights sent to the Parks and Wildlife Service from meat processors.

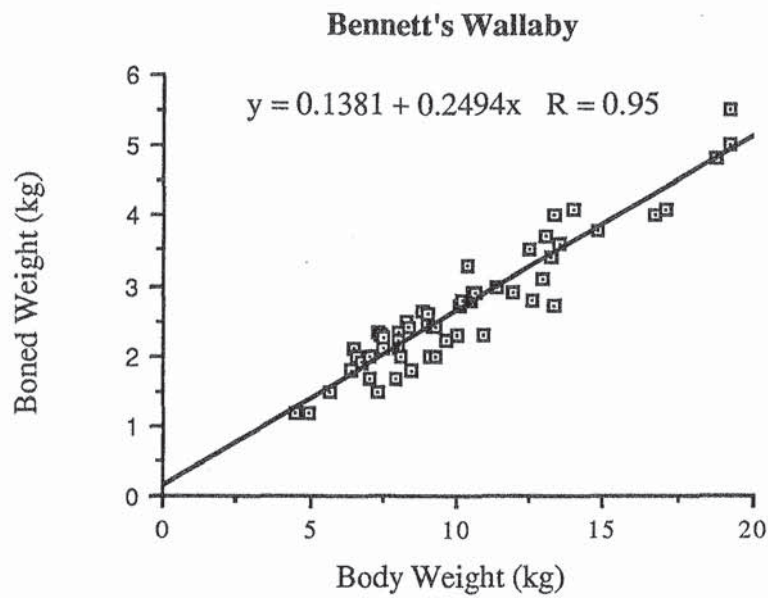


Figure 1 Relationship between boned weight and body weight for Bennett's wallaby ($F = 493.9$, $df = 57$, $p < 0.0001$).

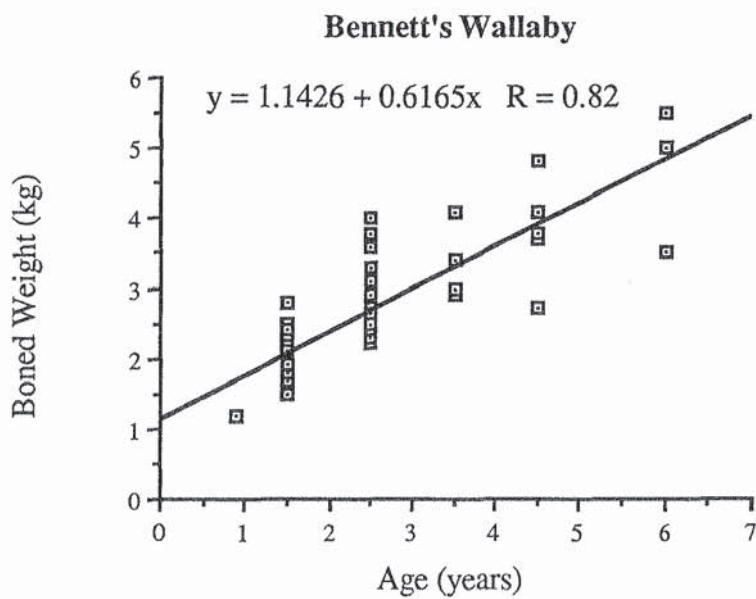


Figure 2 Relationship between boned weight and age for Bennett's wallaby ($F = 118.7$, $df = 31$, $p < 0.0001$).

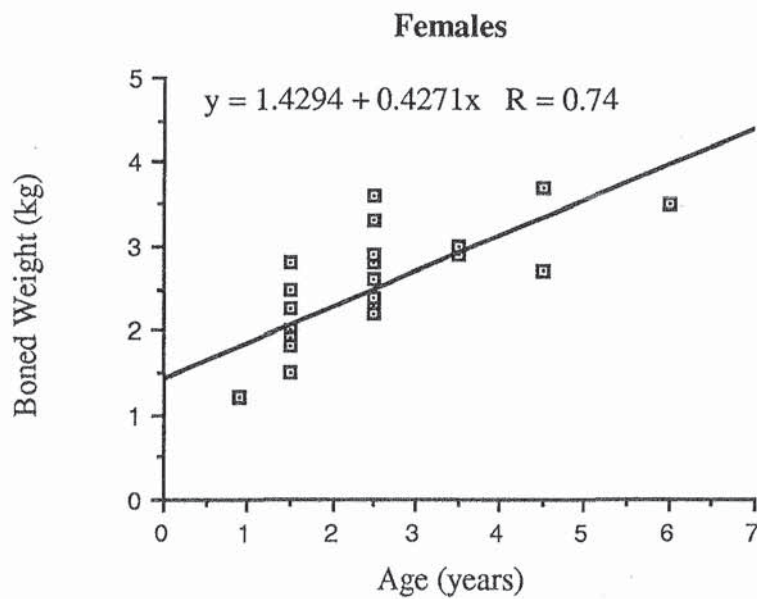
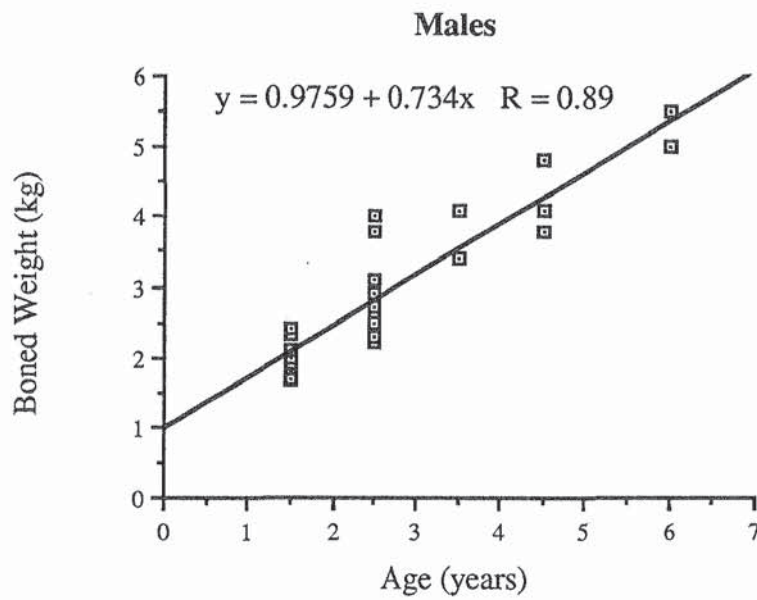


Figure 3 Relationship between boned weight and age for Bennett's wallaby (Males: $F = 118.7$, $df = 31$, $p < 0.0001$; Females: $F = 29.3$, $df = 25$, $p < 0.0001$).

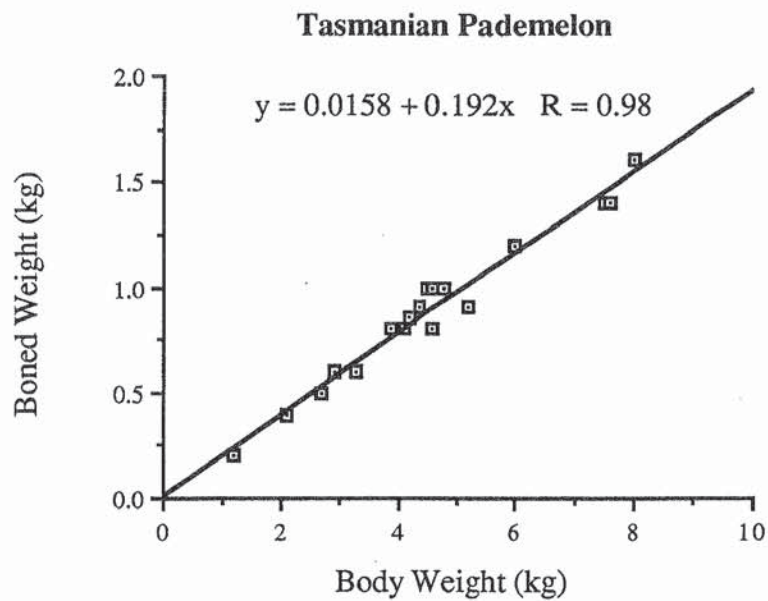


Figure 4 Relationship between boned weight and body weight for the Tasmanian pademelon ($F = 464.1$, $df = 17$, $p < 0.0001$).

