



SOCIO-ECOLOGY OF THE HAIRY-NOSED WOMBAT
(*Lasiorhinus latifrons*) IN THE
BLANCHE TOWN REGION OF
SOUTH AUSTRALIA

by

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Summary

The hairy-nosed wombat *Lasiorchinus latifrons* is a large herbivorous fossorial marsupial active mainly at night.

The wombat is adapted to the arid and semi-arid environment in which it lives by behavioural and physiological mechanisms of energy and water conservation.

Little is known about the demography and social behaviour of this wombat, however. In order to gain some information on the socio-ecology of the population of wombats inhabiting the Blanche Town region of South Australia studies of its ethology, reproductive biology, and ability to survive drought were undertaken to see whether reproduction, social behaviour and survival were apposite for the arid environment.

The ethogram was limited in range of behavioural components when compared with ethograms of similar eutherian mammals such as marmots, and when compared with ethograms of other marsupials. Social interactions were always initiated by males, which were territorial; while female wombats were less active socially than males. The intensity of social behaviour increased during breeding periods and was relatively low at other times, particularly during drought. The limited patterns of behaviour and stable social structure of the wombat may assist it to conserve energy.

There was a definite breeding season from July to December, but when there was drought during this period the wombats did not reproduce. The times of matings and birth were closely associated with patterns of rainfall and pasture growth. When enough rain fell to cause the growth of pasture of good quality, wombats became reproductively active as determined by anatomical and physiological measurements. The patterns of reproduction were interpreted as adaptations which ensured that wombats

did not expend energy in producing young in years in which they were unlikely to survive.

In view of the inherently low rates of water and energy turnover in this wombat, the patterns of reproduction and social behaviour probably explain how they survive droughts of at least 18 months duration which drive away or kill other mammals such as rabbits, sheep and kangaroos. Detailed biochemical, haematological and trace-element measurements showed little change during drought indicating that the wombat is relatively hardy. The fossorial habits of wombats in the arid environment appear to complement remarkably efficient adaptations to aridity, including the linkage of reproduction to the availability of food of good nutritional value.

DECLARATION

This thesis contains no material which has been accepted for any other degree or diploma in any University and to the best of my knowledge and belief, the thesis contains no material previously published or written by myself or any other person except where due reference is made in the text of the thesis.

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Publications

Some of the work described in this thesis has been published previously or has been accepted for publication and is in press. These papers and abstracts are listed below.

- 1) Brooks, D.E., Gaughwin, M.D., & Mann, T., 1978. Structural and biochemical characteristics of the male accessory organs of reproduction in the hairy-nosed wombat (*Lasiorchinus latifrons*). Proc. R. Soc. Lond. B. 201, 191-207.
- 2) Gaughwin, M.D., 1978. Ethology and social structure of the hairy-nosed wombat (*Lasiorchinus latifrons*). (Abstract). Bull. Aust. Mamm. Soc. 5, 28-29.
- 3) Gaughwin, M.D., & Wells, R.T., 1978. General features of reproduction of the hairy-nosed wombat (*Lasiorchinus latifrons*) in the Blanche Town region of South Australia. (Abstract). Bull. Aust. Mamm. Soc. 5, 46-47.
- 4) Gaughwin, M.D., 1979. The occurrence of flehmen in a marsupial - the hairy-nosed wombat (*Lasiorchinus latifrons*). Anim. Behav. 27, 1063-1065.
- 5) Gaughwin, M.D., Lee, V.W.K., & de Kretser, D.M., 1979. Seasonal variation in the reproductive status of the male hairy-nosed wombat (*Lasiorchinus latifrons*). (Abstract). Proc. Aust. Soc. Reprod. Biol. 11, 70.
- 6) Gaughwin, M.D., & Judson, G.J., 1980. Haematology and clinical chemistry of hairy-nosed wombats (*Lasiorchinus latifrons*). J. Wildl. Dis. 16, 275-279.
- 7) Gaughwin, M.D., 1980. The hairy-nosed wombat (*Lasiorchinus latifrons*) in captivity. Proceedings of a symposium of the Australian Mammal Society on keeping Australian mammals in captivity. Healesville, Victoria, January 1979. (in press).

CHAPTER 1

LITERATURE REVIEW

1.1 Wombats, desert environments and fossoriality

The socio-ecology and behaviour of the hairy-nosed wombat *Lasiorchinus latifrons* (Figure 1.1) (one species of the large herbivorous, fossorial marsupial family Vombatidae), has been studied over 4 years in the Blanche Town area of South Australia. *Lasiorchinus latifrons* is found patchily distributed in arid and semi-arid southern Australia (Figure 1.2), west of the river Murray (Aitken 1971). Until Wells (1973, 1978) undertook a study of behavioural and physiological adaptations of *Lasiorchinus* to its arid environment the only published works on the species, other than minor references in some comparative anatomical and physiological texts, were of an anecdotal or taxonomic nature.

Well's study encompassed investigations of activity patterns, thermoregulation and metabolic physiology of the species. He demonstrated that the wombat is adapted to an arid environment by physiological and behavioural mechanisms for conservation of energy and water.

But little is known of the population biology of the species, its social organisation, reproductive patterns or its ability to survive during the regular summer aridity and, frequently, longer droughts. The desert environment represents an extreme to which it appears wombats have become adapted (Wells 1973). Noy-Meir (1973) has recently reviewed the major features of desert ecosystems and considered their main attributes to be: (a) precipitation is so low that water is the dominant limiting factor for biological processes; (b) precipitation is highly variable through the year; occurring as infrequent and discrete events; (c) variation in precipitation has a large, random (unpredictable) component. In hot deserts ambient

Figure 1.1 The hairy-nosed wombat *Lasiorhinus latifrons*; a photograph taken on a sunny day in winter when the wombat had emerged from its burrow to bask in the sun.. The lower photograph is of one of the wombats kept at the Waite Agricultural Research Institute.



Figure 1.2 Habitat of the hairy-nosed wombat in the Blanche Town region of South Australia showing one of the warrens observed as part of the behavioural study.



temperatures are so high that evaporation represents a major source of water loss from the ecosystem. Water is scarce, it is generally available only through plants and it determines the abundance of food. Throughout most of their lives small animals that evolved in and are confined to deserts will not have access to free water.

Desert environments have been studied by biologists interested in adaptation probably because such environments present a biologically limiting zone of survival. The ways in which organisms live and reproduce in the desert are diverse and there is a wide range of adaptations often with great differences between species in behavioural and physiological mechanisms (Macfarlane 1964, Schmidt-Nielsen 1972).

Heat, and shortages of food (energy and protein) and water are the three most potent stresses of the desert, adaptations to which can be morphological, behavioural or physiological, or combinations of these. Adaptive traits may be encoded in genotypes or they may be part of the elasticity inherent particularly in behavioural and physiological processes.

The diverse nature of adaptive mechanisms among desert animals may be illustrated by comparing the ways in which different species cope with the heat of the desert environment. The mammals of deserts can be classified broadly as 'avoiders' or 'endurers' of heat. Wombats, some bandicoots and dasyurids, and small macropods such as the spectacled hare-wallaby *Lagorchestes conspicillatus*, are examples of marsupial 'avoiders', like the eutherian desert ground squirrels, jackrabbits and the small desert rodents, such as *Notomys alexis*. These animals avoid heat by living a large part of their lives in

burrows (wombats, bandicoots) or in dense grass-shelters (wallaby). Burrowing is probably a genetic behavioural adaptation enhanced in some cases by nocturnal habits (wombats and bandicoots). Some desert-dwelling ground squirrels are active during the heat of the day, but they avoid hyperthermia by retreating to their burrows for short periods to unload accumulated body heat (Hudson 1962).

Although these behavioural and genetic adaptations occur, most of the 'avoiders' will die of hyperthermia if exposed to high ambient temperatures for more than a few hours. They lack the morphological and physiological adaptations possessed by those animals which endure the heat, such as camels, the oryx and some kangaroos. These animals are exposed to the extremes of desert temperatures. Some like oryxes and camels sweat but also tolerate a degree of hyperthermia; others shelter in the shade of trees (kangaroos) and pant to maintain body temperature. Highly reflective or insulative coats of body hair are a characteristic feature of these animals also.

Similar complex and diverse adaptations to cope with food and water shortages occur and will be considered later.

The wombat is a uniquely large mammal to have a fossorial escape behaviour. Similarities in morphology, feeding patterns and fossoriality itself suggest that selection has favoured individuals of both *Lasiorchinus latifrons* and *Vombatus ursinus* which have adopted underground habits. The studies on wombat thermoregulation by Wells (1973, 1978) show the importance of living in burrows as a mechanism by which *Lasiorchinus* avoids extremes of day-time temperatures which would otherwise kill most individuals. Observations by McIlroy

(1973) suggest that a similar situation is true for *Vombatus ursinus*.

While fossoriality may be an adaptation in itself it is likely that this trait would influence other aspects of lifestyle. For example Crook et al. (1976) note that anything which forces animals to forage radially from a fixed point or refuge, seems to have a great influence on social structure.

If the ancestors of the Vombatidae (some of which were the size of large pigs) were not fossorial and lived in agreeable environments, then increasing aridity, or scarcity of food may have favoured evolution towards fossorial habits. The main advantages of living beneath the ground for part of the day in arid regions are avoidance of heat and conservation of energy and water.

The occupation of a burrow places many constraints on the physiology of a mammal because the design and location of burrows will significantly affect the diffusion of respiratory gases within them. Many of the physiological characteristics of *Lasiorchinus* such as lowered metabolic rate and tolerance of hypothermia, can result in expansion of the steady-state respiratory space which is otherwise restricted in a typical burrow (Wilson & Kilgore 1978). Thus, such functions may in part represent adaptations to a fossorial existence as well as to an arid environment. It may be necessary for fossorial animals to modify the structure of their burrows to allow greater diffusion of respiratory gases within them. If this is the case such modifications may have major effects on social structure and reproductive patterns.

Any interpretation of reproductive patterns, social structure or demography of a species such as the wombat should consider the influence fossoriality has on lifestyle.

The studies of Wells (1973, 1978) have clearly indicated some of the major physiological and behavioural adaptations of *Lasiorhinus* to an arid environment. Against the background of conservatively low energy and water turnover rates it is useful also to examine those aspects of wombat biology which affect its population dynamics, especially survival during drought, reproduction and social behaviour. In addition, the study of a major family of marsupials markedly different from the intensively studied macropods should broaden the base of knowledge of the Marsupialia as a whole. Because *Lasiorhinus* is an inhabitant of arid regions, it provides a unique opportunity to consider the evolution in a marsupial of a life-history pattern under the influence of fossoriality and aridity.

1.2 Adaptations and survival of herbivorous marsupials during drought

Drought is a common extreme of arid environments and is likely to act as a strong selective agent through its effects on both individual survival and on group reproduction. There is an increasing amount of palaeontological evidence to suggest that drought and increasing aridity were the causes of the extinction of much of the Australian megafauna (Horton 1978). Two thirds of the Australian environment is arid or semi-arid and has a high frequency of drought. Despite this many species of mammals survive and reproduce under these conditions (Ride 1970). Some species have benefitted from the provision of water by man while many others have become extinct because the environmental changes brought about by man

were beyond their capacity for adaptive change (Newsome 1975).

Individual survival under conditions of drought is determined by a number of factors, but those individuals adapted to habitats with little food and water would be more likely to survive and reproduce.

Perhaps the most intensive investigations of adaptations for desert life have been of a physiological nature, and for mammals a number of general adaptations have been described including low water turnover, low metabolic rate, and efficient thermoregulation and urine-concentrating mechanisms (Schmidt-Nielsen 1972).

Macfarlane (1978) has described three main types of desert inhabitants based on their ability to survive without water. They include those species which evolved in dry conditions, others more broadly adaptive but with less desert specificity and those that evolved in wet conditions, but survive opportunistically by behavioural means and are vulnerable to heat and drought.

Among the indigenous Australian mammals a similar range of desert inhabitants can be found (Brown 1974, Ride 1970) but it is possible that some marsupials are in one sense pre-adapted for desert life because many have low metabolic rates (Dawson & Hulbert 1969). Desert wombats (Wells 1973, personal communication) and the bandicoot (Hulbert & Dawson 1974), like desert eutherians, ^(Macmillen & Lee 1970) have lower metabolic rates than similar species inhabiting less arid environments.

The tolerance of heat by some arid-zone kangaroos is not needed by burrowing mammals such as bandicoots and wombats. The number and degree of the stresses to which a species has to accommodate may determine its ability to survive conditions of drought.

There have been few studies of survival of marsupials in arid or semi-arid regions during drought. Observations have been concentrated on the Macropodidae including the euro *Macropus robustus*, red kangaroo *Macropus rufus*, and the quokka *Setonix brachyurus*.

The quokka was not regarded by Brown (1974) as an arid-zone species; nevertheless it is often found in regions where regular summer droughts (and occasionally longer ones) occur (Main 1971).

The population biology of the quokka and the factors influencing individual survival on Rottnest Island have been studied in great detail (reviewed in Main 1971, Tyndale-Biscoe 1973, Barker et al. 1974). The pattern that emerged from these studies was that during, and shortly after the summer drought many quokkas died, mostly young animals, but in extended droughts adults also died. The causes of this mortality were probably the effects of chronic water deprivation (Tyndale-Biscoe 1973) and a debilitating anaemia related to inadequate nutrition (Barker et al. 1974). Barker et al. (1974) found experimentally, that quokkas on a low nitrogen diet lost 13-17 per cent of their body weight over an 8-week period and developed anaemia. Eight of the 11 animals subsequently died at the end of the experiment when they were exposed to cold weather.

In the field Holsworth (in Main 1971) found that individual quokkas could lose 30-40 per cent of their body weight during drought and they usually died after this. Barker et al. (1974) found that male and female quokkas lost 28 and 18 per cent body weight respectively over a 5-month period (October-March). Any extension to autumn of the regular summer drought which occurs

on the island, resulted in considerable mortality and data on population-size support this (Niven 1970).

Physiologically the quokka possesses many characteristics including low metabolic rate and small nitrogen requirements (Fraser & Kinnear 1969) suiting it to arid conditions. It is able to tolerate high ambient temperatures (Bartholomew 1956), but it probably expends much body water in the process. In the water-deficient environment of Rottnest Island this requirement for water contributes significantly to the poor condition of the animals in summer (Tyndale-Biscoe 1973).

In contrast to quokkas, the larger kangaroos seem better adapted for survival in drought conditions although in different ways. Male and female red kangaroos (with access to water provided for stock) in north-western New South Wales lost 27 per cent and 18 per cent of their body weight respectively during a 12-month (c.f. quokkas) drought (Myers et al. 1976). These authors considered protein, energy and water deprivation to be the causes of death. Significant mortality during that drought may have occurred, probably in the adult males of the population. Male deaths seem to be characteristic of most red kangaroo populations, which is indicated by a marked imbalance in the sex-ratio favouring females (Myers et al. 1976, Newsome 1977a). This piece of evidence suggests that the greater weight loss of adult males is an important factor contributing to their mortality. The data of Storr (Main 1978) suggest that in regard to water, larger males are at a disadvantage compared with females on a body weight basis; that is, males lose any metabolic advantage of large body size in reducing energy and nitrogen metabolism. Starvation however, is probably the ultimate cause of

death in red kangaroos because the populations that have been studied have had access to water provided for stock.

Storr's data (Main 1978) also showed that male euros in Western Australia lost 25 per cent of their body weight over a 7-month dry period whereas females showed no significant weight loss. Interestingly, in the same environment female red kangaroos lost no weight, compared to a 33 per cent reduction in males. Ealey & Main (1967) attributed weight loss in euros to negative nitrogen balance reflected in low concentrations of haemoglobin in blood. The euro appears to be slightly better adapted to arid conditions than the red kangaroo, both in nitrogen requirements and because of its behaviour in seeking the shelter of caves, apparently a genetic trait. Taxonomically the euro and red kangaroo appear to be rather close in their common ancestry (Calaby & Poole 1971) possibly reflected in the similarity of some of their functions, including water turnover under standard conditions and in response to dehydration (Denny & Dawson 1975a,b). Euros probably require less nitrogen and energy for maintenance than red kangaroos (Hume 1974) which is suggested also by their ability to survive on pastures of low nitrogen content where red kangaroos are not found (Newsome 1975).

The interpretation of the ability of euros and red kangaroos to survive drought is complicated by the effects of pastoral practice on their habitat (Newsome 1975). Probably, euros in non-pastoral areas could only survive drought by using rock shelters, while red kangaroos are reported to seek refuge in flood-outs at the ends of creeks. Newsome (1975) in discussing the comparative ecology of the two species, suggests that diet was the important ecological factor affecting the distribution and survival of the species. The additional

water requirements of red kangaroos as a result of living in the open necessitate an association with water much of which they get through choosing green feed. It is probable that under natural conditions the population density of both species remained relatively low and that mortality during drought occurred mainly in large males (and juveniles).

One pattern that emerges from these studies on macropods is that large body size is a distinct disadvantage during drought since it is associated with rapid weight loss and mortality.

Because the behavioural activities of an animal represent a large source of energy expenditure above that required for maintenance (Moen 1973), it is relevant to consider social structure and social ethograms when trying to understand patterns of survival and mortality.

Before considering the role of reproduction in desert adaptation it is valuable to note the importance of the high rates of water and energy use by juveniles and sub-adults. Main (1978) has emphasized that juveniles may lack the full development of functions for the desert and consequently would be less likely to survive a long drought than adapted adults, which have lower rates of demand on food and water. The works cited previously suggest a high juvenile mortality. It is in this light that the importance to population recruitment of reproductive rate and adult survival should be considered.

1.3 Reproduction

1.3.1 Patterns of life-history and reproduction

If components of a gene pool are to multiply in a population,

phenotypic reproductive success is essential, as well as adaptation to environmental conditions. Because an individual can survive under adverse conditions it does not necessarily follow that successful reproduction will occur. Reproduction of genes can be the result of a wide variety of phenotypic reproductive patterns (Williams 1966, Wilson 1975) but their success or failure can only be measured in terms of the size of the population and its age structure. Reproductive efficiency can be predicted with a knowledge of fecundity, lifespan and age-specific mortality.

An adaptive reproductive process favours maximum genetic representation in successive generations. This can be achieved by a variety of means measured by the fitness of genotypes, and quantified by the Malthusian parameter (Fisher 1958) or relative rate of population increase r in the equation $\int_0^{\infty} l_x m_x e^{-rx} dx = 1$, where l_x and m_x are the proportions of individuals alive and dead at age x respectively. Wilson (1975) notes that classical theories of natural selection are concerned mainly with its effect on r in situations independent of population density. This may in part represent a confusion of terms since Brown (1975) notes that the relative rate of population increase r for genotypes is also increased in density dependent situations. He prefers the term r -max (minimal deaths other than those due to old age) which does become smaller with density.

The two aspects of a selection mechanism, density dependent and density independent have been formalized in the theory of r and K (carrying capacity of the environment) -selection (MacArthur & Wilson 1967). Fisher was probably aware of K -selection because

he noted that any net advantage gained by an organism will be conserved in the form of an increased population and not an increase in r which, due to environmental effects is always kept near zero. Changes that do occur during selection result in a change in r ; but in K-selection, genotypes that achieve a higher r as a result of lowered death rate are more successful (because increased birth rate would add too many individuals competing for resources). The population grows from an old to a new and higher K (carrying capacity). During growth, r is positive but it returns to zero when the new K is reached. Afterwards K is higher but birth rate and r -max are likely to be lower (Brown 1975). Consistent with this sort of selection would be increased specialization to the prevailing environment. For example, in an arid environment K could be increased by selection favouring a lower metabolic rate since each animal requires less food.

A number of ecological consequences or associations follow from these theories. The studies of Lack (1966) on birds have often been cited (Brown 1975, Wilson 1975) as an example of a situation where selection has favoured the production of an optimum rather than the maximum number of young, which ensured maximum possible genetic reproduction. A mammalian example of this is possibly the Olympic marmot *Marmota olympus* which breeds every second year, apparently below its maximum reproductive rate (Barash 1974).

While many examples can be found to fit the MacArthur-Wilson model (Brown 1975, Wilson 1975) one noticeable problem in its application is a lack of knowledge of the degree of predict-

ability in species' environments. The basic idea behind r-selection is unlimited available habitat, and for K, a saturation of the carrying capacity of a habitat; but in deserts the situation is not so precise, since the environment may range unpredictably from conditions of drought to an abundance of food.

In unpredictable situations a measure of year to year variation in reproductive effort is possibly more relevant to an understanding of life-history mechanisms and selection processes (Swingland 1977). Most models or theories are limited in their application; though many of the tenets of the theory of r and K-selection have wide application particularly when considered in terms of an r-K continuum (Pianka 1970), the importance of temporal variations in reproductive events (often a feature of desert environments) and possible variable shifts within individuals of reproductive patterns, have not been considered (Nichols et al. 1976). Recently, more attention has been given to the evolution of demographic processes in randomly fluctuating environments (Schaffer 1974, Wilbur et al. 1974) and the conclusions drawn appear relevant to desert organisms. Both Schaffer and Wilbur et al. note the importance of determining whether reproductive success or adult survival is principally affected by environmental fluctuations. In general Schaffer (1974) proposes that for iteroparous populations, variation in fecundity selects for reduced reproductive effort in all individuals while variation in adult survival selects for increased breeding. Wilbur et al. (1974) suggest that if juvenile survival is low and unpredictable there should be strong selection for long adult life, delayed maturity and iteroparity.

Entirely different ecological circumstances can select for apparently similar life-histories (and this is a reason for caution in acceptance of r-K tenets). Wilson (1975) was aware of this when he said that 'longevity and low fertility are compensatory traits favoured by natural selection under either one or two opposite environmental conditions' such as a highly productive and predictable, stable, environment or a harsh unpredictable environment. It is interesting to note that in the latter situation the best theoretical option for organisms is to engage in opportunistic, irregular reproduction keyed to occasional times of plenty (Holgate 1967).

Desert environments are highly variable, but it is likely that their lower resource levels will be one of the major determinants of population structure. Selection could act differentially in producing reproductive and somatic adaptations. Lower metabolic and water turnover rates and the other physiological characters of desert animals are clearly adaptations to lower resource levels, but highly irregular reproduction is a flexible adaptation to both high and low resource levels which cannot be considered as a fixed part of an r-K continuum.

A genetically determined life-history process can be considered to reflect the average effect of the environment on individual survival and reproduction in previous generations. In a surviving, reproducing population an optimum mechanism can be considered to have evolved. In many temperate zone animals, for instance, photoperiod control of breeding season is thought to have evolved to allow production of weaned offspring at a time favourable to their survival (Sadleir 1969). With the

rotation of the earth as the key environmental determinant of such reproductive patterns there is a reliably regular signal.

Before considering published works on reproduction in larger herbivorous desert marsupials it is relevant to note that Weir & Rowlands (1973) concluded, after reviewing physiological and anatomical aspects of mammalian reproduction that 'there are no obvious patterns of mammalian reproduction that can be correlated with taxonomy or habitat'.

Against this background it is useful to examine apparent differences between eutherian and marsupial mammals in reproductive functions.

1.3.2 The marsupial mode of reproduction

At the anatomical and physiological level the characteristic features of marsupial reproduction which distinguish it from the eutherian mode relate to gestation and its endocrine control, and to the different characteristics of the ova. There are no apparent functional differences between male marsupial and eutherian modes of reproduction (Tyndale-Biscoe 1973, Parker 1977).

Why the marsupial condition should have evolved at all is a complex question. Recent workers have emphasized the role of different selective mechanisms that could have led to the evolution of the marsupium in the eutherian/marsupial stock rather than isolation (Kirsch 1977, Parker 1977). Examples of the success of the marsupial mode of reproduction both in its own right and in competition with placental mammals are given by Low (1978).

Despite this, the comments of Weir & Rowlands (1973) are still relevant and it is not possible to specify even a few of the possible selective factors which favoured marsupial reproduction.

Low (1978) suggested that marsupials have long been under selection imposed by frequent loss of offspring. This is plausible, but she emphasises too strongly the adaptive nature of embryonic diapause in kangaroos (clearly characteristic of macropods) and gives little consideration to other marsupials without diapause, which weighs against this hypothesis.

No authors have been able to show that different ecological conditions existed for placental and marsupial mammals in the Cretaceous and later, which may have (in the long-term) favoured different modes of reproduction. Any mechanism that works is effective, since selection is on young produced, not on how they are produced (Nalbandov 1973).

One outstanding feature of marsupial reproduction, the concentration of maternal effort on lactation rather than embryonic development (Low 1978), could theoretically, have been favoured by uncertain environments (Schaffer 1974), but it is difficult to conclude that this ecological circumstance alone favoured the marsupial mode of reproduction when both groups probably experienced similar conditions in America during the Cretaceous.

Once the marsupial mode of reproduction became established it was not subject to great evolutionary modification probably because it was adequate for maintaining populations.

1.3.3 Patterns of reproduction in desert marsupials

Among the larger herbivorous desert marsupials patterns of reproduction among the macropods have again been the most studied. A consistent finding is that drought inhibits reproduction since it affects the survival of young and aspects

of the physiology of reproduction.

In central Australia, reproduction in the red kangaroo is non-seasonal and opportunistic (Newsome 1965, 1975). In this species ovulation depends on a flush of green pasture, and often, conditions suitable for reproduction do not occur. The environmental requirement for the production of a mature kangaroo appears to be a series of 2-3 years of good food supply (Newsome 1977b). In prolonged droughts the majority of female kangaroos become anoestrous, and no diapausing blastocysts are found (Newsome 1964).

The euro is less dependent on green feed for reproduction and can 'breed on a diet low in nitrogen content' (Newsome 1975). Newsome's observations and prediction that the euro is displacing the red kangaroo in central Australia suggest that it is able to survive and reproduce on lower quality food than *Macropus rufus*. Reproduction in the euro is, nevertheless, related to availability of food, and the proportion of breeding females decreases during drought (Ealey 1963, Sadleir 1965, Newsome 1975).

In both species reproduction is non-seasonal, presumably because the environments in which these animals have evolved has been irregular and in low latitudes where photoperiod changes little. As Sadleir (1965, 1969) notes, the optimal weaning season bears no fixed relation to any previously occurring climatic phenomenon, so it is not predictable.

The quokka, in the seasonally arid environment of Rottnest Island, shows a restricted seasonal pattern of breeding, but not in the more favourable regions of mainland Australia where breeding is continuous (Shield 1964).

The grey kangaroos (*Macropus fuliginosus*, *Macropus giganteus*) and the tammar wallaby *Macropus eugenii* are strictly seasonal breeders even in semi-arid environments (Kirkpatrick 1965, Sharman et al. 1966, Poole 1973, Tyndale-Biscoe et al. 1974). Photoperiod has been demonstrated to play a role in the reproductive pattern of the tammar wallaby (Sadleir & Tyndale-Biscoe 1977).

Genetic reproductive characters, habitat and their interactions are the major determinants of breeding patterns. Embryonic diapause and post-partum conception confer reproductive advantages on the larger desert macropods, but whether this is an accidental advantage of a group characteristic or whether selection has in fact favoured the pattern is open to question. That the grey kangaroos found in southern temperate zones show defined periods of seasonal oestrus and generally do not carry diapausing blastocysts (but can occasionally do so) supports the idea that in desert kangaroos the mechanism has been 'taken over as an additional adaptation to desert life' (Tyndale-Biscoe 1973), or has been latent, and comes into action under duress.

The environments of the larger desert macropods are unpredictable but this may not be the case for other marsupials in the same or similar environments. The fat-tailed dunnart, *Sminthopsis crassicaudata* shows similar patterns of reproduction in arid and mesic environments (Morton 1978); Smith et al. (1978) have shown that photoperiod influences the reproductive pattern of this species. Photoperiod influences the availability of insects which is seasonal in both desert and mesic environments. An observed pattern of reproduction should thus be considered in regard to the overall biology of the species - particular traits such as insectivory in *Sminthopsis crassicaudata*, allow seasonal reproduction to be

efficient even in an arid environment. Other physiological and behavioural adaptations may also influence the evolution of a reproductive pattern.

In summary, it is difficult to assign a particular reproductive pattern to desert marsupials and while Richardson (1975) considered red and grey kangaroos to be examples from each end of the r-K continuum respectively, temporal variations in reproductive patterns appear to be of greater relevance in understanding life-history processes of the desert marsupials that have been studied.

1.4 Behaviour and social organisation

The behaviour of an animal, its activity patterns, feeding and social interactions reflect the integration of the internal physiological state and genetic adaptations to particular physical and social environments.

1.4.1 Activity patterns, the ethogram and energy expenditure

The activity patterns of a species reflect the way in which the individuals organise their days, months or years into sectors within which other behaviours are performed. Because any activity of an animal involves some energy expenditure, activity patterns will have some influence on individual survival and reproduction.

In some species, particularly desert forms, activity patterns contribute largely to the survival and reproduction of individuals. Specific examples include crepuscular activity in desert kangaroos (Russell & Harrop 1976), nocturnality in the hairy-nosed wombat (Wells 1973, 1978) and spectacled hare-wallaby (Dawson & Bennett 1978).

In the case of wombats it can be demonstrated that activity

patterns are of vital importance to survival of individuals - they die if exposed to ambient temperatures above 32°C for prolonged periods (Wells 1973, 1978). There is little doubt that in other desert forms similar if not such acute situations apply.

A behaviour pattern is a coordinated neuro-muscular event and those patterns characteristic of a species represent adaptations to physical and social environments. Some behaviour patterns (standing or walking) can evolve under minimal influence of social environment while others (pair-grooming in monkeys) have clearly been influenced to a large degree by the social environment.

determined by

Social environment is social structure or organisation the determinants of which are 'demographic parameters (birth rates, death rates, and equilibrium population size), the rates of gene flow and coefficients of relationships' (Wilson 1975). Crook et al. (1976) have suggested that social structure can be best described after examination of mating, rearing, resource-exploitation and predator-avoidance components. These components of a social system will vary in importance in determining the social structure.

Social structure and behaviour will vary in complexity depending upon the number and type of selective forces which have favoured individual survival and gene reproduction as a result of group living. The survival (and hence reproductive) value of social behaviours is in some cases clear - alarm calls, flocking, and cooperative hunting - but this is not so in others (displacement behaviour in kangaroos). Complexity in social structure is usually

associated with complexity in number and types of social signals (Wilson 1975).