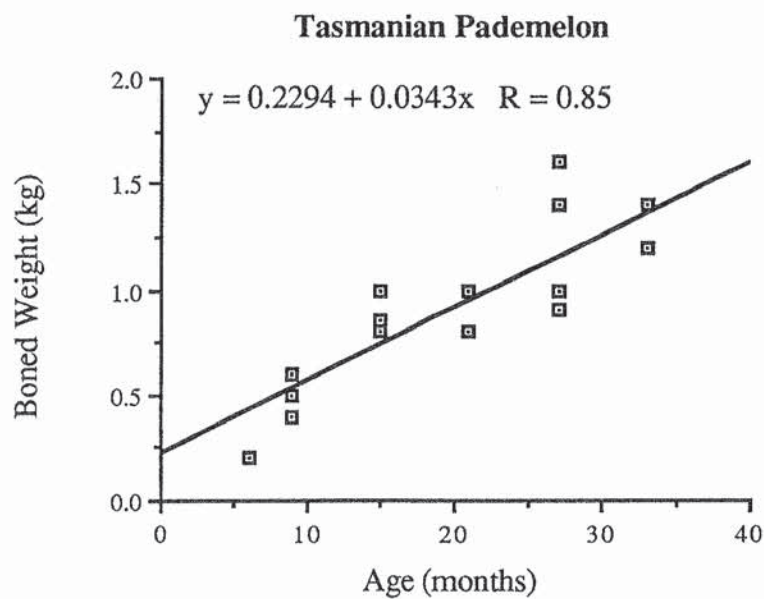


Figure 5 Relationship between boned weight and age for the Tasmanian pademelon ($F = 40.3$, $df = 17$, $p < 0.0001$).

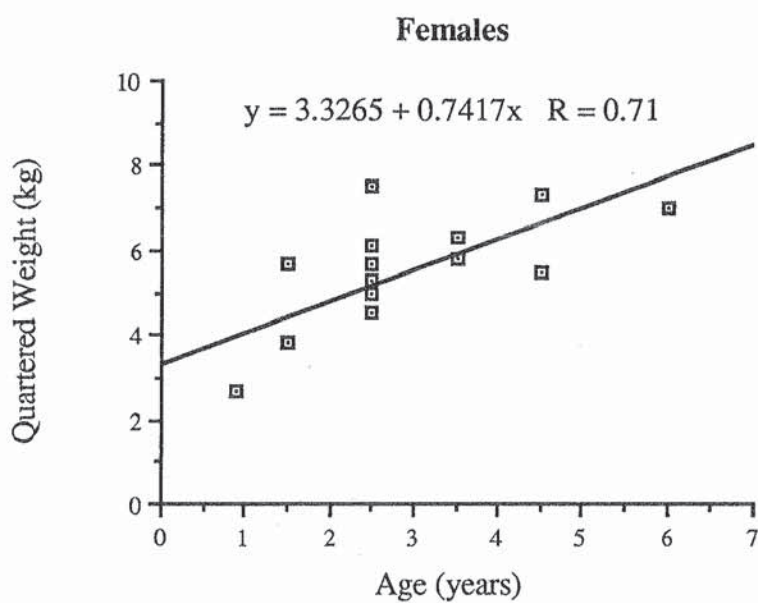
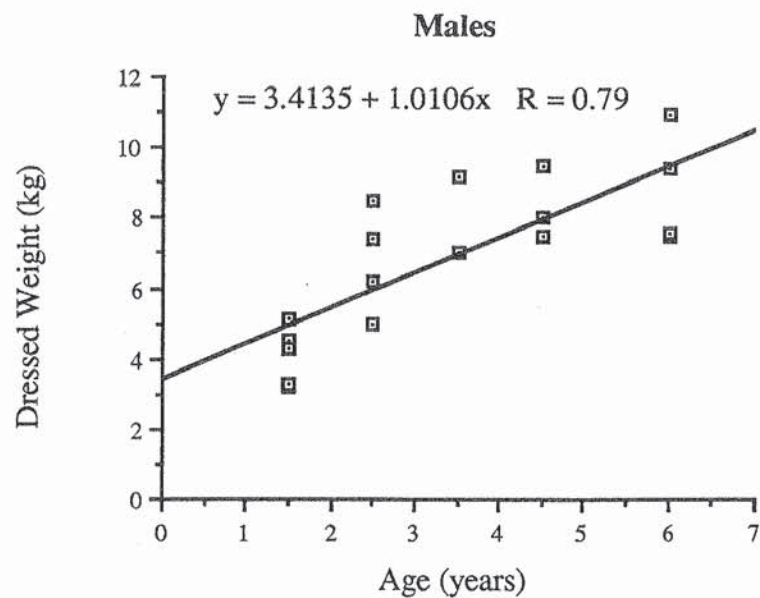


Figure 9 Relationship between dressed weight and age for Bennett's wallaby (Males: $F = 25.7$, $df = 17$, $p < 0.0001$; Females: $F = 13.5$, $df = 14$, $p = 0.0028$).

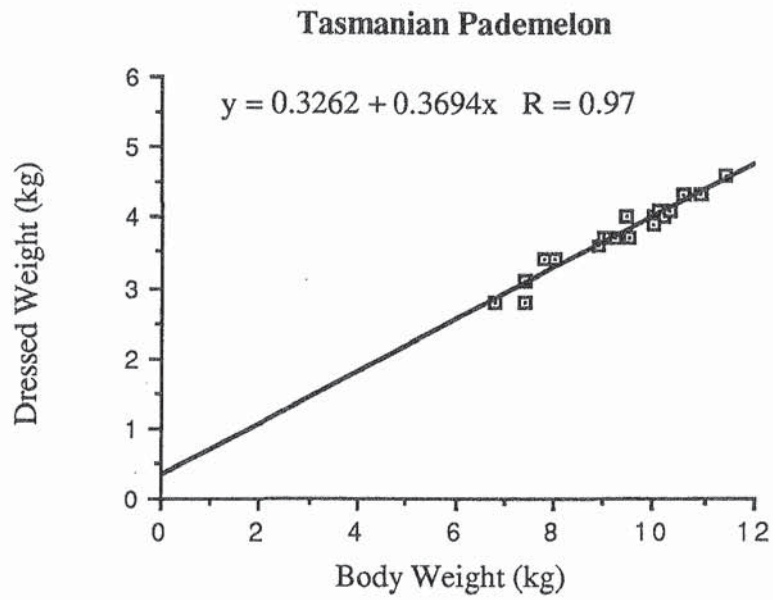


Figure 10 Relationship between dressed weight and body weight for the Tasmanian pademelon ($F = 364.8$, $df = 20$, $p < 0.0001$).

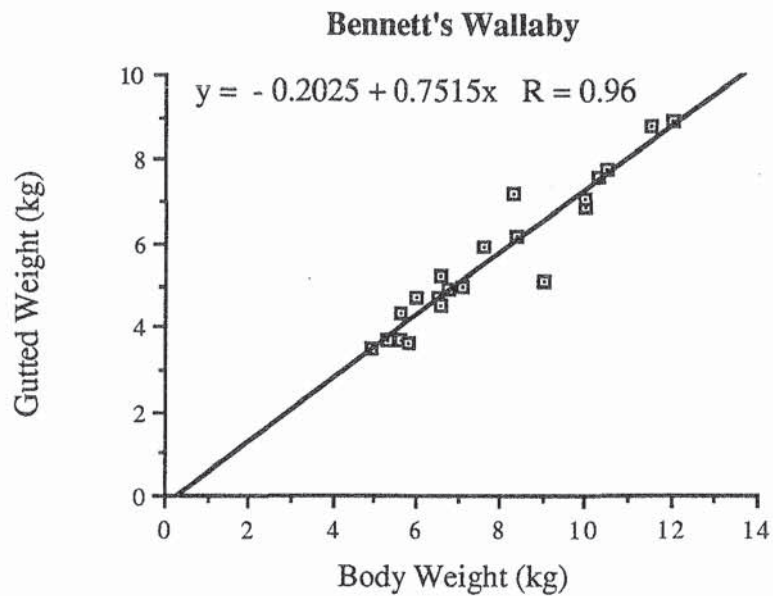


Figure 11 Relationship between gutted weight and body weight for Bennett's wallaby ($F = 204.2$, $df = 20$, $p < 0.0001$).