Wilson (1975) has pointed out that social organisation is among the most labile of traits. Accordingly it is probable that the fixed action patterns characteristic of a taxonomic unit reflect genetic components of social structure more than a measure such as interaction rate which is likely to reflect the influence of environmental conditions on social structure. The social ethogram or behaviour patterns characteristic of a species are not likely to change markedly in the lifetime of individuals, so possibly they give a better insight into the social evolution of a species than social structure itself.

The range of social behaviour patterns a mammal can perform varies greatly and is in part determined by morphological characteristics. Monkeys, like man, with dexterity of movement and coordination, can perform many more complex social behaviour patterns than ungulates or even social carnivores such as wolves. The determinants of morphology will influence patterns of social behaviour, and it is likely that the 'need' to perform a particular function will, in an evolutionary sense, determine morphology.

"Ritualisation" occurs where particular behaviour patterns become very important in social communication and these can in some cases be considered analogous to the development of horns or elaborate body markings (Geist 1971, Wilson 1975). Highly social primates, ungulates and carnivores use elaborate displays in social communication (Walther 1974, Fox 1975, Wilson 1975) while asocial, solitary species may show no more social behaviour than chasing each other (Bronson 1964, on woodchucks, *Marmota monax*).

In species showing a moderate degree of spatial separation even within a flock or herd, social behaviours can be analysed in terms of the effect they have on the distance separating social partners (Barrette 1977). Thus Barrette refers to the distance-decreasing, proximity-maintenance and distance-increasing behaviour patterns of the muntjac, *Muntiacus reevesi*.

In a representative social unit of a species, the proportion of proximity-maintenance (usually close-quarter behaviours) to distance-increasing behaviours may be a useful measure of sociality. In some solitary, asocial species close-quarter interactive behaviours may not occur at all. The performance of a behaviour pattern will be influenced by the genetic constitution of the animal and prevailing environmental circumstances, conveyed to the neural circuits determining the choice (McFarland 1977). A behavioural event requires energy, which has to be allocated from the many biological systems within the animal. Net energy gain or loss figure largely in the theoretical models formulated to explain behavioural and learning decisions of animals (McFarland 1977).

In theory a behaviour should be performed when it is required and when it subserves some functions useful to the performer. In the evolutionary sense, where the energy cost of performing a behaviour is outweighed by the advantages attained in terms of survival and reproductive success then evolutionary fixation of particular behaviours can occur. In the theories of McFarland (1977) and Moen (1973) performance of behaviours on a day to day basis is also largely determined by energy status.

These arguments are relevant to consideration of the behaviour of animals in deserts. Activity patterns have been discussed previously, but in addition to locomotion another source of potentially large additional expenditure is social behaviour.

If the environment is poor in resources and minimization of energy expenditure has become a major part of adaptation to it, selection may favour reduced elaboration of physical and behavioural paraphernalia in favour of precise social signals and a social structure with little ambiguity.

The presence or absence of interactive behaviour patterns in the ethograms of desert mammals may be a useful guide to their social evolution. It is likely, however, that the level of sociality (as well as energy considerations) will also play a major role in determining the evolution of behavioural patterns.

Some evidence from the literature supports the above ideas. Geist (1974a) links the low calorific value of the plants eaten by tropical deer and bovids with their generally smaller antlers or horns compared with those from temperate zones; and tropical ungulates do not engage in very vigorous social interactions. Territoriality is favoured under tropical conditions and this may explain why many ungulates are territorial in equatorial regions where in such a social structure it is suggested that 'costs in time and energy expenditure and risks of injury leading to reduced life expectancy are probably lower' (Owen-Smith 1977). Geist (1971) provides some evidence that in undernourished ungulate populations the intensity and frequency of display, combat and courtship are lower than in populations with access to adequate

forage. It is not known if the differences between sheep populations have a genetic component but Schaller's & Mirza's (1974) short comparative review of combat patterns in several kinds of *Ovis* suggests that there are few differences between ethograms of desert sheep like the Punjab urial and those of northern temperate zone sheep. This may reflect the comparatively short evolutionary history of sheep, from an ancestral stock of high quality. Ungulates that evolved in tropics or deserts may show more limited ethograms or increased ritualisation of behaviour, minimizing the energetic costs of performing vigorous movements.

Circumstantial evidence also suggests that differential mortality of males in some species may be related to their greater social involvement (Geist 1974a). It is also interesting that the sizes of groups of desert bighorn sheep (Leslie & Douglas 1979) and African buffalo *Syncerus caffer* (Sinclair 1977) decline during periods of reduced availability of food and water. Desert baboons form small groups, and dominant males do not tolerate the presence of many subordinate males; but the converse is true of savannah baboons (Kummer 1968). A consequence of these behaviours would be a reduction in the potential number of social interactions per individual which may conserve energy.

A recent study of the nesting behaviour of iguanas (*Iguana iguana*) concluded that limited available energy causes iguanas to display rather than fight and to use simple rather than elaborate displays (Rand & Rand 1976).

1.4.2 Ecology of social behaviour

One function of sociality is to allow conspecifics opportunities to copulate, but the advantages of sociality are varied.

Individual advantages can be gained from group living if detection and avoidance of predators is enhanced; more efficient hunting may be the result of sociality in wolves and lions (Mech 1970, Schaller 1972). There are also disadvantages of group living such as increased competition for resources, including mates, and a greater likelihood of disease and transmission of parasites (Alexander 1974).

While morphology and ancestral behaviour traits undeniably play a role in determining social structure the importance of prevailing ecological conditions as a determinant of social structure has only been realised recently. Crook (1970) noted that similar species in different environments had different social structures while different species in similar environments were alike in their social organisation. More recently Jarman (1974) illustrated the relationships between body size, dispersion and quality of feed plants, predator avoidance mechanisms and the sociality of African antelopes. Similar associations were found by Estes (1974) for African bovids. In a theoretical paper Geist (1974b) listed what he believed to be the main ecological and physical determinants of social structure in ungulates. He emphasized the importance of body size in avoidance of predators while metabolic rate, food requirements and particularly, energy conservation for females, figured largely in his theories.

Many ecological factors change seasonally, and often the same species is found in a variety of habitats. This accounts for the lability of social structures and their responsiveness to prevailing ecological circumstances.

Seasonal changes in the abundance of food are common in

temperate regions an ecological pattern which often affects the timing of reproduction and hence the timing of sexual behaviour (Sadleir 1969, Geist 1971). Major qualitative changes in social structure may occur seasonally such as separation of the sexes during winter in mountain sheep, which has been postulated to be energetically advantageous to pregnant and lactating females (Geist & Petocz 1977). Other minor quantitative changes in social structure may be manifested as variation in rates of social interaction like that occurring among marmots (Barash 1973), ground squirrels (Betts 1976) and monkeys (Drickamer 1975).

The regularity of some seasonal temperate environmental changes (such as spring growth of pasture) selects for social structure changing seasonally while the constancy of some tropical environments appears to have favoured more rigid social systems including, in some cases territoriality and continuous breeding. Among larger herbivorous mammals which evolved in deserts, selection may have favoured social systems which enhance adaptation to the most frequently occurring ecological condition (usually drought), but they must be sufficiently labile to take advantage of good conditions when they occur.

In considering social structures and levels of sociality it is important to note that a solitary existence does not necessarily imply an asocial character, as Barrette (1977) points out. The muntjac and some of the solitary carnivores are readily social, particularly during the breeding season and possess elaborate behaviour patterns for purposes of social communication (Barrette 1977, Wemmer 1977). Many of the more complex behaviour patterns are associated with courtship and mating, and probably function to reduce

the tendency of individuals to avoid each other, and thus they allow mating to take place.

Some animals may appear to be social when in fact they are not. Aggregation may occur because some important resource such as burrow sites or favoured food occurs in fixed areas, but there may still be no great advantage in adopting a high degree of sociality. Some of the asocial colonial rodents could be cited as examples of this (Nel 1975). In these species the concept of 'individual distance' (Hediger 1964) applies and generally, social interactions when they occur do so at a distance with little or no contact between adult conspecifics outside copulation. Aggression may not be seen in these species because the individuals avoid each other before contact is made.

1.4.3 Social behaviour of marsupials

The behaviour of marsupials has been studied less than the physiological and anatomical aspects of the biology of the order. While there have been specific studies on behaviour of captive and wild marsupials there have been only a few long-term observational investigations of social structure of the type Wilson (1975) considers necessary for adequate analysis of social relationships. Predictably the macropods have received most attention particularly the whiptail wallaby *Macropus parryi* (Kaufmann 1974a), rock wallaby *Petrogale puella* (Davies 1979) and euro (Croft 1979). Of these only the euro can be regarded as an inhabitant of the arid zone. Winter (1976) has described the social organization of the brushtail possum, *Trichosurus vulpecula*.

It is not yet possible, therefore, to make generalisations about differences between marsupial and eutherian behaviour patterns

or social structures, unlike traits such as metabolic rate and reproductive physiology. If such physiological differences do exist at the higher taxonomic level of Mammalia it is likely that behavioural differences would be present also.

However, Johnson (1977), in reviewing marsupial brain structures, concluded that functionally there are probably few differences between the marsupial and eutherian brain; brain structures are similar and there is a similar range of brain size to body weight ratios and of neocortical expansion (except among the primates).

At the level of social relationships where studies have been made on wild populations, well-known behavioural traits such as territoriality and dominance are found in marsupials (Kaufmann 1974a, Russell 1974). At the level of the ethogram and behaviour patterns the situation is less clear. Some marsupial carnivores have, like their eutherian counterparts, many relatively complex social signals (Ewer 1968, Aslin 1974, Eisenberg et al. 1975) with a vocal repertoire equivalent to their eutherian counterparts (Eisenberg et al. 1975). The marsupial equivalent of the eutherian ungulates, the kangaroos do not appear to have the variety of displays of the eutherians (Kaufmann 1974a, cf Walther 1974) and Russell (1974) notes the absence of cohesive behaviour patterns such as mutual grooming. She points out, however, that such behaviours may not be important in maintaining a society of kangaroos.

It is tempting to speculate that there is some relationship between marsupial metabolic rate and behaviour patterns, with selection favouring a low basal metabolism and minimizing energy expenditure above that needed for maintenance. Such traits could

be correlates of evolution in an energy-restricted environment. Alternatively, the trend in marsupials toward nocturnality may be associated with the lack of visual social signals.

Kaufmann (1974a,b) after reviewing what is known of macropod social organisations concluded that it was not possible to show the marked correlation between social development and ecological conditions described by Estes (1974) for African bovids. Importantly, he notes that most macropods have not achieved (or required?) the combination of other adaptations which make possible sociality.

1.5 Conclusions

It is clear, from the foregoing review of literature on social behaviour, reproduction and survival of herbivorous marsupials in drought that these aspects of population biology can be regarded as adaptations to an environment in the same way as can be more well-known physiological, biochemical and morphological traits. The nature of the adaptations and importance of them varies among species, but often the interactions of behaviour, reproduction and physiology play the principal role in adapting individuals to environments.

These ideas and the existing knowledge of the adaptiveness of certain aspects of the physiology of wombats form the basis on which the socio-ecology and behaviour of the hairy-nosed wombat in the Blanche Town region of South Australia have been investigated.

Specifically, it is postulated;

- (a) that physiological and social behavioural processes of wombats are adapted to the unpredictability and irregularity of their

arid environment; and that they are also adapted to the seasonal characteristics of their environment;

- (b) that rainfall and growth of pasture are major determinants of reproductive patterns and associated social behaviour;
- (c) that somatic, reproductive and behavioural adaptations interact to enable wombats to survive in times of drought.

CHAPTER 2

METHODS

2.1 Study area

Hairy-nosed wombats (*Lasiorhinus latifrons* Owen) were studied on the Brookfield Conservation Park and on pastoral properties nearby. The park is situated 14 km west of Blanche Town (approximately 140 km north-east of Adelaide, South Australia) in the valley of the Murray river. This region is part of the semi-arid zone and is characterised by high summer temperatures up to 50°C (mean maximum, 38°C) and irregular rainfall (mean, 265 mm) (Specht 1972, Wells 1973). A drought frequency of more than 70 per cent (Trumble 1948) has been recorded for the region.

2.2 Animals

2.2.1 Procedures - Brookfield Conservation Park

Wombats were caught alive in steel cage-traps (1 m long × 0.5 m square) designed by Wells (1973). The traps were placed at the entrances of burrows and left unset except when animals were needed for study.

After capture wombats were anaesthetized with an intramuscular injection of ketamine hydrochloride ('Ketalar', Parke Davis, Australia) at a dose of 15-20 mg kg⁻¹ body weight. Each wombat was then weighed and its body length (excluding tail) was recorded. A small stainless-steel numbered tag was attached to an ear of each wombat captured. Fur on the flank of those wombats observed in the behavioural study (Chapter 3) was bleached with hydrogen peroxide providing symbols to enable identification of individuals at a distance.

Biopsy samples of testicular tissue were obtained by making an

incision of 1-3 mm length in the scrotum and tunica albuginea and extruding the tissue by applying slight pressure to the testis. Sterile conditions were maintained throughout this procedure. The appearance of the marsupium was described, and if a young wombat was present its body length was measured.

Wombats were released at the site of capture after they had recovered from anaesthesia.

2.2.2 Procedures - pastoral properties

Wombats were killed (under license of the South Australian National Parks and Wildlife Service) by shooting them in the head or neck while they were grazing or resting. The following procedures were carried out on these animals within 1 h of death.

2.2.2.1 Blood sampling

The chest cavity was opened and blood samples were taken from the heart within 2 min of death. Blood (in tubes containing heparin or EDTA) and plasma samples were stored on crushed ice; the plasma was separated from blood cells within 30 min of collection. Samples required for haematological and chemical measurements were at the laboratory within 18 h of collecting them in the field, while plasma samples for hormone analyses were stored frozen until required for the assays.

2.2.2.2 Morphological measurements

Measurements of total body weight, gut weight, body length and skin thickness of the rump were obtained from each wombat. An index of fatness scaled from 0 (no fat) to 5 (abundant deposits of mesenteric, renal, peritoneal and subcutaneous fat) was estimated. Skin thickness was measured from top of epidermis to lowest region of dermis

A 'condition' index was calculated by expressing the body weight of wild wombats as a fraction of the weight-for-length of healthy, fat wombats maintained in captivity. Weight-for-length of 8 captive wombats was given by the equation $y = 0.73x - 34.5$, $r = 0.84$ $P < 0.01$, where y is body weight (kg) and x is body length (cm).

2.2.2.3 Tissue, stomach and faecal samples

Reproductive organs and a portion of the liver were dissected from wombats and stored frozen. Representative samples of the various glands were fixed (while fresh) and stored in Bouin's fluid prior to histological processing. Faecal pellets collected from the rectum, and the contents of stomachs were stored frozen in plastic containers.