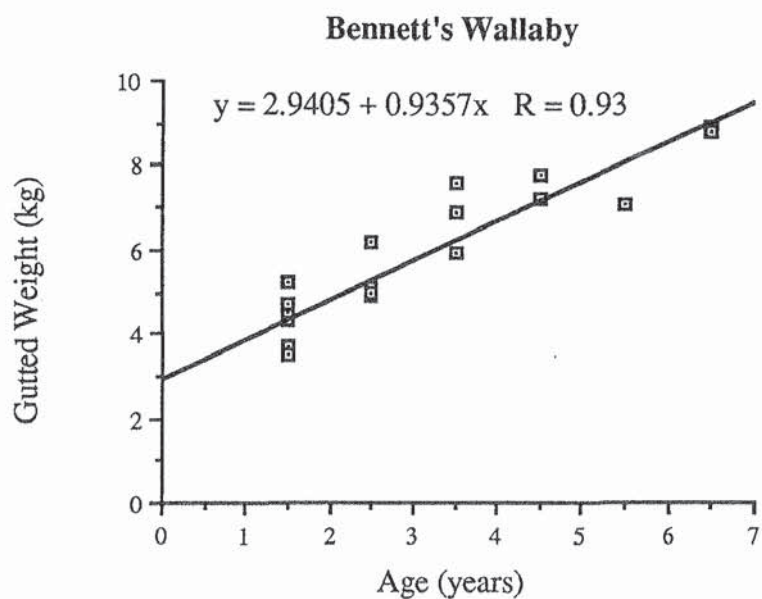


Figure 12 Relationship between gutted weight and age for Bennett's wallaby ($F = 116.6$, $df = 20$, $p < 0.0001$).

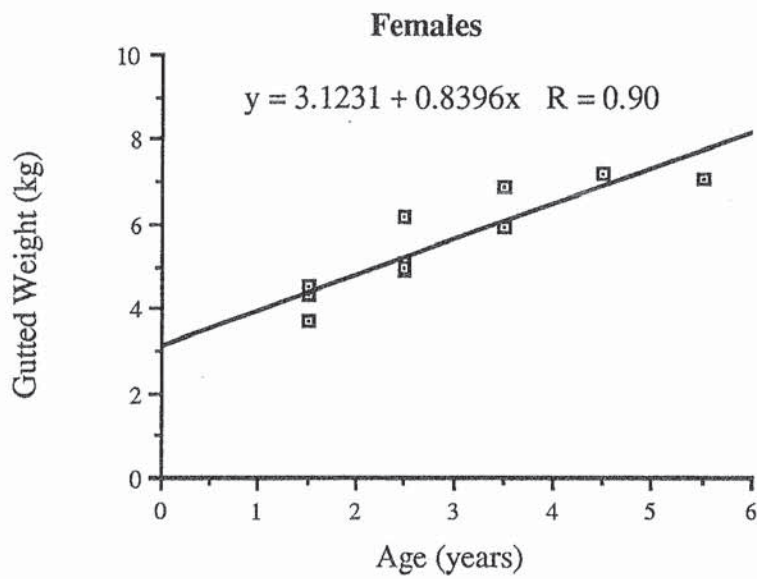
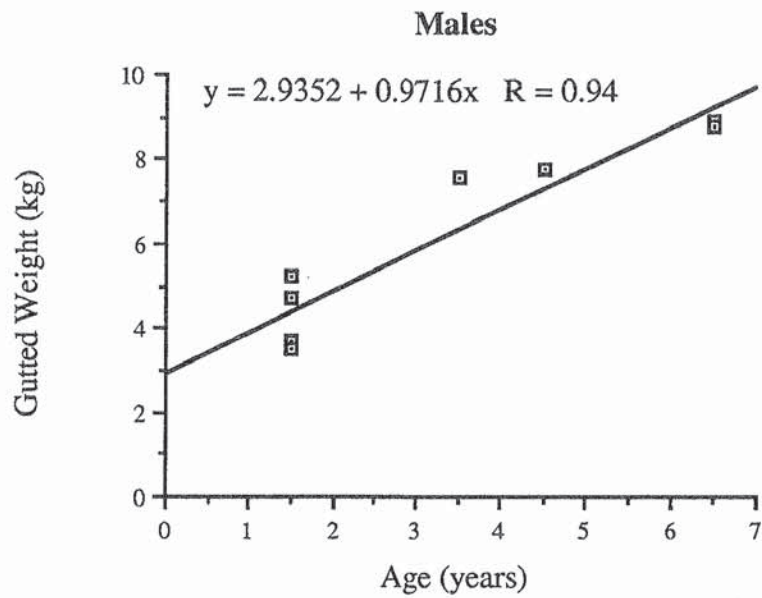


Figure 13 Relationship between gutted weight and age for Bennett's wallaby (Males: $F = 62.3$, $df = 9$, $p < 0.0001$; Females: $F = 37.0$, $df = 10$, $p = 0.0002$).

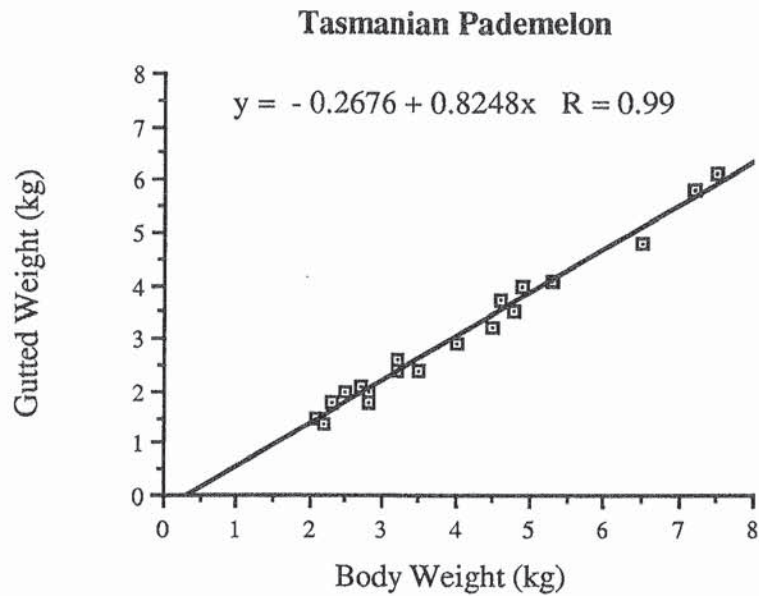


Figure 14 Relationship between gutted weight and body weight for the Tasmanian pademelon ($F = 965.4$, $df = 18$, $p < 0.0001$).

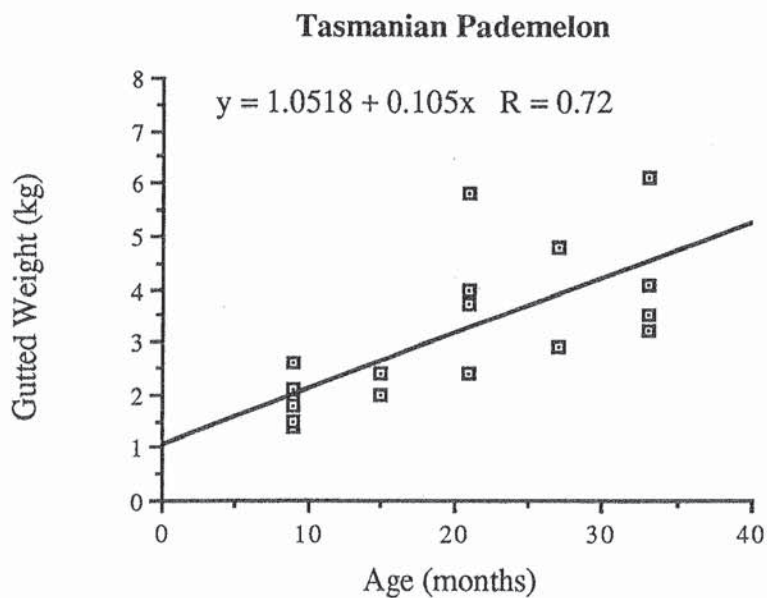


Figure 15 Relationship between gutted weight and age for the Tasmanian pademelon ($F = 18.6$, $df = 18$, $p = 0.0005$).