2.2.3 Wombats in captivity

A few wombats were maintained in captivity and details of their husbandry have been described elsewhere (Gaughwin 1980). Four wombats with small pouch-young (2-3 cm body length) were caught and returned to the laboratory in order to monitor the growth of the young wombats. Only 1 young survived (for 10 weeks) and its body length was recorded at intervals of 2 weeks. Its growth in body length up to the week prior to its death was linear and given by the equation $y = -17.33 + 8.75x$ $r = 1.00$ $P < 0.01$ where y is age (days) and x is body length (cm). The length of the hairy-nosed wombat at birth is approximately 2 cm; the foregoing equation was used to estimate the dates of birth of 30 wild wombats whose body lengths ranged upwards from 2-15 cm. It is recognized that there is variation in growth rate among pouch-young,

but the equation has been used only to estimate the month of birth.

2.3 Environmental data and other records

Records of rainfall and pan-evaporation at Blanche Town were obtained from the Bureau of Meteorology, Adelaide. From them, a plant growth index was calculated (Specht 1972). It is an index of evapotranspiration and is strongly correlated with plant productivity particularly in arid and semi-arid regions (Specht 1972, Noy-Meir 1973).

The lengths of 11 pouch-young preserved in ethanol at the South Australian Museum were measured, and records of the dates of capture of these wombats were related to the field data.

Dr. R.T. Wells made available his unpublished records of dates of capture, and the morphology of the wombats he studied on the conservation park from 1969 to 1973.

The records of the Museum and of Wells were used to supplement data collected in this study on dates of birth, approximate growth rates and the proportion of females with young.

2.4 Ethological methods

Observations of the behaviour of wombats were made on the Brookfield Conservation Park. More than 1,500 h of observation were undertaken from April 1975 to April 1977. For 5-8 days of each month, during the phase of full-moon, wombats were observed at night from a 7 m -high tower situated 30 m from 2 separate warrens (see Figure 3.1).

A group of wombats occupied these burrows. A warren was taken to comprise the surface and underground structures associated

with this complex of tunnels.

Wombats walked about the warrens occasionally encountering other wombats at various distances from each other. The distance of closest proximity between wombats was termed an encounter (in practice, less than 25 m apart) and any social interactions were recorded. Full descriptions of the patterns of social behaviour were made also.

Wombats were observed with the aid of binoculars, and an image-intensifying 'night-vision' television camera was also used in conjunction with a videotape recorder. When a wombat was seen for the first time a red spotlight was trained on it for a few seconds to determine its identity.

An expression for encounter frequency which could be compared from month to month by taking into account changes in the populations of the warrens, was formulated. The numbers of total encounters (encounters with no social interactions plus encounters with social interactions) between wombats which occurred at a distance of 10 m or less were added together for the number of nights of uninterrupted observation from sunset to sunrise in each month. This ranged from 4-6 nights depending on the season. The values obtained from each warren were then divided by the number of possible combinations of different encounters which was determined by the population of wombats inhabiting a warren, and is given by the expression $n(n-1)/2$. The values for each warren were then divided by the number of complete nights of observation, and the two values averaged to give the number of encounters per night (encounter frequency) for both warrens under observation.

This derivation can be depicted in the following way (see page 36a)

The probability of an interaction occurring (per cent interactions) was estimated by expressing the number of social interactions observed as a percentage of the total encounters.

The amount of use of particular burrows was estimated by expressing the number of times a wombat used a particular burrow (including each emergence and entrance but only if the wombat had been, or stayed in a burrow for more than 30 min) as a percentage of the total number of times a wombat used burrows in its home warren. Preferred burrows were those with highest percentage use.

Captive wombats were observed opportunistically and some behaviour patterns were recorded on 16 mm cine film. Vocalizations were recorded on a Tandberg tape-recorder (model 11) at a tape speed of 19 cm sec⁻¹ and were subsequently analysed on a Kay Sound Spectrograph 6061B.

2.5 Treatment of tissues and analytical methods

Tissues for histological processing were fixed in Bouin's fluid, embedded in wax and 7 μ m sections were stained with haematoxylin and eosin. Morphological measurements on organs or tissues, and sections were made with vernier callipers and an ocular micrometer respectively. Frozen organs or parts of them were weighed and thawed before extracts of constituents were made.

2.5.1 Haematology and blood biochemistry

The haematological and blood biochemical methods used in this study have been referred to by Gaughwin & Judson (1980). These were the standard methods used at the Institute of Medical and Veterinary Science in Adelaide.

2.5.2 Trace elements and vitamins

Plasma for copper and zinc estimations was deproteinized by adding 2 volumes of 10 per cent trichloroacetic acid to 1 volume of plasma, the trace elements were measured in the supernatant by atomic absorption spectrophotometry.

Samples of liver for trace element assays were dried at 60°C and ground with a stainless-steel laboratory mill (Wiley, U.S.A.). Samples of bovine liver (National Bureau of Standards, Standard Reference Material No. 1577) were included with each batch of assays as an external quality control.

Concentrations of liver selenium were determined by the fluorometric procedure of Watkinson (1966). Dried liver (0.1 g) was predigested with nitric acid overnight at room temperature before digestion with perchloric acid. In the assay of other trace elements 0.1 g of liver was predigested overnight at room temperature with an acid mixture containing 1.0 ml nitric acid, 0.5 ml perchloric acid and 6 drops sulphuric acid. The mixture was digested by heating and the residual sulphuric acid containing the trace elements was diluted to 5.0 ml with distilled water before assay for copper, zinc, manganese and iron by atomic absorption spectrophotometry.

Concentrations of vitamin A in liver were measured by the technique of Carr & Price (1926) and serum vitamin B₁₂ by the method of Tibbling (1969).

2.5.3 Chemical composition of stomach contents and faeces

Dry matter, organic matter, water and cell wall contents were determined in stomach contents and faeces by methods outlined in Siebert & Hunter (1977).

2.5.4 Biochemical constituents of the reproductive tract of the male wombat

Biochemical methods used in the study of the reproductive tract of the male wombat have been described by Brooks et al. (1978).

2.5.5 Determination of concentrations of androgens and progestins in plasma

2.5.5.1 Chemicals and apparatus

Phosphate buffers with and without sodium azide and gelatin were prepared from laboratory reagent-grade chemicals in distilled water. A charcoal suspension was prepared from neutral charcoal and dextran T70 (Pharmacia Ltd., Uppsala, Sweden). Sephadex G75 (Pharmacia Ltd.,) columns were prepared as described by Challis et al. (1971).

Testosterone and progesterone were obtained from the Sigma Chemical Company, U.S.A. (1,2,6,7 (n) - ^3H) testosterone and (1,2,6,7 (n) - ^3H) progesterone (specific activity 83 Ci mmol^{-1}) were obtained from The Radio-chemical Centre, Amersham, Bucks, U.K. Solvents (other than those used in scintillation counting) were of laboratory or reagent grade and were redistilled before use. Scintillation fluid was prepared by dissolving 5.0 g of PPO (2,5 diphenyloxazole) in 1 l of laboratory reagent-grade toluene. Pipetting was carried out using Finpipettes (Helsinki, Finland). Radio-immunoassays (RIA) and competitive protein-binding (CPB) assays were performed in 12 x 100 mm Pyrex test-tubes (Corning, Sydney, Australia). Radioactivity was determined using a Packard Tri-Carb Liquid Scintillation Spectrometer.

2.5.5.2 Assay of androgens

Androgens were assayed by radioimmunoassay using testosterone as standard. The antiserum was provided by Dr. R.I. Cox, Hormone Assay Group, CSIRO, Division of Animal Production, Sydney and was raised in sheep to testosterone-3CMO-BSA. Antibody dilution curves were prepared to obtain the dilution for approximately 50 per cent binding, which was 1:10,000. The specificity of the antiserum from sheep 6050 was characterized previously by the CSIRO Hormone Assay Group and they provide the following percentage cross-reactions: testosterone, 100; epitestosterone, 0.11; etiocholanolone, 0.10; androsterone, 0.02; androstenedione, 1.3; dehydroepiandrosterone, <0.01; 5 α dihydrotestosterone, 31; 4-androsten 3 β 17 β diol, 30; progesterone, 0.004, 17 α -hydroxyprogesterone, <0.003; pregnenolone, 0.0004; 17 α hydroxypregnenolone, <0.003; cortisol, 0.003; oestrone, <0.003; oestradiol, 0.10; oestriol, <0.003.

Extraction and assay procedure were as follows: 50 to 500 μ l of plasma were added to screw-cap Pyrex test-tubes. To this was added 0.1 ml of 2.5 per cent NaOH - this step was necessary to avoid extraction of large amounts of lipid which interfered with the assay at a later stage. Five ml of a mixture of ethylacetate and cyclohexane (15v:85v) was added and tubes were shaken for 10 min. The tubes were then centrifuged, the plasma phase was frozen and the solvent phase was decanted into Pyrex test-tubes. The solvent phase was evaporated to dryness under nitrogen or in a vacuum oven. At the same time a series of tubes containing 0 pg, 10 pg, 25 pg, 50 pg, 100 pg and 200 pg of testosterone in ethanol was prepared. The ethanol in these tubes was evaporated to dryness also. To the tubes

containing standards and samples 0.1 ml (^3H) testosterone (approximately 12,000 cpm) was added, the contents of the tubes were mixed and allowed to stand for 10 min at room temperature. The testosterone antisera in 0.1 ml of 0.05M phosphate, 0.1 per cent gelatin, 0.1 per cent sodium azide buffer (pH 7.4) was then added to the tubes, mixed and allowed to stand for 30 min at room temperature before incubating them at 4°C for 18 h. After incubation 0.8 ml of a charcoal suspension (250 mg charcoal and 25 mg dextran T70 dl^{-1} phosphate buffer) was added at 4°C. The contents of the tubes were mixed and allowed to stand at 4°C for 5 min before they were centrifuged at 1200 g for 20 min. The supernatant was decanted into scintillation vials and counted in 5 ml of scintillation fluid after allowing 5 h for equilibration.

A standard curve of the percentage of (^3H) testosterone (Y axis) bound to the standard amounts of testosterone (X axis) was constructed. The values for plasma samples were determined by interpolation from this curve. The qualitative sensitivity of the standard curve was 10 pg. Samples and standards were assayed in duplicate. Samples of plasma obtained from male wombats caught in 1976 and 1977 were assayed together while 3 samples from wombats caught in 1978 were assayed separately. Unfortunately there was not enough of the pooled wombat plasma which was assayed with the first samples, to be included with the second so a measure of inter-assay variation was not obtained. Both assays showed good standard curves and reasonable recoveries so it is unlikely that the results obtained are anomalous.

The recover of (^3H) testosterone added to plasma was 73 per cent for the first assay and 85 per cent for the second; sample values were

corrected accordingly. The intra-assay coefficients of variation (per cent standard deviation) of both assays were less than 12 per cent. The recoveries of 10 pg, 20 pg, 50 pg and 100 pg of testosterone added to a sample of pooled plasma were 82 per cent, 68 per cent, 89 per cent and 84 per cent respectively. Blank values for 5 ml of extracting solvent treated in the same manner as plasma samples were less than 10 pg.

2.5.5.3 Assay of progestins

Progestins were determined by CPB assay using the method of Challis et al. (1971) with progesterone as the standard. Samples were assayed in duplicate in one assay and variation between duplicates was less than 10 per cent.

2.5.6 Determination of concentrations of gonadotrophins in plasma

Gonadotrophins were assayed under the supervision of Dr. V.W.K. Lee in the Reproductive Biology Laboratory of the Medical Research Centre, Prince Henry's Hospital, Melbourne, Victoria. Samples of wombat plasma were treated in the same manner as clinical samples from the hospital. Concentrations of luteinizing hormone (LH) and follicle stimulating hormone (FSH) were measured by RIA using reagents for the rat LH and FSH systems provided by the National Institute of Arthritic Metabolic and Digestive Diseases (NIAMDD) National Institute of Health, Bethesda, Maryland, U.S.A. Standards for LH and FSH assays were NIAMDD rat LH-218 and NIAMDD rat FSH-RP1 respectively. All the samples for each assay were processed at the same time and the intra-assay coefficients of variation were less than 10 per cent. The assays were validated for wombat gonadotrophins by measuring the concentrations of FSH

and LH in different volumes of plasma. For both hormones there were good correlations ($r > 0.95$) between the volumes of plasma used and the concentrations of gonadotrophin measured.

2.6 Statistical analyses

Statistical analyses were performed using calculators manufactured by the Hewlett-Packard Company (Models 29C and 65) in conjunction with programs for statistical tests available for use with these calculators.

There were no statistically significant differences between male and female wombats in biochemical, haematological and trace element measurements, or in morphological measurements so the data from both sexes were pooled. Unless otherwise indicated the data in tables and figures has been obtained from adult, sexually mature wombats.

CHAPTER 3

ETHOLOGY AND SOCIAL BEHAVIOUR

3.1 Introduction

Comparative and ecological studies of mammalian social behaviour in recent years have left little doubt that the demographic characteristics of a species influence and are influenced by social structure and behaviour patterns (see reviews in Wilson 1975, Clutton-Brock & Harvey 1978).

It is the aim of social ethology (Crook & Goss-Custard 1972) to determine the behaviours characteristic of a species, how they help form social structures and how they adapt individuals to the ecological and social environment. Behaviour can be an adaptation to the ecological or the social environment, or both.

One link between ecology, behaviour and survival is energy expenditure. In a biological system energy is allocated to various sectors as required. Behaviours represent a large source of expenditure of energy above that required for maintenance; if intake of energy does not balance expenditure then in the short-term health and wellbeing may deteriorate. Modification of behaviour may be enough to restore the balance. Consequently behaviour can have an important role in adapting individuals to various energy regimes.

The importance of energy, however, cannot be considered in isolation because according to Dawkins (1976) the biological 'aim' of organisms is reproduction of genes, and behaviour highly wasteful of energy could evolve if reproduction of genes were compatible with it.

If energy is in surplus there is little limitation to expenditure of it, so elaborate behaviours or high metabolic rate

could evolve and persist. If energy is, or has been (on the evolutionary time-scale) in short supply it would seem to be detrimental to waste it. If enough time in a low energy environment has passed, behavioural mechanisms for saving energy could become encoded in the genotype, as has occurred with many physiological traits. Analysis of the ethogram and social structure of a species may help to indicate whether a species evolved in an energy-rich or a deficient environment.

Modification of social structure can significantly alter the amount of energy available to an animal, as is seen when a decreasing supply of food induces males and females of some species of sheep to occupy different home ranges (Geist 1971). Changes in social structure that alter the frequency at which individuals interact with each other, and changes in motivational state are also likely to influence expenditure of energy.

Some aspects of the behaviour of both genera of wombats have been studied in detail, especially activity patterns (Wells 1973, 1978, McIlroy 1973). Both authors found the species to be mainly nocturnal with a seasonal variation in the time at which individuals were active.[†] McIlroy's study of *Vombatus ursinus* obtained quantitative data on home range and use of burrows, with a few qualitative observations on territoriality and agonistic behaviour. An important observation was that of multiple use of burrows including simultaneous sharing of burrows by *Vombatus*.

Wells (1973) made general notes on aspects of social behaviour

[†]Wells postulated that the activity patterns of hairy-nosed wombats enabled them to conserve energy and water.

of *Lasiorchinus* also, but until the present study there has been no systematic observation of the species.

3.2 Results

3.2.1 Warrens and warren composition (Table 3.1)

Each warren was composed of a number of burrows. The large warrens examined had up to 10 major burrows centred on a crater and prominent mound. Smaller warrens had from 1 to 5 major burrows. Many of the burrows were inter-connected. A large warren could be inhabited by up to 10 wombats, although all of the individuals were not present at all times. Although in the warrens examined there were a few more male wombats than females the differences were not statistically significant. Warrens were characterised, also, by dung piles where wombats habitually defaecated; by grooming posts and by trails leading from the warrens to adjacent pastures.

3.2.2 Burrow use

The wombats inhabiting each warren made use of a large number of the burrows, but had a marked preference for 3 or 4 (Table 3.2). In the first year of observation, females were present significantly ($P < 0.001$) more often in their most preferred burrow than males in theirs. It appears likely that the reproductive status of female wombats in part determines the use of burrows by both males and females. For example, female 4 when she was weaning her 1974 young, occupied burrow 4 (one of a group of 3 some distance from the rest of the burrows in warren 1 (see Figure 3.1). At times these 3 burrows were also occupied by the other individuals of warren 1, but not warren 2. Individual

Table 3.1 Numbers of male and female wombats inhabiting 5 warrens on the conservation park.

Warren	Major burrows [†]	Adult males	Adult females	Total number of wombats
1*	6	3	2	5
2*	6	2	2	4
3	9	5	4	9
4	10	5	5	10
5	8	3	2	5
Totals	39	18	15	33

[†] Burrows with craters and mounds
 * Observation warrens

Table 3.2 Use of preferred burrows.

	Preferred burrow					Number used	Recorded usages
	1	2	3	4	5-10		
Adult males (4)	28	20	14	12	25	7-13	385
Per cent use	*						
Adult females (4)	41	19	13	10	20	5-11	275

* $\chi^2_1 = 12.1$, $P < 0.001$ for males v. females (most preferred burrow)

Table 3.3

Wombat

	Warren 1									<u>Burrow</u>	Warren 2												
	12	11	29	B	15	16	4	C	O		17	21	19	30	TC	BB	TF	22	N18	18	24	5	27
Male X		*						*	*														
Male 1		*						*	*														
Female 4	*					*		*															
Female D	*					*		*															
Male U											*				*						*		
Male G											*			*							*		
Female T											*				*						*		
Female H											*	*		*									




* Preferred burrows of wombats.

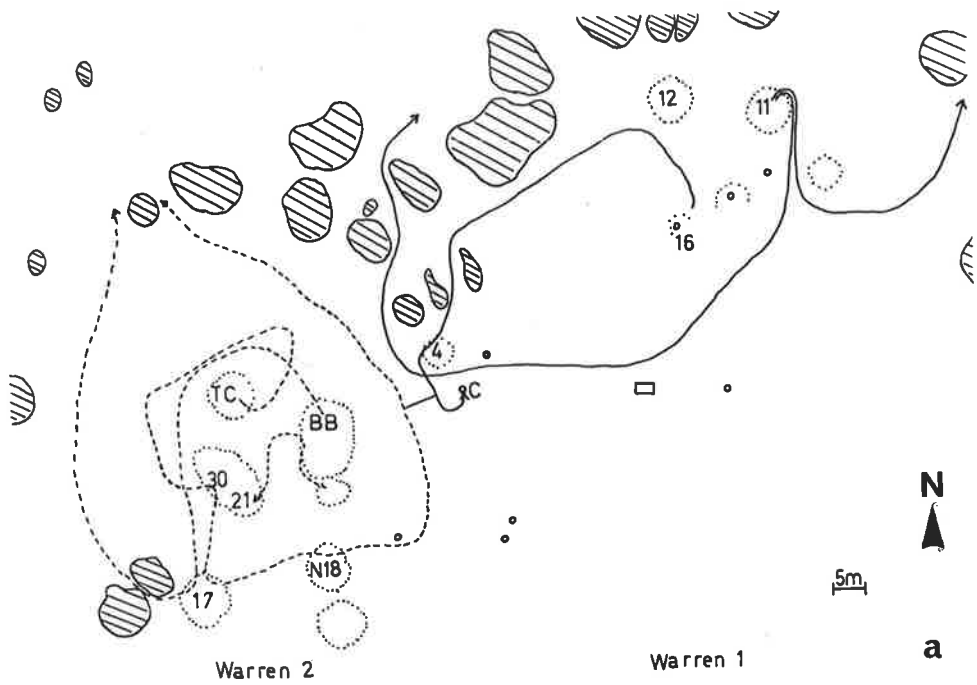
Table 3.3 Distribution of 8 wombats in 2 warrens during 1975.

wombats did not own burrows and often 2 or more wombats used the same burrow entrance during periods of observation. It can be seen from Table 3.3 that each warren represents a stable aggregation of wombats and that there is considerable common use of preferred burrows. Female wombats may not be as restricted to particular warrens as are males. Females 4 and D from warren 1 resided in warren 2 for periods of up to 2 months in 1976 and 1977, but males from each warren were never seen to occupy warrens other than their primary one. Four wombats (X,U,T and 4) have inhabited the warrens observed for 8 years and it is likely that male X has been resident at warren 1 for in excess of 10 years (R.T. Wells, personal communication).

3.2.3 Movements about warrens

After wombats emerged from their burrows they usually walked about the warrens for some time before moving off to graze in adjacent pastures. Movements at the warrens, particularly of males, indicated the geographical extent of each warren (Figure 3.1a). Wombats of each warren were unrestricted in their movements about their own warrens and the pattern of movements of males, at least in the mating season, was determined in part by the location of the preferred burrows of the females. At warren 1 male X regularly visited burrow 4, occupied by female 4, while at warren 2, male U regularly visited burrows 17, BN18 and 30, the preferred burrows of the females of that warren (see Table 3.3). The movement, also, of U at the periphery of warren 2 brought him close to burrow 4 of warren 1, and on one occasion in September, 1975, within 5 to 10 m of male X (Figure 3.1a).

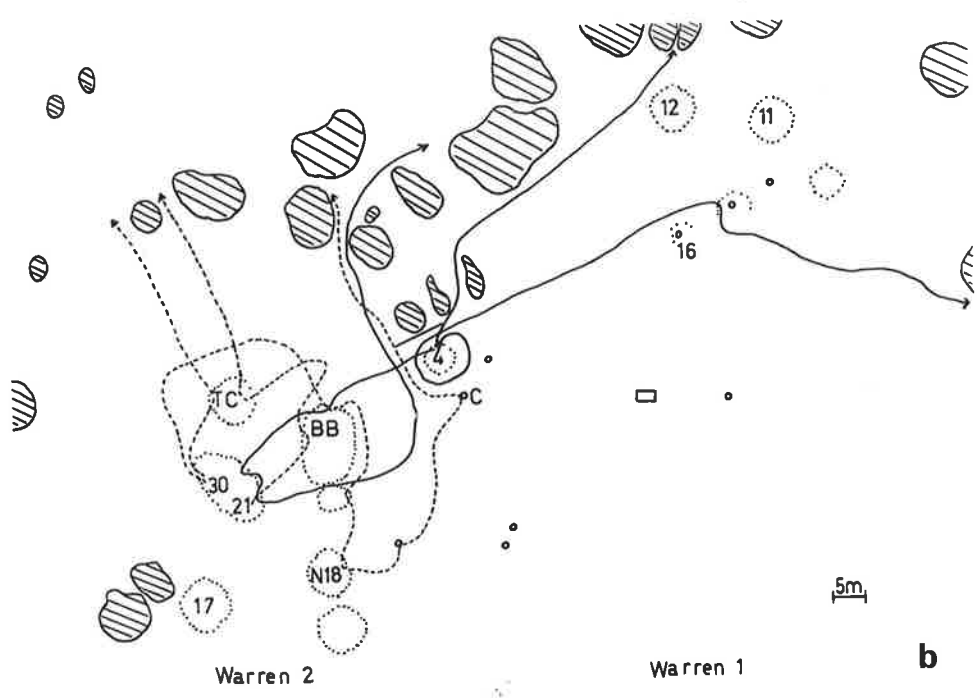
Figure 3.1 Movements of 4 wombats after their first emergence from burrows on 3 nights in September 1975. a) — = Male X, --- = Male U b) — = Female 4, --- = Female T. Encounters are indicated by solid lines joining the paths of the wombats. Hatched areas represent trees and the position of the observation tower is indicated by . Major burrows are depicted as  and minor burrows as . Vertical lines on the scale indicate the direction of due North.



Warren 2

Warren 1

N
5m
a



Warren 2

Warren 1

5m
b

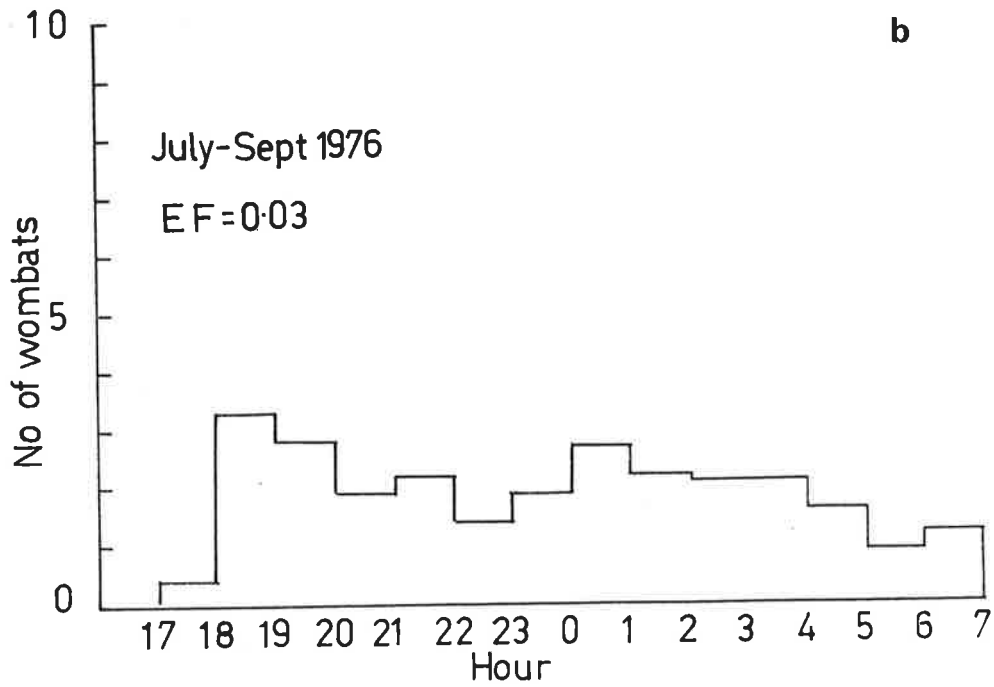
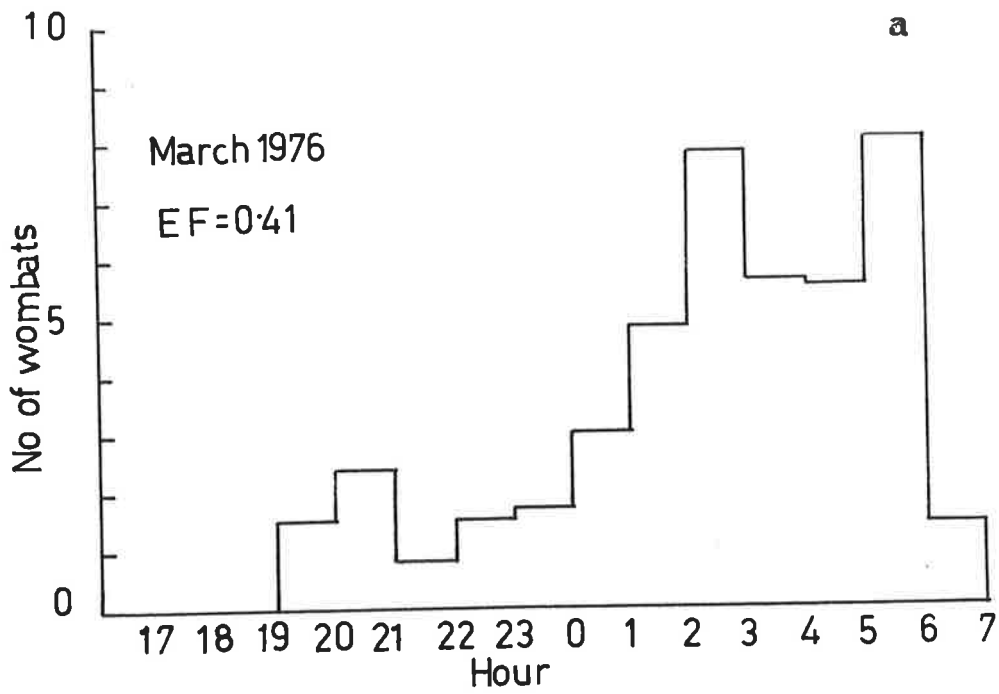
Female wombats generally moved about their own warrens, but female 4 occasionally made short incursions to warren 2 from burrow 4 (Figure 3.1b). Females also visited other burrows and female T of warren 2 often moved near burrow 4, encountering female 4.

Wombats of each warren generally moved off in specific directions to graze. Individuals from warren 2 moved in a north, north-west direction from that warren while the wombats of warren 1 moved north, north-east or east from that warren to graze. Some individuals from warren 2 often moved due south from the warren for food.

3.2.4 Activity patterns

Activity patterns have been the most closely studied aspect of wombat behaviour (Wells 1978, McIlroy 1973) and for *Lasiorchinus* consistent seasonal patterns of activity were evident. In the summer months most wombats emerged from their burrows late at night, around 1 a.m. whereas in the winter months first emergence was much earlier, around 6 p.m. In addition to the thermoregulatory aspect of such behaviour postulated by Wells (1978), patterns of activity appeared to affect social behaviour by influencing the frequency at which wombats encountered each other when above ground. Synchronous emergences either early or late resulted in many wombats being present at a warren within a short space of time and hence there was a greater probability that a wombat would encounter another (Figure 3.2a). Asynchronous emergences and wider separation of times of appearance above ground resulted in few encounters at the warrens (as in July to September,

Figure 3.2 Average number of wombats observed overnight at 2 warrens during each hour of observation in (a) March 1976 $n = 6$ nights and (b) July to September 1976 $n = 17$ nights. EF is encounter frequency.