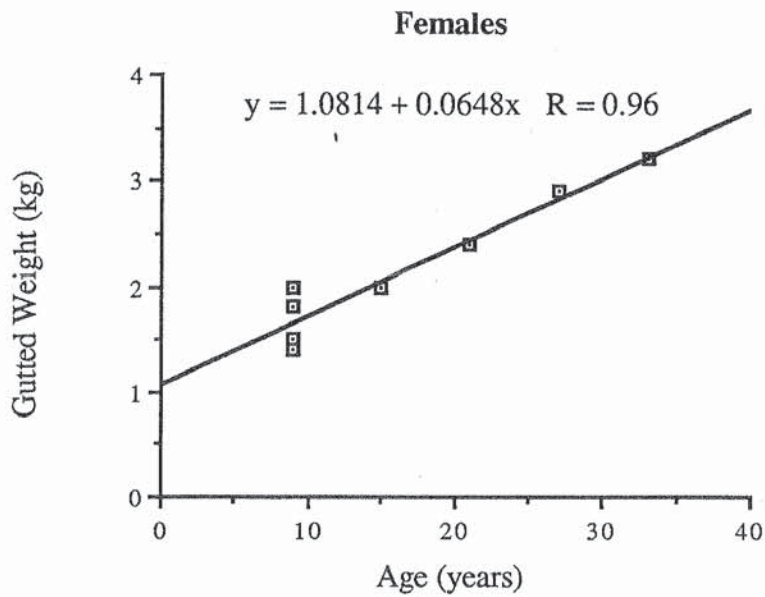
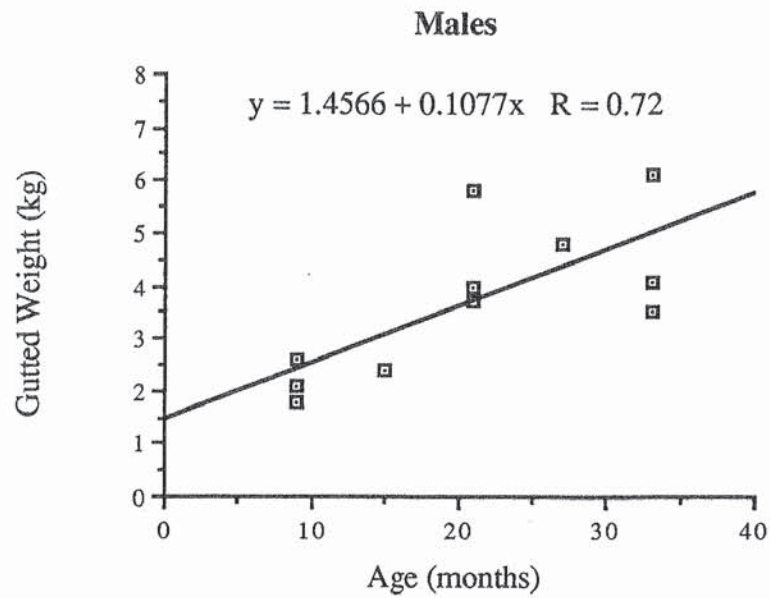


Figure 16 Relationship between gutted weight and age for the Tasmanian pademelon .
 (Males: $F = 9.9$, $df = 10$, $p = 0.0118$; Females: $F = 66.7$, $df = 7$, $p < 0.0002$).

3. Correlations Between Skin Measurements and Age

Wallabies have been harvested in Tasmania for their skins since the earliest days of European settlement. The size of this harvest has fluctuated greatly depending upon the strength of overseas markets which determine the price paid to hunters for skins. Thus during the late 1970s and early 1980s skin prices improved which lead to a massive increase in the trade of skins. Since 1986 the trade has virtually ceased due to the loss of access to overseas markets.

The aim of the section is to determine the usefulness of obtaining age structures of wallabies from skin measurements.

Bennett's wallaby skins were obtained from the Lemont and Nunamara study areas. Tasmanian pademelon skins were obtained from the Nunamara study area. In addition to skin weight, skin measurements were taken as shown in Figure 1. All skins were air dried for six weeks before the measurements were taken.

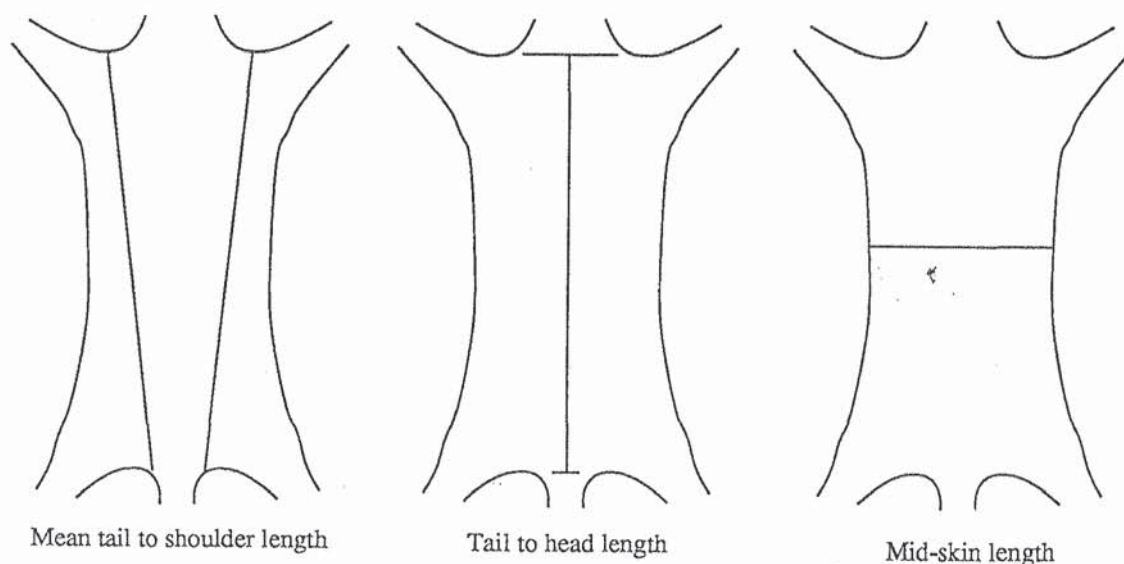


Figure 1 Skin measurements

The various correlations between skin measurements and age are shown in Figures 2-9. As sex can not be determined from the skins males and females were combined. For Bennett's wallabies significant correlations were obtained between age and skin weight, mean tail to shoulder length and tail to head length. However, the regressions only accounted for 30-40% of the variation. No significant regression was found between mid-skin width and age for Bennett's wallaby. For the Tasmanian pademelon significant correlations were obtained between age and mean tail to shoulder length and tail to head length. The regressions accounted for 50-60% of the variation. No significant regressions were found between age and mid-skin width and skin weight. The regression equations for Bennett's wallaby were statistically more significant than those for the Tasmanian pademelon. This is probably due the greater size range found in Bennett's wallaby.

The relationship between skin measurements and age is confounded by a number of factors:

- 1) A significant difference in size between males and females.
- 2) Different skinning and pegging-out methods among hunters which introduce major errors. For example the distance skins are stretched will greatly influence results.
- 3) Wallabies of the same age may vary significantly in size depending on the locality in which they were obtained (see chapter 4).
- 4) Weights of skins may vary depending on the drying time and the quality of the fur.

Consequently skin measurements can not be used to determine the detailed age structure of populations of either Bennett's wallaby or the Tasmanian pademelon. It may be possible to determine the ratio of adults to juveniles.