1976 Figure 3.2b).

3.2.5 Social ethogram (Figure 3.3, Appendix 3)

The most characteristic feature of the ethogram of *Lasiorchinus latifrons* is the lack of close-quarter patterns of either greeting or fighting. Social behaviours are relatively simple movements toward or away from other wombats. Kangaroos lack many of the more sophisticated and elaborate behaviour patterns of their eutherian counterparts, the ungulates, but display predominantly ritualistic upright fighting as a major behaviour (Kaufmann, 1974a). *Lasiorchinus* is, however, even less endowed with such behaviour than kangaroos. Social interactions, defined as any situation where the presence or actions of one wombat resulted in an overt responsive behaviour being shown by another wombat, were relatively simple. Among 143 social interactions observed between April 1975 and March 1977, a large proportion (nearly 70 per cent) resulted from overt avoidance due to the presence (AR - actor response interaction) or approach (APR - approach response interaction) of another wombat (Table 3.4). A smaller proportion was due to overt aggressive behaviour. Addressor or actor-response interactions were indicative of and consistent with well defined dominance relationships within the warrens, whereas SR (simultaneous response) interactions were characteristic of the social interactions between adult females where no dominance was evident (see later). Over 90 per cent of social interactions occurred when wombats were less than 10 m from each other, and there was a greater possibility of an encounter becoming a social interaction, the closer wombats were to each

Behaviour patterns:

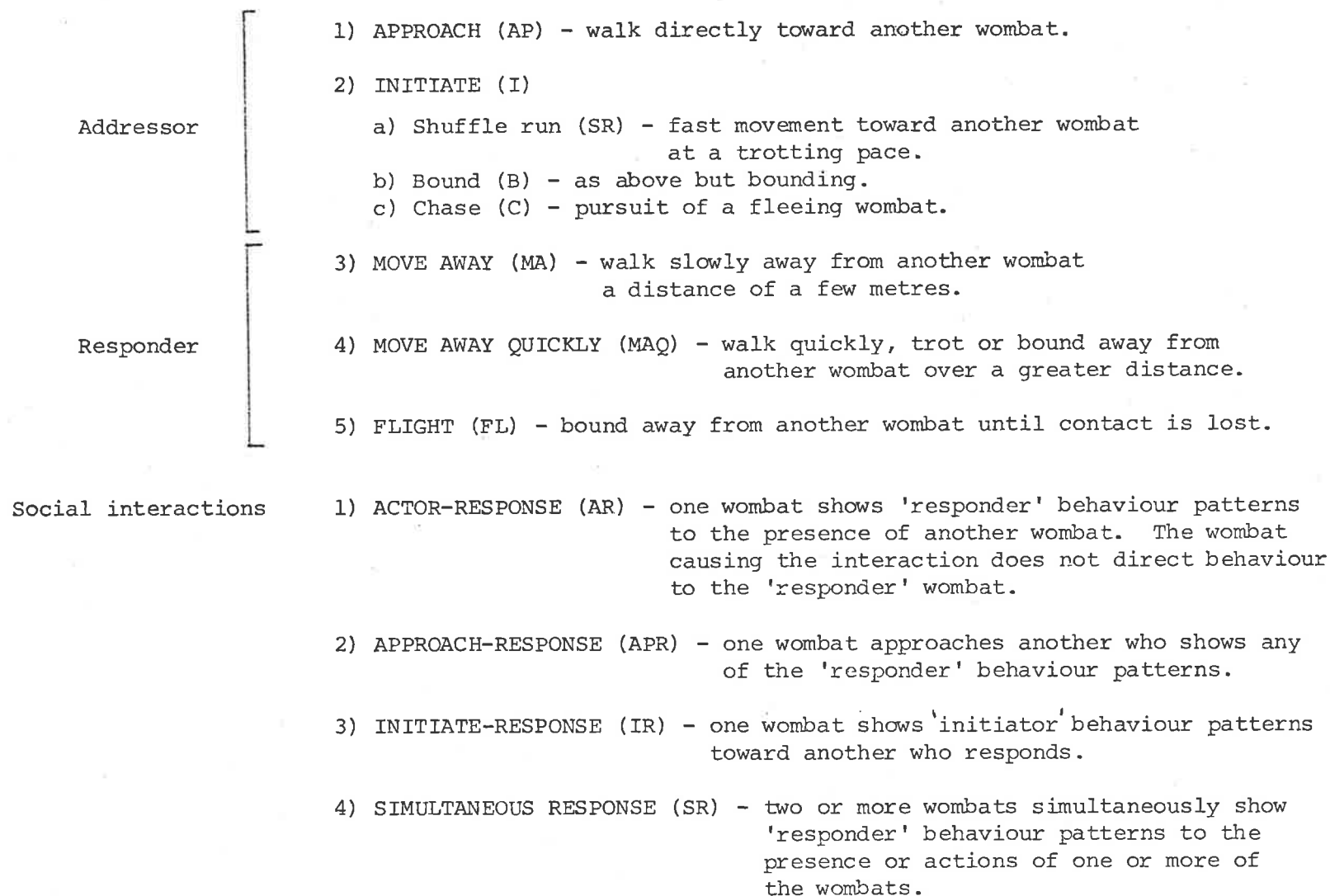


Figure 3.3 Social ethogram of *Lasiorchinus latifrons*.

Table 3.4 Numbers and proportions of the types of 143 social interactions among adult wombats observed between May 1975 and March 1977.

	Type of interaction			
	Actor response	Approach response	Initiate response	Simultaneous response
No. of interactions	45	54	34	10
Per cent	31	38	24	7

Table 3.5 Distances at which 65 male - male, and male - female, social interactions occurred.

	Distance			
	0 - 5	5 - 10	10 - 15	> 10 - 15
No. of interactions	45	14	4	2
Per cent	69	22	6	3

other (Tables 3.5,3.6). Wombats were not in close proximity frequently or for long periods of time and it appeared that situations where an encounter resulted in no interaction were as socially important as the interactions themselves. Thus, in the first year of observation, nearly 50 per cent of encounters at a distance of less than 10 m did not become social interactions. Behaviour patterns and social interactions indicate that *Lasiorhinus* is an animal with a well defined individual distance, but nevertheless it is reasonably tolerant of conspecifics.

3.2.6 Fighting

Fighting at the warrens was rare and was seen only twice in more than 1,500 h of observations over 2 years. It had no significance as a day to day social signal, and appears not to have evolved into a ritual like the formal fighting of kangaroos (Kaufmann 1974a). The major offensive behaviour of wombats was to lunge at and bite the opponent, the defence to which was presentation of the rump.* Measurement of the skin thickness of wombats has shown (Figure 3.4) that the skin is thickest on the rump and it is likely that this evolved as a defence. Geist (1971) suggested that the pneumated skulls of rams and thick rump-skin of mountain goats evolved as a consequence of fighting. Fighting among wombats is more likely to occur in the mating season when males compete for females. In the mating seasons of 1975 and 1976 males were quite scarred, presumably because they had been fighting.

3.2.7 Vocalizations

Only one type of vocalization was heard in the field. It

* see page 49a

Table 3.6 The numbers of interactions and encounters at distances of 0 - 5 m and 5 - 10 m.

	Distance	
	0 - 5	5 - 10
Encounters	60	49
Interactions	45	14
Per cent interactions	75	* 29

* $\chi^2_1 = 23.42, P < 0.001$

Table 3.7 Association between the occurrence of vocalizations and the type of social response.

	Type of social response	
	Move away	Flight
No. of responses	28	27
No. of responses with vocalizations	10	23
Per cent with vocalizations	36	* 85

* $\chi^2_1 = 14.02, P < 0.001$

Figure 3.4 Skin thickness (mm) of *Lasiorhinus latifrons*.

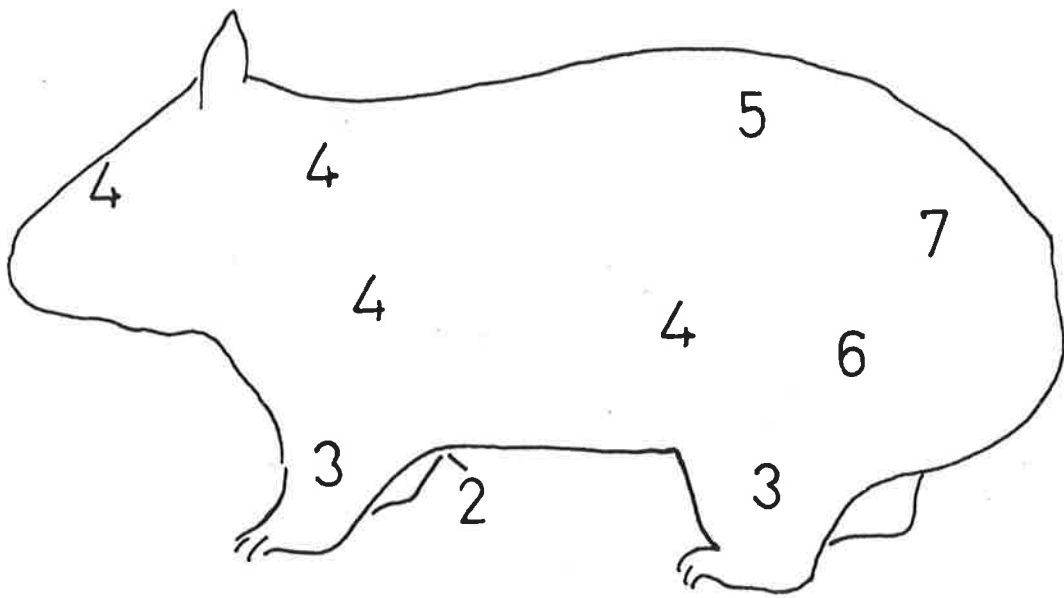
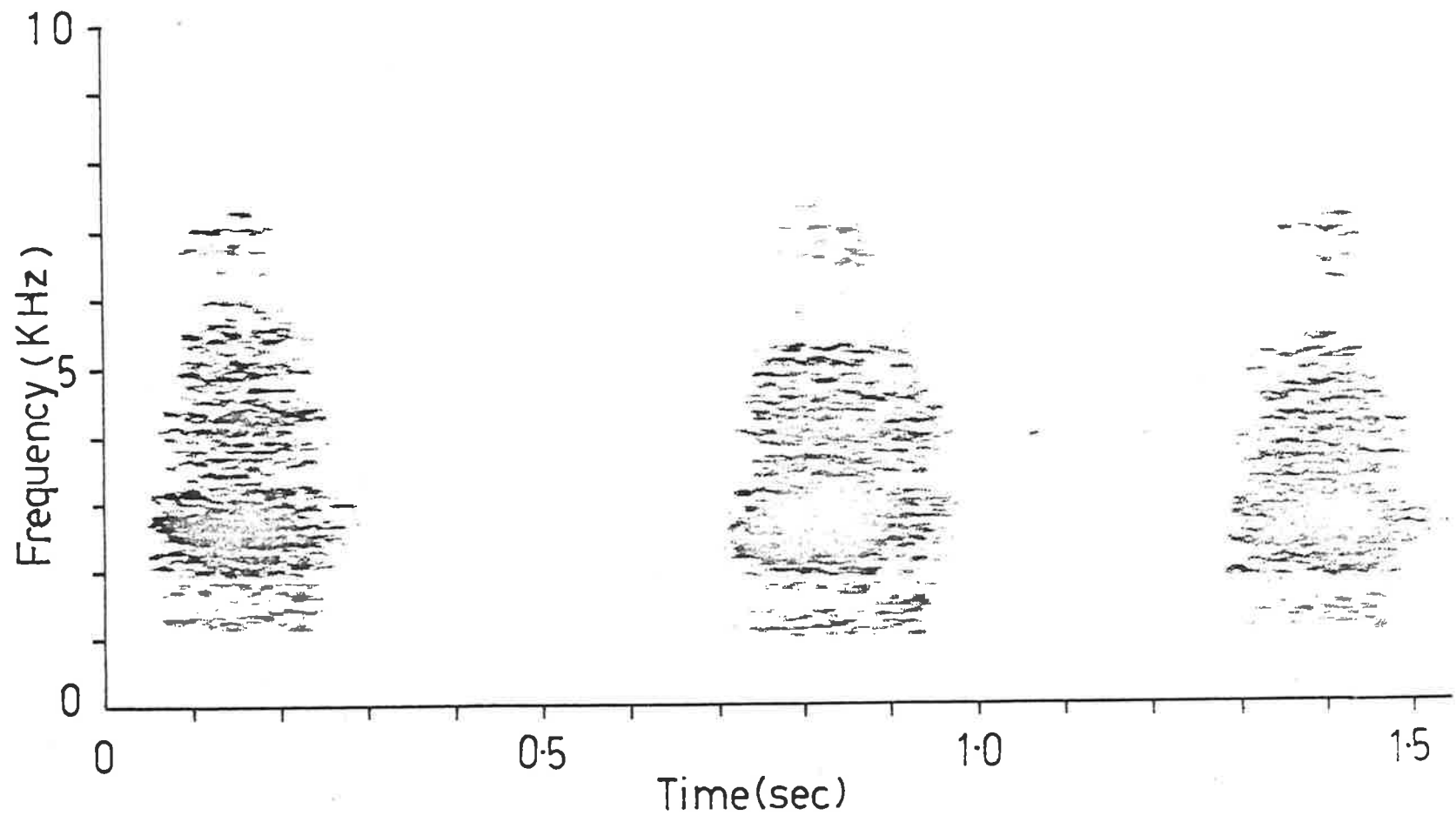


Figure 3.5 Sonograms of the vocalization of *Lasiorhinus latifrons*.



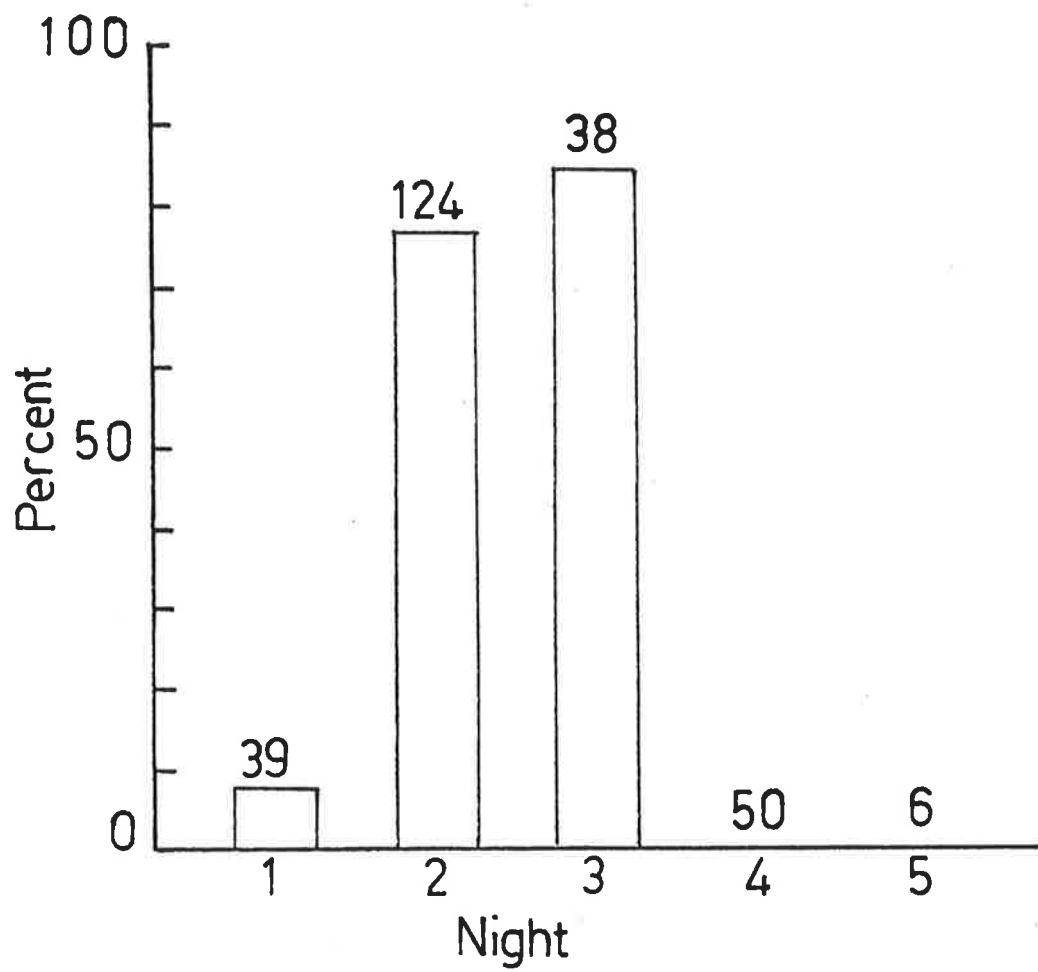
was always associated with social interactions. Of 65 social interactions observed between adults from June 1975 to March 1976, 40, or 62 per cent involved vocalization. These vocalizations were uttered by the wombat showing 'responder' behaviour patterns and the probability of a vocalization occurring depended on the type of social response. Thus 85 per cent of flight responses, but only 36 per cent of move-away responses, were associated with vocalizations (Table 3.7). Sonograms of the vocalization uttered by a captive female wombat (Figure 3.5) show that it is a short call (150-300 msec) of broad frequency (1-8 KHz) with a preponderance of energy at 2-3 KHz. It lacked significant harmonic structure. This is the typical non-specific vocalization of many mammals produced by forcefully expelling air through the larynx (Bartholomew & Collias 1962) like a heavily breathed 'h'. Wombats also uttered this sound when manually restrained after capture; this observation and the social context of the vocalization suggest that it is an expression of alarm or distress. Often, wombats ran to their burrows when they were disturbed by objects unfamiliar to them, such as humans or motor vehicles, but they did not vocalize on these occasions.