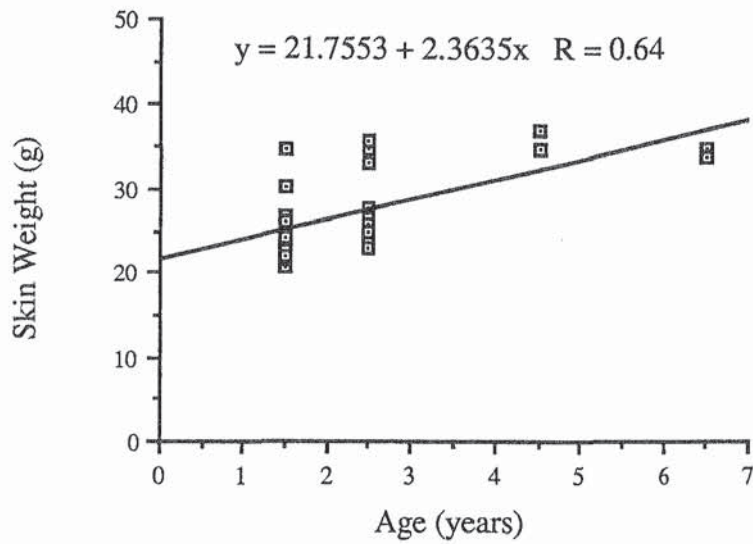


Figure 2 Relationship between skin weight and age for Bennett's wallaby ($F = 17.3$, $df = 26$, $p = 0.0003$).

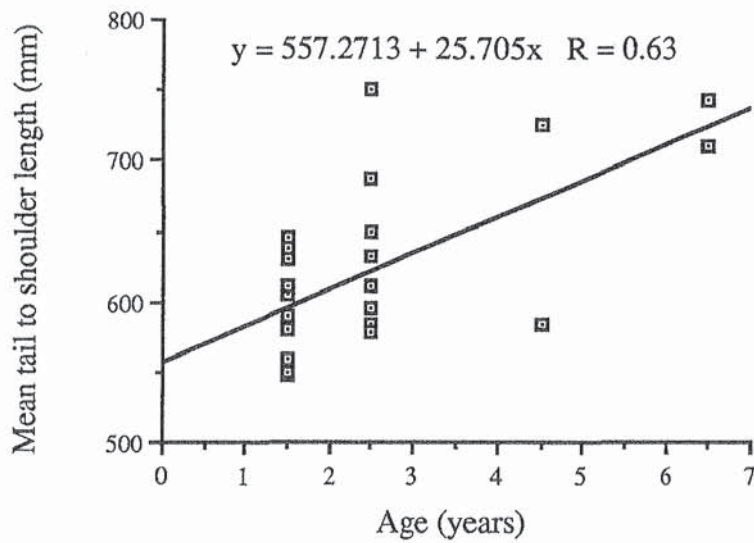


Figure 3 Relationship between mean tail to shoulder length and age for Bennett's wallaby ($F = 16.1$, $df = 26$, $p = 0.0005$).

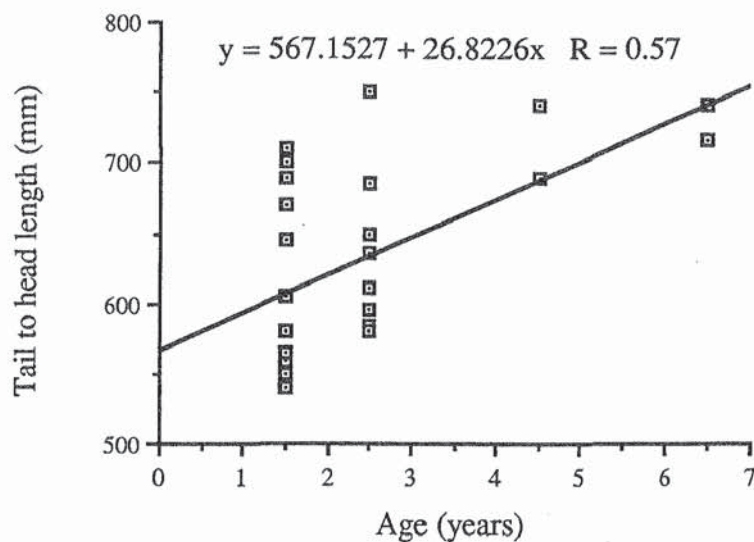


Figure 4 Relationship between tail to head length and age for Bennett's wallaby ($F = 12.2$, $df = 26$, $p = 0.0018$).

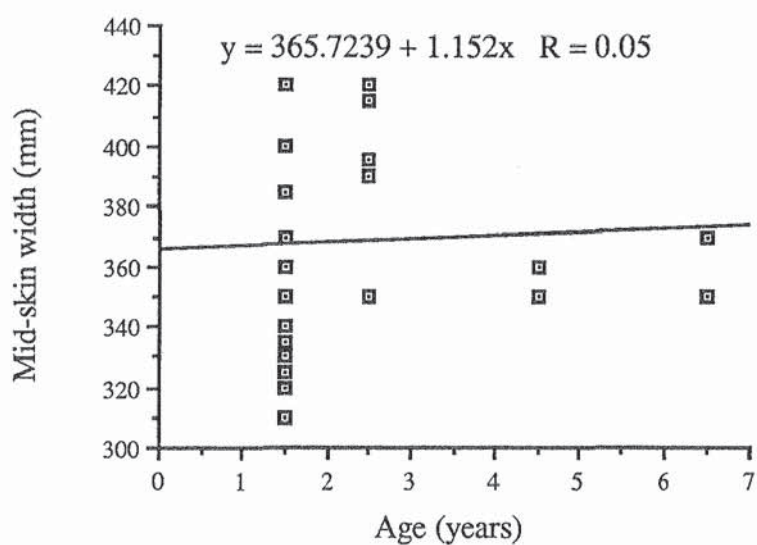


Figure 5 Relationship between mid-skin width and age for Bennett's wallaby ($F = 0.071$, $df = 26$, $p = 0.7917$).

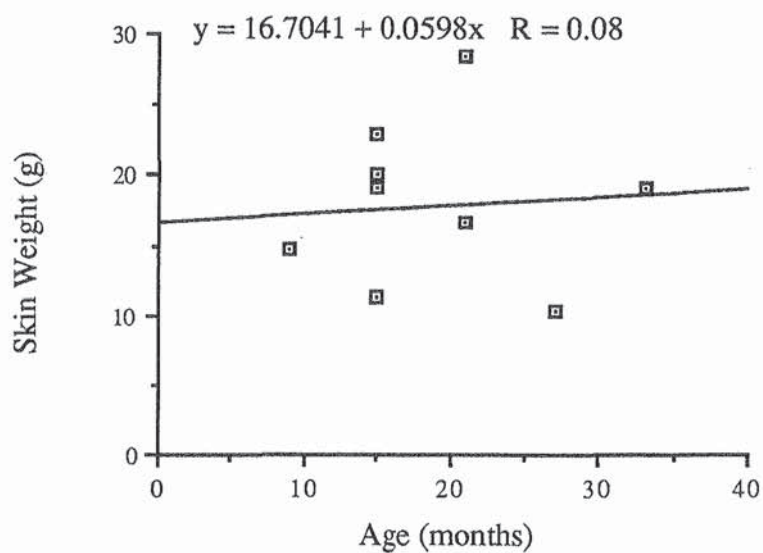


Figure 6 Relationship between skin weight and age for the Tasmanian pademelon ($F = 0.06$, $df = 9$, $p = 0.8186$).

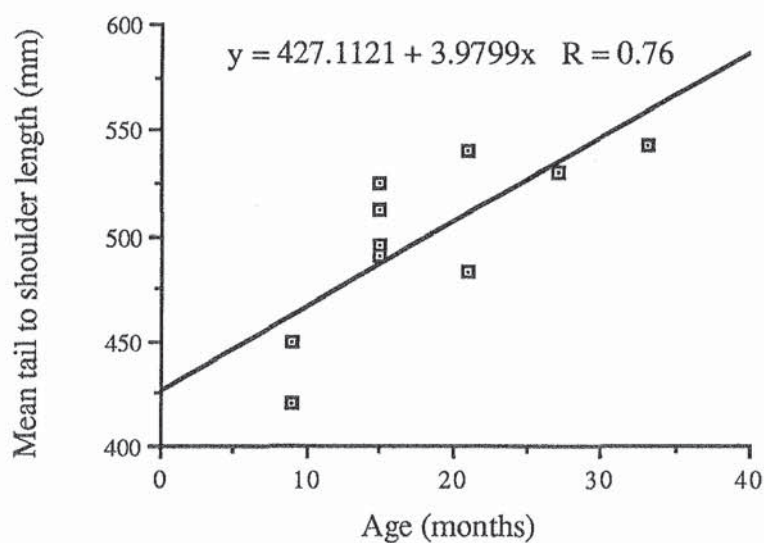


Figure 7 Relationship between mean tail to shoulder length and age for the Tasmanian pademelon ($F = 10.8$, $df = 9$, $p = 0.0111$).

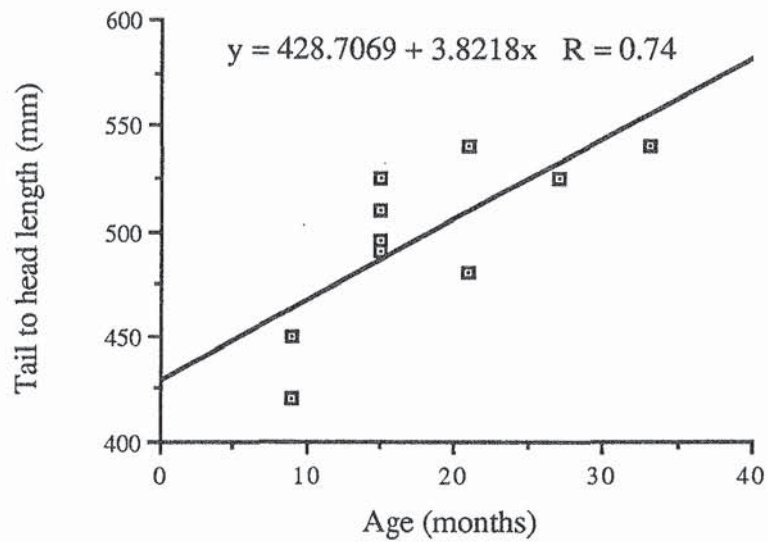


Figure 8 Relationship between tail to head length and age for the Tasmanian pademelon ($F = 9.7$, $df = 9$, $p = 0.0143$).

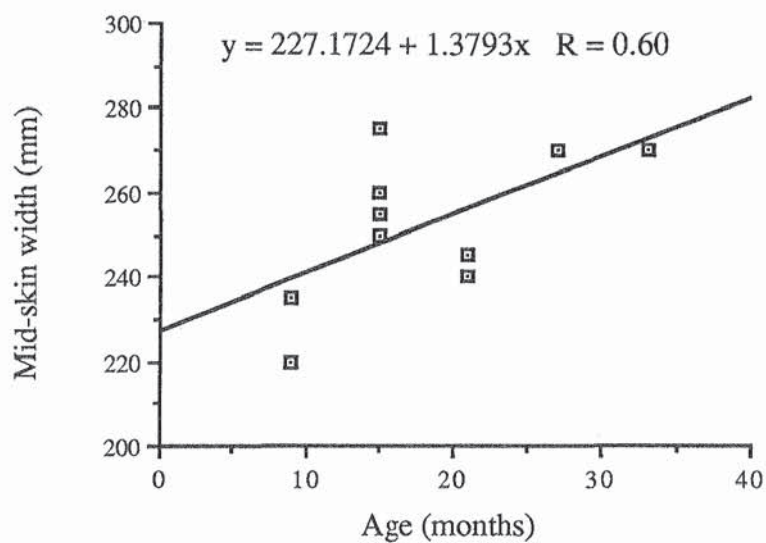


Figure 9 Relationship between mid-skin width and age for the Tasmanian pademelon ($F = 4.5$, $df = 9$, $p = 0.0668$).

4 . Size at Sexual Maturity

Probit analysis was used to assess weight at sexual maturity in same way that age at sexual maturity was determined in Chapter 5. The results are shown below.

Species	Sex	Median Weight at Maturity (kg)	95% Confidence Limits	
			lower	upper
Tasmanian Pademelon	Male	4.5	4.4	4.7
	Female	3.1	2.9	3.2
Bennett's Wallaby	Male	10.5	10.2	10.8
	Female	7.1	6.9	7.4

5. Testes Measurements

During this study a number of external testes measurements were taken in order to determine their relationship with testes weight. This information would prove useful for field studies involving live animals. The relationship between testes + scrotum weight and testes weight was also determined as the former weight is quicker to determine.

Testes were severed at the part of the peduncle closest to the body. The testes were kept frozen until the measurements were taken. Testes height, width and length are illustrated in Figure 1. All measurements were made using vernier callipers. Testes volume was measured by calculating the amount of water displaced by the testes when they were placed in a graduated volumetric cylinder.

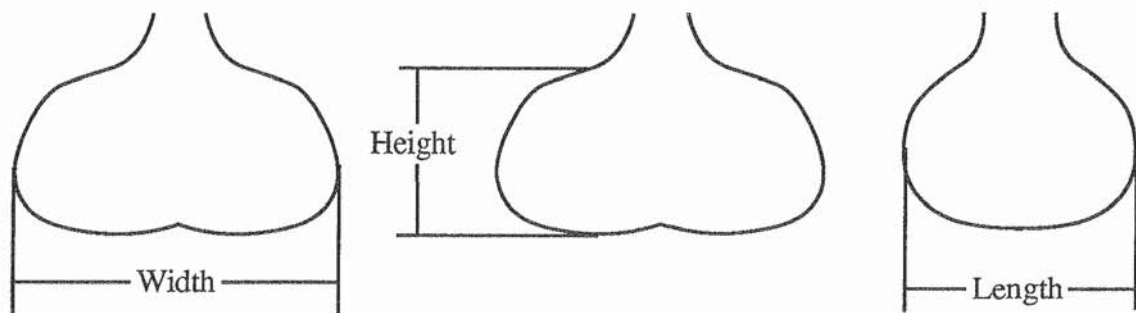


Figure 1 External testes measurements.

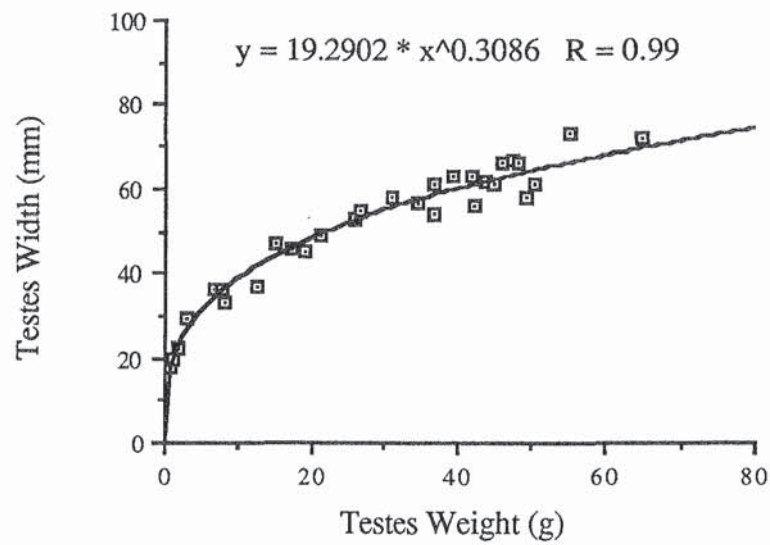


Figure 2 Relationship between testes width and testes weight for Bennett's wallaby (sample size = 34).