3.2.8 Sexual behaviour

Female 4 was observed during oestrus in October 1975. On 2 of 5 consecutive nights of observation the largest adult male from her own warren (male X) was within 10 m of her and followed her for over 70 per cent of the time she was observed (Figure 3.6). This appeared to alarm her since she vocalized incessantly, frequently moving back toward and entering her preferred burrow,

followed by the male. The fact that male X did not attempt to copulate with female 4 while they were observed above ground suggests that copulation occurs underground. Observations of the copulatory behaviour of captive wombats (copulation occurs with both animals lying on their sides, the female resisting the male's attempt at copulation until he has securely pinned her to the ground and achieved intromission; see Appendix 3) reinforce this interpretation. Olfaction probably plays a major role in the determination by males of a female's reproductive state. Female 4 resided in a small warren with 3 burrow entrances 30 m from warrens 1 and 2 but considered part of warren 1 (including burrows 4 and C, Figure 3.1). This warren was also periodically occupied by the 2 adult males of warren 1 (Table 3.3). If not occupying her warren, these males visited her burrow, both while she was resident and while she was away grazing, at a frequency of once every 2-3 nights during periods of observation in the 3 months prior to October 1975. Since female 4 was weaning her previous year's young, she would perhaps be expected to be nearing oestrus. The attractiveness of female 4 was not restricted to male X since 2 other males from both warrens attempted to move close to her on 3 separate occasions while she was in oestrus but were effectively prevented from doing so by X. Significantly, this occurred only on the third night she was attractive to males. Mating probably occurred during that night because none of the males showed interest in her after that. Some patterns of fighting^{behaviour (lunge and retreat)} occurred between X and the other males when they were competing for female 4.

Figure 3.6 Percentage of the time that male X was within 10 m of oestrous female 4 on 5 consecutive nights of observation in October 1975. Numbers above the histograms are the numbers of minutes that female 4 was observed.



In addition, a well-known olfactory behaviour of ungulates associated with sexual investigation, flehmen, which has never been previously described for a marsupial, was observed once in the field and as part of pre-copulatory behaviour of a captive male wombat (Gaughwin 1979, Appendix 3).

3.2.9 Social relationships (Figure 3.7)

Most encounters were between wombats from the same warren and approximately 10 per cent were between wombats from the adjacent warrens. These encounters all occurred in the vicinity of burrow 4, which is near the 'demarcation' line between warren 1 and warren 2.

Within each warren it was apparent that precise relationships existed among the wombats. Among adult males in each warren well-defined dominance relationships were evident. Males 1 and G always retreated from and avoided males X and U respectively, and on 70 per cent of the occasions they came within 10 m of each other (1 within 10m of X and G within 10m of U) an interaction occurred. Male 3S, observed to be a juvenile and sub-adult wombat in the early part of the study, was subordinate to both X and 1 when he had achieved adulthood.

Both dominant and subordinate males from each warren dominated all the females in the warrens, but quantitatively the manifestation of this dominance was less apparent and females retreated from or avoided males on only 48 per cent of the times they encountered them (Table 3.8).

Among female wombats no dominance relationships were apparent. Females interacted on about 36 per cent of the times they encountered each other. When they did react, only simultaneous response

Figure 3.7 Sociogram of adult wombats in the first year of observation (1975). Solid lines indicate total encounters. Dashed lines indicate social interactions of the actor, approach-response types - the direction of the arrow indicates the direction of dominance. Dotted lines indicate simultaneous response interactions.

Table 3.8

	Sex class		
	Male- male	Male- female	Female- female
Total encounters	26	83	25 $\chi^2_1 = 1.37, P > 0.05$ [†]
Interactions	19	40	9 $\chi^2_1 = 6.30, P < 0.05$
Per cent interactions	73	48	36
	$\chi^2_1 = 4.94, P < 0.05$ →		
	ns →		
	$\chi^2_1 = 9.42, P < 0.01$ →		

[†] Goodness of fit test. Expected ratio 1 : 4 : 1 based on the numbers of male and female wombats in each warren.

Table 3.8 Encounters and social interactions of adult male and female wombats at distances of less than 10 m.

(SR) interactions were observed and the category of behavioural response was 'move away'. Females interacted infrequently and were very tolerant of each other. It was also interesting to note that SR interactions did not occur between males where the most rigid dominance relationships were evident, but they occurred more frequently in male-female interactions and were characteristic of all the interactions between females. In addition, when SR interactions occurred between males and females it was between the subordinate males and females and not the dominant males (Figure 3.7).

In the first year of observations only one interaction took place between males from different warrens. This was in September, 1975, when male G was promptly chased out of burrow 4 by male 1 until he was well into the main area of warren 2. This was the first indication that perhaps male wombats were territorial with respect to their warrens.

As indicated in the section on warrens and burrow use, female wombats appear to be able to take up residence in warrens other than their own. In September 1976 the females 4 and D from warren 1 moved to warren 2, leaving only 3 adult males occupying warren 1. It is significant that even though females avoid or retreat from males less often than males from each other, the fact that females can take up residence in another warren indicates a more important qualitative relationship between males and females. Presumably it is reproductively advantageous for males to have many females with which to mate and so they should readily accept females in their warrens and be less aggressive to them while they are there. This situation, for obvious reasons cannot apply between adult males.

Five interactions between the males of warren 1 and warren 2 in 1976 as well as an interaction between male X and an unidentified (presumably male) wombat temporarily residing in warren 1 confirmed the idea that territoriality was the major inter-warren relationship between adult males.

Territorial interactions occurred in the mating season (September-November). In October 1976 after females 4 and D had taken up residence in warren 2, males X and 3S entered warren 2 on 5 separate occasions only to be chased out by the resident males G and U. Patterns of fighting behaviour occurred between X and G, but in the other territorial interactions the resident males merely chased the fleeing intruders until they entered their own warren. Male X, the dominant and very large male of warren 1, was attacked and successfully chased from warren 1 by G, a younger and smaller male. Male X also chased an unmarked wombat from warren 1 when he met it there. It is not known whether territoriality extends to the feeding areas adjacent to the warrens, although 3S was chased to an area north of warren 1 by U when he encountered 3S at a distance of 50-70 m directly north of warren 2.

Encounters within warrens occurred at random and this was consistent with the observed lack of burrow ownership and freedom of movement of individual wombats within their own warrens. Differences between male and female wombats in their participation in social interactions (compared with the expected probability of their occurrence on a random basis) can be attributed to the different social relationships discussed previously (Table 3.8).

No differences in the basic qualitative relationships were noted when females were carrying pouch young. While the qualitative

relationships of dominance and territoriality did not vary, there were large variations over the 2-year study-period in the frequency of individual encounters and interactions.

3.2.10 Variation in social behaviour

The number of instances of vocalization (and hence social interactions) which were heard during nights of observations varied markedly over a 20-month period spanning 2 breeding seasons (Figure 3.8). Vocalizations could be heard from wombats interacting within a radius of approximately 400-600 m of the observation tower and thus were a useful guide to overall social activity in the area.

High levels of social activity occurred in October-November of each year and this coincided with periods of mating activity. Presumably they reflected increased male-female interactions (of a sexual nature) as well as increased interactions between males, both within and between warrens as they sought and competed for oestrous females. Male wombats at these times were often quite scarred particularly on their rumps, from having been bitten. Less social activity occurred when females were carrying pouch-young or were anoestrous when male sexual development was minimal (see Chapter 4). Variations in social activity were due to variation in the frequency at which wombats encountered each other (encounter frequency) and were due to variation in the probability of a social interaction occurring once they had met each other (Table 3.9). When the probability of an interaction occurring was high and the encounter frequency was also high, then very high levels of vocalization were heard as in October-November, 1976.

Figure 3.8 Monthly variation in the mean (\pm S.E.) incidents of vocalization heard in the study area. Analysis of variance $F_{18,72} = 19.9$ $P < 0.001$.

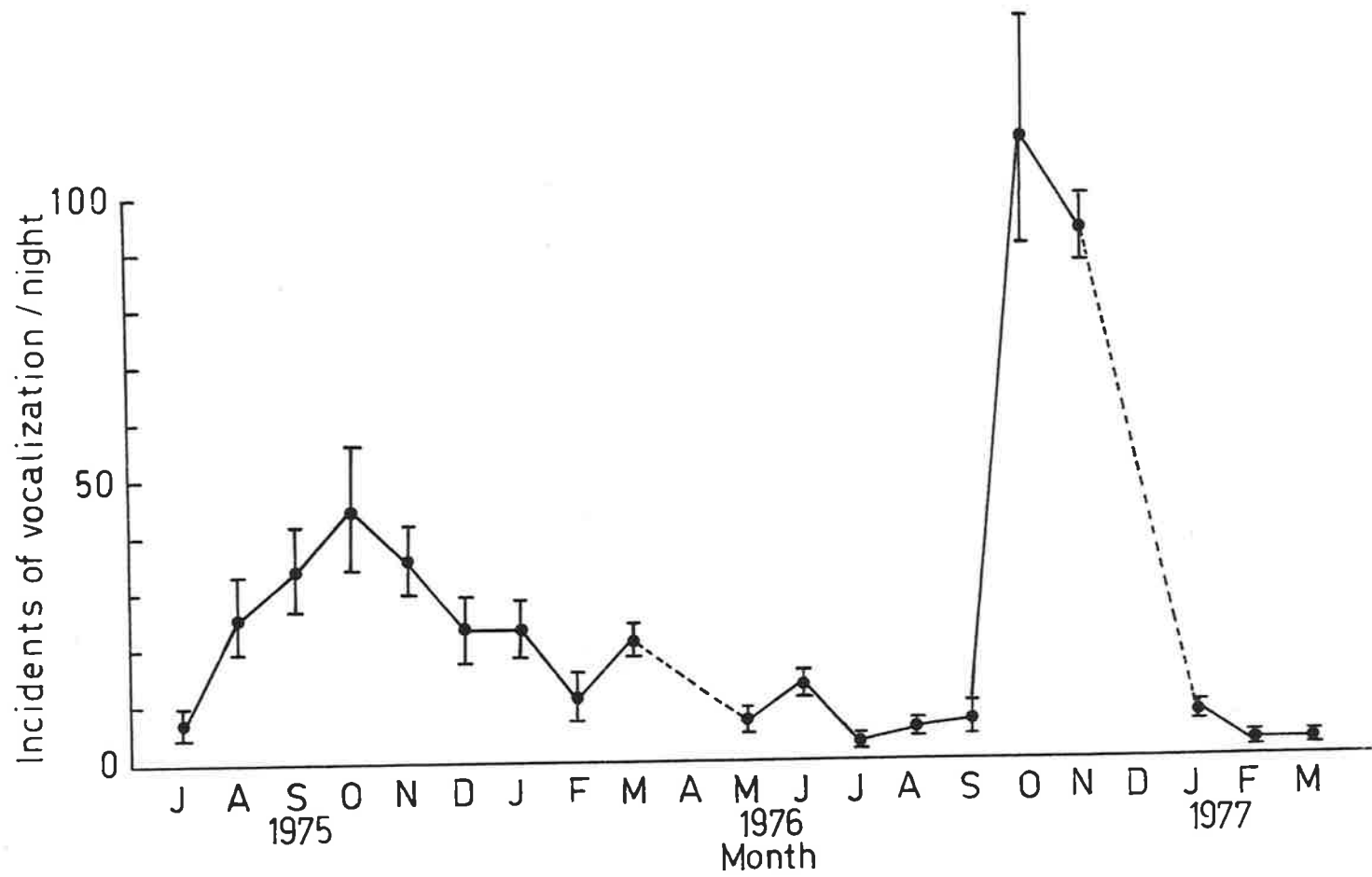


Table 3.9

Parameter	Unit	Month				
		Sept '75	March '76	July-Sept '76	Oct-Nov '76	March '77
Vocalization	No. of incidents per night (\pm SE)	34 \pm 7	21 \pm 2	5 \pm 1	101 \pm 10	3 \pm 1
Encounter frequency	Encounters per night	0.15	0.41	0.03	0.51	0.42
Per cent interactions	$\frac{\text{Interactions}}{\text{Encounters}} \times 100$	83 ***	37	57	70 ***	21

χ^2 analysis * $P < 0.05$, *** $P < 0.001$

† See Methods for description.

Table 3.9 Variations in the social behaviour of wombats.

When the probability of interaction was high but the encounter frequency was lower, then the level of vocalization was lower, even within a breeding season as in October-November, 1976. If the encounter frequency was low and the probability of an interaction occurring was also low, then very low levels of overall social activity in the area were observed (July-September, 1976).

Factors which influence activity patterns such as temperature, relative humidity and possibly available food, as well as the distance of grazing areas from a warren, will all influence the frequency at which wombats encounter each other. It is more likely, however, that the probability of interaction is related to age and sex class, the type of interaction such as territorial or dominance, and the motivational state of the individuals, influenced by such factors as reproductive condition and health.

3.3 Discussion

Behaviour patterns are vital in the adaptation of wombats to their arid environment. Undoubtedly, burrowing or the fossorial habit is the most important behaviour. When combined with other behaviours such as feeding at night and other activity patterns there is an effective mechanism by which wombats can avoid the extremes of heat and cold as well as conserve energy and water. The studies of Wells (1973,1978) have clearly shown that without these behaviours wombats in the Blanche Town area would die.

The observations described in this chapter suggest that the adaptive value of these fundamental aspects of behaviour is enhanced by aspects of social behaviour.

One of the most striking features of the social behaviour of

Lasiorhinus latifrons is the simplicity and effectiveness of the behaviour patterns used in social communication. Comparison with other marsupials (Kaufmann 1974a), or the eutherian counterparts of wombats, the ground squirrels (Barash 1973, Steiner 1975, Betts 1976) shows that a major part of wombat social behaviour is tolerance of individuals without regular greeting ceremonies (Steiner 1975) or ritualized aggression.