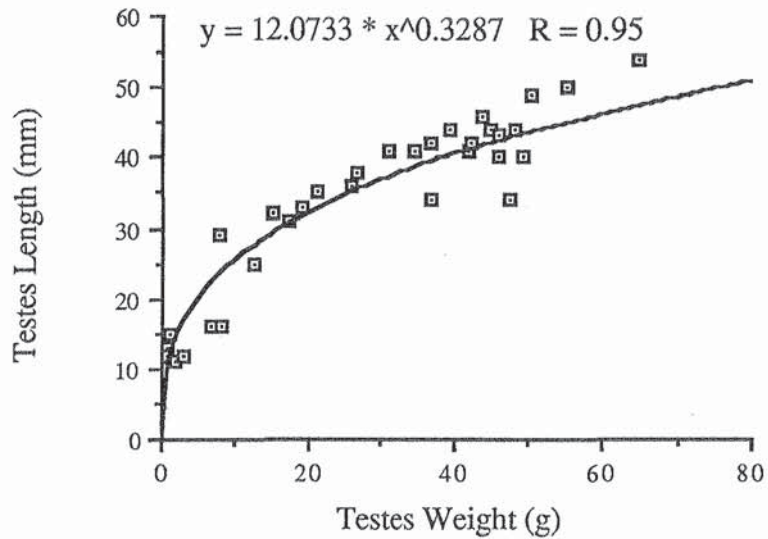


Figure 3 Relationship between testes length and testes weight for Bennett's wallaby (sample size = 34).

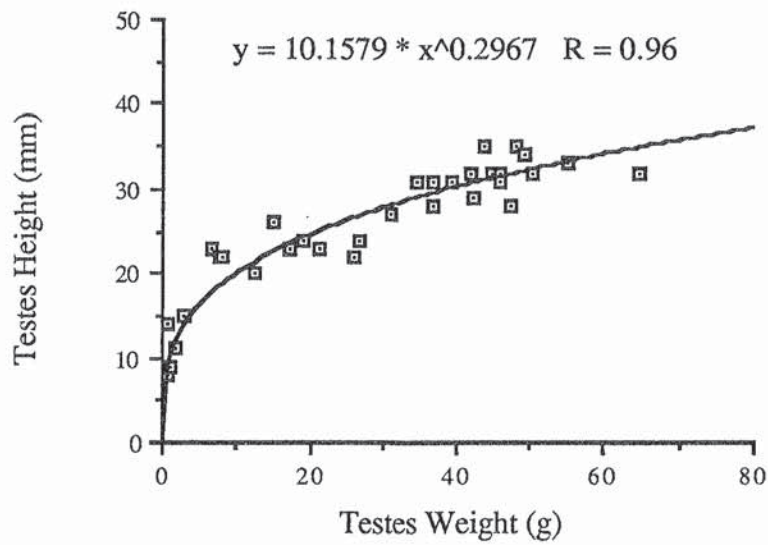


Figure 4 Relationship between testes height and testes weight for Bennett's wallaby (sample size = 34).

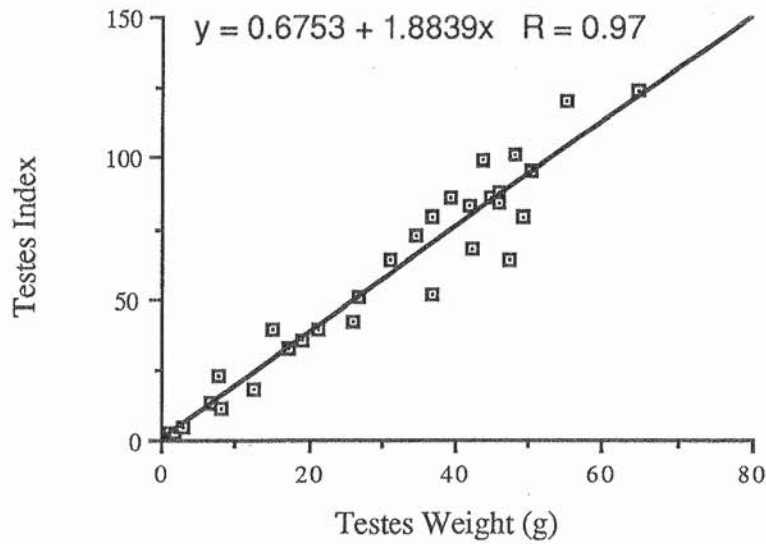


Figure 5 Relationship between testes index (width x length x height) and testes weight for Bennett's wallaby (sample size = 34).

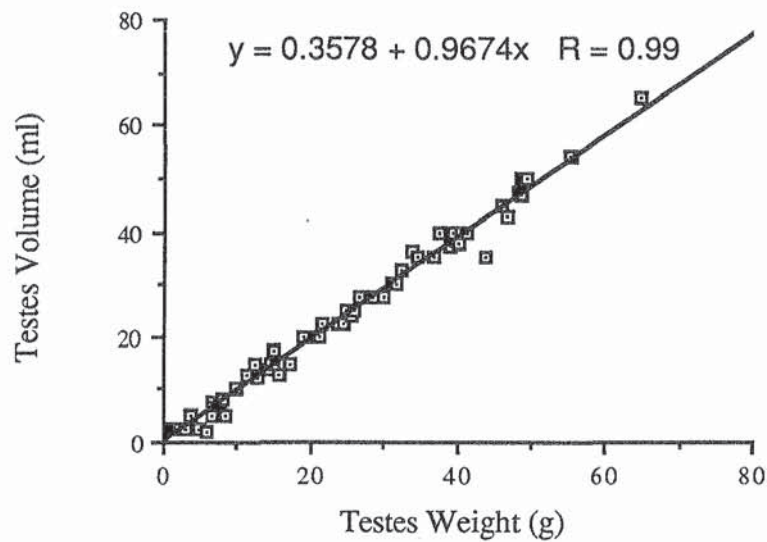


Figure 6 Relationship between testes volume and testes weight for Bennett's wallaby (sample size = 69).

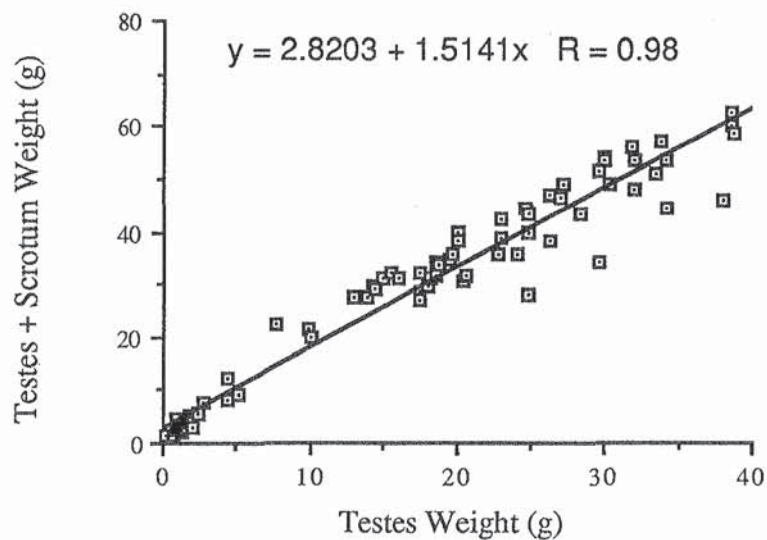


Figure 7 Relationship between testes and scrotum + testes weight for Bennett's wallaby (sample size = 90).

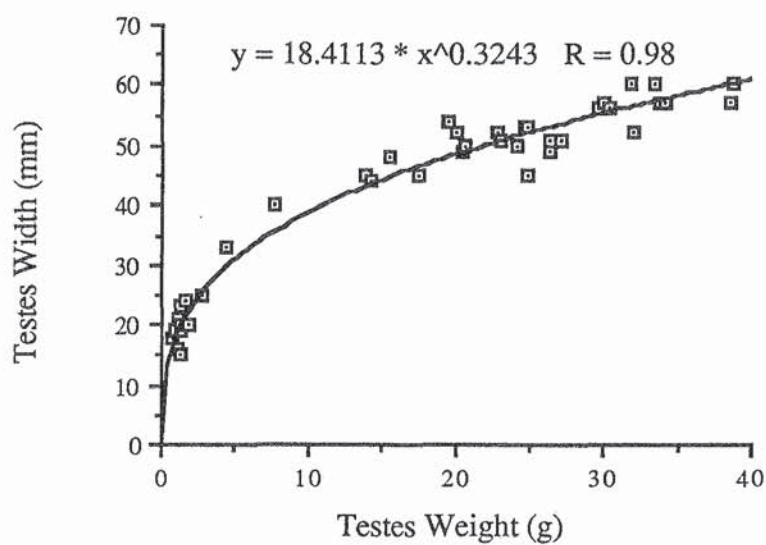


Figure 8 Relationship between testes width and testes weight for the Tasmanian pademelon (sample size = 45).

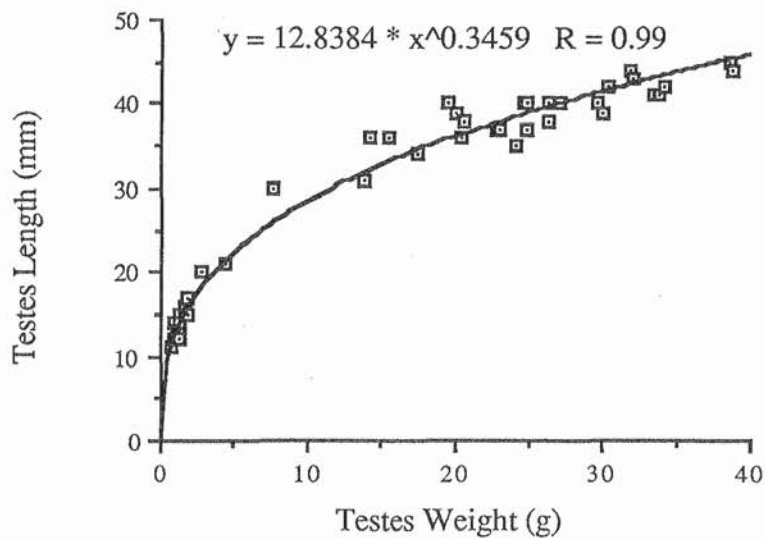


Figure 9 Relationship between testes length and testes weight for the Tasmanian pademelon (sample size = 45).

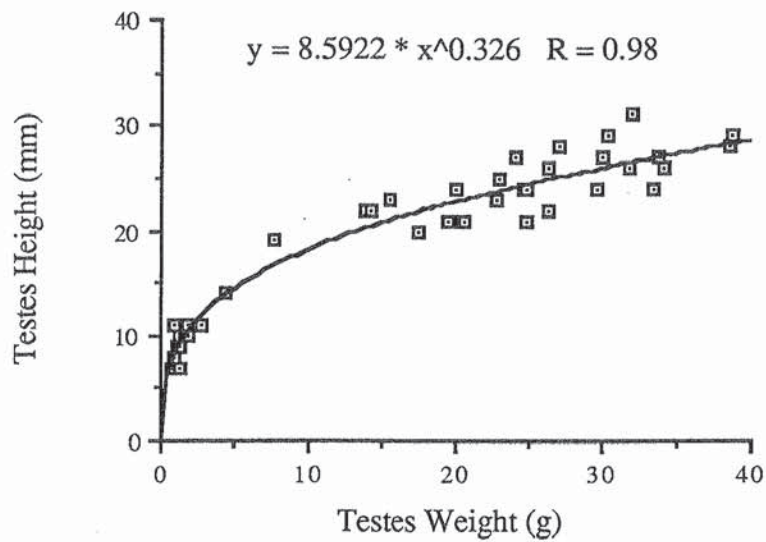


Figure 10 Relationship between testes height and testes weight for the Tasmanian pademelon (sample size = 45).

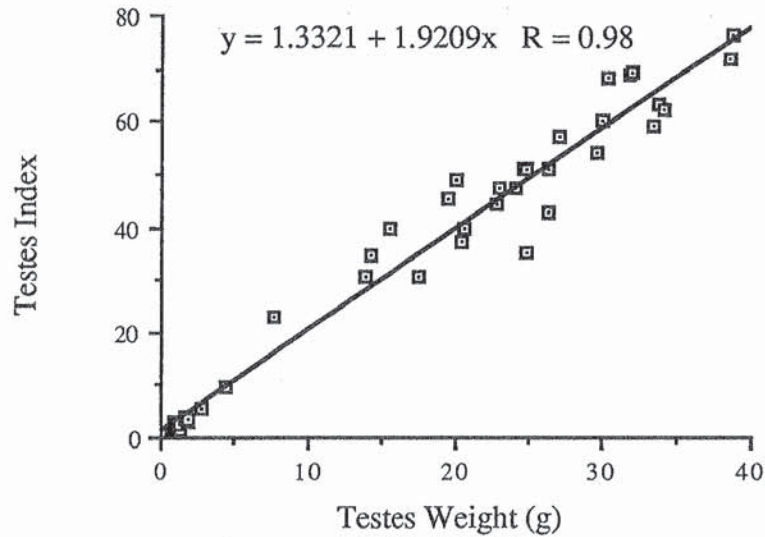


Figure 11 Relationship between testes index (width x length x height) and testes weight for the Tasmanian pademelon (sample size = 45).

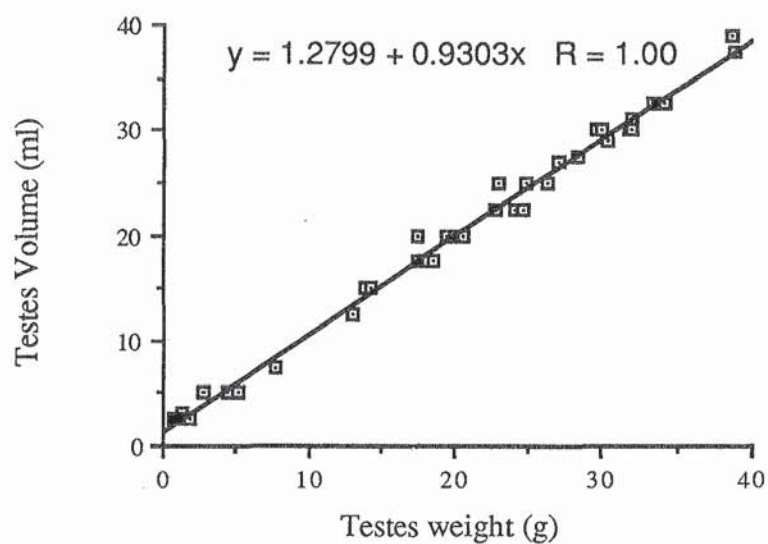


Figure 12 Relationship between testes volume and testes weight for the Tasmanian pademelon (sample size = 83).

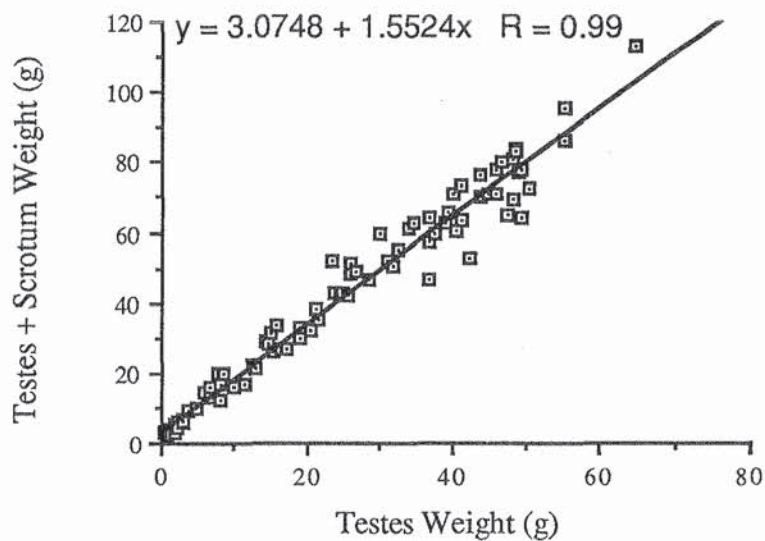


Figure 13 Relationship between testes + scrotum weight and testes weight for the Tasmanian pademelon (sample size = 86).