Nearly all social interactions consist of behaviour patterns associated with increasing or decreasing the distance between individuals, but close-quarter behaviours of an interactive type occur rarely.

There are few quantitative data on other species with which to make comparison, but Kaufmann's study (1974a) of the whiptail wallaby showed that for adult males displacement behaviour (similar to wombat social interactions) accounted for only 18 per cent of agonistic interactions; the remainder were ritualized aggression at close-quarters. Barash (1973) has emphasized the importance of close-quarter greeting behaviour as an indicator of sociality in the Olympic marmot, *Marmota olympus*, where this behaviour forms a large proportion of the social behaviour observed. For adult yellow-bellied marmots (*Marmota flaviventris*) greeting behaviours outnumber flight by 93 to 50 (Armitage 1974). For the least social of the marmots, the woodchuck, *Marmota monax*, greeting behaviour has not been described (Bronson 1964, Barash 1974).

Approximately 50 per cent of encounters between wombats at a distance of less than 10 m did not result in social interactions. Given the repulsing or dispersive nature of the basic social interactions of wombats, this probably reflects a degree of tolerance of

conspecifics, taking the place of the overt amicable behaviour seen in many other species.

It appears that selection has favoured a limited ethogram in *Lasiornhinus*, evident especially when comparisons are made with kangaroos, or with the marmots, a group of mammals with similar structure. It is likely that morphology and nocturnal habits are associated with the lack of visual signals, and with simple behaviours, but the fact that the wombat ethogram is more limited than in other species suggests that morphology or nocturnality alone could not account for the differences.

Fighting occurred rarely. Given the form it takes its use as a day to day social signal would be detrimental to the well-being of individuals because of the energy expenditure involved and the physical damage that might be sustained.

Social relationships among adult wombats were relatively complex and similar to those of the macropods that have been studied (Kaufmann 1974a, Croft 1979). That female wombats could take up permanent residence in warrens other than those of their initial preference suggests that their relative position of subordination to all males allows their incorporation into many warrens without the need to establish themselves in a social hierarchy by interacting extensively with other individuals. Freedom of movement of females and diversity of their residences probably confer reproductive advantages on male wombats and possibly resource advantages on females such as a greater choice of burrows.

Both dominance and territoriality are well-defined characteristics of the social relationships of male wombats. Males inhabiting

the same warren occupied a position in a social hierarchy based on individual recognition of each other. The displacement behaviour of wombats confirmed and maintained an individual's social position. Territoriality was an effective means of excluding non-resident males from a warren; the subordinate resident wombat of one warren could effectively evict the older, larger, dominant male of another warren. Territorial behaviour occurred infrequently, suggesting that the observed avoidance by males of warrens not initially preferred by them was maintained by some other mechanism, possibly olfaction. The wide distribution of dung piles about warrens supports this idea; it is a characteristic aspect of territoriality in another colonial, fossorial mammal, the rabbit *Oryctolagus cuniculus* (Mykytowycz & Gambale 1969).

A commonly suggested function of dominance is to allow dominant individuals preferential access to a resource. The observed sexual behaviour of wombats confirmed that an oestrous female could be regarded as such a resource and it was obvious that the dominant male had far greater access to and control of the oestrous female than other males. Kaufmann (1974a) and Croft (1979) have suggested dominance functions in a similar manner in kangaroos.

In wombats, territoriality probably played a similar role since it reduced the number of males that could permanently occupy a warren.

Females of the same and different warrens were very tolerant of each other with no evidence of dominance or territorial relationships.

At a fundamental level it is apparent that a social group of wombats is maintained using a very simple set of overt behaviour

patterns in precise social relationships. In the arid environment inhabited by these animals this may conserve energy. For example, the fact that females show no dominance relationships and can move from warren to warren means that potentially, they have 2 fewer types of social interactions in which to engage than males. Such a situation supports Geist's (1974a&b) predictions that conservation of energy is a major driving force determining the social structure of female herbivores.

Less overt, but probably important aspects of behaviour such as olfaction may also conserve energy. Two examples may be cited. Territoriality may be maintained by the odour of dung piles, reducing the number of territorial interactions that occur; and initial investigation by males of a female's sexual status may be facilitated by olfactory investigations of the environment of her burrow. This was suggested by field observations and if so would reduce the number of times females would be harassed by males. A notable feature of social organisation of kangaroos is the sniffing of females' genital areas by males, which means that female kangaroos would be engaged in many more social interactions of a sexual kind than female wombats.

Wells (1978) has demonstrated that *Lasiorchinus latifrons* has one of the lowest metabolic rates of any marsupial and has postulated that variations in activity patterns minimise energy and water expenditure; in short, there is rigorous energy conservation. At times this was tediously obvious since often, in a week of all night observation, only one or two social interactions were seen.

Despite the limited nature of the overt communicative patterns of wombats and the high stability of social relationships, wombats

had a great capacity to alter the frequency and intensity of their social behaviour, as shown by the data on encounter frequencies and vocalization. It is likely that such changes in behaviour were a consequence of changes in reproductive status which in turn was related to the availability of fresh pasture (see Chapters 4,5).

In the northern temperate zone where environmental conditions are predictable on a seasonal and yearly basis, increased behavioural complexity and hence expenditure of energy above that required for maintenance could evolve in the mammals. For the herbivores, periods of lush pasture growth occur regularly and compensate for energy shortage at other times. The shortages of energy in feed that do occur each year can be met adaptively either by hibernation as in ground squirrels, or by short term behavioural shifts in home-range, reduction in the intensity of social behaviour and even by alteration of social structure. Barash (1973) noted a decline in the sociality of Olympic marmots as they near hibernation. Geist (1971) described a decline in vigour of social interactions of mountain sheep in poor years, as well as the regular home-range shifts and changes in social structure that occur throughout the year in these sheep.

In these species short-term changes in social behaviour and social structure enable the individual to cope with its environment. Such regularly occurring extremes of environment cannot be expected to select for one fixed type of social behaviour, of either high or low intensity.

Unlike ground squirrels, wombats do not hibernate.

They lack the mobility of larger herbivores so the adaptive mechanisms described previously would be

Lasiorchinus

difficult for wombats to effect. *Lasiorchinus* are confined to arid areas and a year to year irregularity of available feed. A drought frequency of 70 per cent has been recorded in the Blanche Town region (Trumble 1948) so the likelihood is high that wombats experience more bad years than good in the 15-20 years that they live. From the observations presented in this chapter there appears to be much evidence to support the idea that the physiological adaptations of wombats to an arid environment are further enhanced by economy of social behaviour.

The social behaviour of *Lasiorchinus* may be interpreted as an adaptation to minimise the potentially large increases in above-maintenance expenditure of energy that may result from group living. The question of why wombats are colonial remains, however, to be answered.

There is no evidence to suggest that predation has influenced wombat sociality or gregariousness. No alarm vocalizations have evolved, though ground squirrels (Betts 1976) and even some of the asocial colonial rodents like *Paratomys brantsi* (Nel 1975) acquired them. Contemporaneous association of large Pleistocene predators with *Lasiorchinus* has not been demonstrated even though Hecht (1975) has suggested that the giant varanid lizard *Megalania* may have preyed upon some of the wombats now extinct (*Phascolonus* species) which were extant with *Lasiorchinus*.

Many warrens are located on the edges of clay-pans where digging may be easy, but the fact that warrens rather than single burrows are found elsewhere where digging is difficult suggests that availability of burrow sites is not the only determinant of aggregation of burrows.

It is possible that the better ventilation in warrens is attractive to wombats. Decaying faecal matter is likely to produce offensive if not noxious odours and I have observed that after rain many wombats 'clean out' their burrows bringing great piles of dirt and dung above ground.

Some evidence suggests that this is the case in the warrens of hairy-nosed wombats. Taylor (1977) has found that the carbon dioxide concentration in the air of warrens is less than that in the air of single burrows. Together with the observations that social factors per se do not appear to have influenced aggregation of wombats, this observation makes more attractive the hypothesis that wombat social behaviour is an adaptation enabling essentially solitary mammals to live in a group without increasing energy expenditure too much.

In summary, the limited ethogram, the simple and precise social relationships forming a highly stable social structure, and the ability to adjust behaviour quickly to changes in the environment are the outstanding features of the behaviour of wombats. At one level these social behaviours appear to enhance other behavioural and physiological adaptations of wombats to their arid environment. At another level, when environmental conditions are appropriate, they allow wombats to engage in important activities such as reproduction which necessarily require a large supply of energy.

CHAPTER 4

ANATOMICAL AND PHYSIOLOGICAL ASPECTS OF WOMBAT REPRODUCTION

4.1 Introduction

A knowledge of the structure and functional appearance of the reproductive tracts of both males and females during various stages of the reproductive cycle (breeding and non-breeding periods, pregnancy, or lactation) is needed if demographic and reproductive patterns of a population are to be understood.

In female mammals this involves gross anatomical as well as histological examination of ovaries and uteri (see the studies by Kean et al. (1964) on the brushtail possum; Newsome (1964) on red kangaroos and Hughes et al. (1965) on the common ringtail possum *Pseudocheirus peregrinus*). Among male mammals, assessment of spermatogenesis is important, but it is often necessary to be able, also, to assess the functional status of the accessory sex glands which provide the liquid vehicle for transport of spermatozoa to the reproductive tract of the female (Mann & Lutwak-Mann 1976).

Mammalian reproductive activity is dependent upon a functional hypothalamic-pituitary-gonadal axis (Turner & Bagnara 1976). Measurement of the plasma concentrations of pituitary and gonadal hormones can be of value if correlations can be established between reproductive status and the concentrations of particular hormones. Some recent work with marsupials has shown the value of gonadal and pituitary hormones as indicators of reproductive status (see Tyndale-Biscoe et al. (1974) on macropods; Cook et al. (1978) on the brushtail possum).

In the absence of experimental studies, which are not often possible with wild mammals, correlative studies can be useful for determining whether reproduction is controlled in the typical mammalian manner. A notable absence in the literature on marsupial

reproductive biology is reference to the Vombatidae. There are no studies of the reproductive physiology of the two genera, but there are some gross anatomical and histological observations on the male and female reproductive tracts, mainly of *Vombatus ursinus*, with occasional reference to *Lasiorchinus*.

MacKenzie & Owen (1919) described the reproductive tracts of male and female *Vombatus ursinus* as did Pearson (1944) for the female of this species. There are some differences in these authors' descriptions of the female reproductive tract particularly their descriptions of the median vagina or vaginal cul-de-sac. A drawing of the female wombat's reproductive tract in Parker & Haswell's textbook of zoology (1943) depicts two pairs of 'rectal glands' not described by other authors.

There are some histological studies on the ovaries of wombats also. O'Donoghue (1914) described the appearance of the ovaries of *Vombatus ursinus* at various stages of gestation. He also noted the presence of well-developed ovarian interstitial tissue in a number of marsupial species including the wombat (O'Donoghue 1916). Fraenkel (1905) described the ovaries of one female *Lasiorchinus latifrons* also noting the presence of much interstitial tissue. These authors commented upon the large size of the corpus luteum in *Vombatus* and its prominence throughout lactation. The vasculature of the reproductive tract of female *Vombatus* has been described recently by Lee & O'Shea (1977).

Until recently less was known of the reproductive biology of male wombats. Hughes (1965) described the spermatozoa of *Vombatus ursinus* while Sharman (1961) briefly mentioned what he thought to be the position of the testes of *Lasiorchinus latifrons* in breeding

and non-breeding seasons. McIlroy (1973) measured the diameter of *Vombatus* testes through the scrotum and detected a seasonal change.

Brooks et al. (1978) gave a detailed account of the reproductive tract of the male hairy-nosed wombat, including analyses of the chemical composition of the accessory sex glands. Gaughwin et al. (1979) described changes in the concentrations of reproductive hormones and the size of reproductive organs in breeding and non-breeding seasons. These studies form part of this dissertation (Chapter 4).

Understandably, the poor breeding performance of wombats in captivity (Gaughwin 1980) has made investigations of some aspects of their reproductive biology difficult. Crowcroft & Soderlund (1977) at the Brookfield Zoo, where some breeding success has been obtained, were able to show that *Lasiiorhinus latifrons* has a gestation period of 21 days and that the species is polyoestrous. Peters & Rose (1979) reported that the common wombat is polyoestrous with a cycle length of 33 days.

4.2 Results

4.2.1 Morphology of the reproductive tract of the male wombat

In general, the gross anatomy of reproductive organs in the hairy-nosed wombat resembled that of the common wombat *Vombatus ursinus* as described by MacKenzie & Owen (1919).

4.2.1.1 Scrotum, testis, epididymis and ductus deferens

The testes are held in a pre-penile scrotum. The surface structure of the scrotum was variable. In some animals the scrotum was relatively thick-walled and covered with fine hair (as in Plate 3,

Figure 4.1), while in others it was thin-walled and almost hairless (Plate 4, Figure 4.1). In the former case, the testes were held close to the body wall and were difficult to palpate.

In no instance could the scrotum have been regarded as pendulous. Nor was there evidence of pigmentation in the parietal tunica vaginalis, although this has been observed in some other marsupials (Biggers 1966). The tunica albuginea of the testis had a silvery appearance. The pampiniform plexus was relatively undeveloped. The cauda epididymis was notable in being tightly enclosed within a separate pocket formed by the tunica vaginalis. In animals with a scrotum largely devoid of hair, the position of the cauda epididymis was easily seen (Plate 4, Figure 4.1). The ductus deferens led from the epididymis to the urethra and there was no ampullary swelling (Plates 1,2, Figure 4.1).

The histological appearance of the testes varied with the reproductive state of individuals (Plates 1-6, Figure 4.2). When the weight of a testis was greater than 5 or 6 g, sperm were produced in seminiferous tubules of diameter greater than 180-200 μm . When it was less than 5 or 6 g, sperm production tended to cease and the various germ-cells except spermatozoa could be seen in seminiferous tubules of diameter 100-180 μm . In the smallest testes (2-3 g) only spermatogonia were present in tubules without a lumen. This was typical of the testes of juvenile wombats.

The appearance of the interstitial or Leydig cells also varied with the reproductive state of the wombats. Leydig cells of wombats in breeding condition (indicated by large testes and accessory glands) were enlarged and rounded, with finely granular cytoplasm, and the

Figure 4.1 The male reproductive tract and spermatozoa of the hairy-nosed wombat, *Lasiorhinus latifrons*.

- Plate 1. Male reproductive tract, dorsal view. A magnified picture of the tip of the penis showing backward facing spines is shown as an inset.
2. Male reproductive tract, ventral view.
 3. Ventral aspect of a male wombat with the scrotum (relatively thickly covered in hair) in the upper half of the picture and the short tail in the lower half. The cloaca lies between the two but is obscured by hair.
 4. Ventral aspect of a male as in Plate 3 but with the scrotum largely devoid of hair. The arrow indicates the position of the cauda epididymis.
 5. Spermatozoon recovered from the urine and stained with nigrosin and eosin. Note the recurved head.
 6. Head and midpiece of a spermatozoon.
 7. Head and midpiece of a spermatozoon viewed at 90° to that shown in Plate 6.

Abbreviations: A Cowper's gland A; B Cowper's gland B, C Cowper's gland C; b bladder; c.p. crus penis; p penis; p prostate; r.p. retractor penis muscle; u ureter; u.b. urethral bulb.

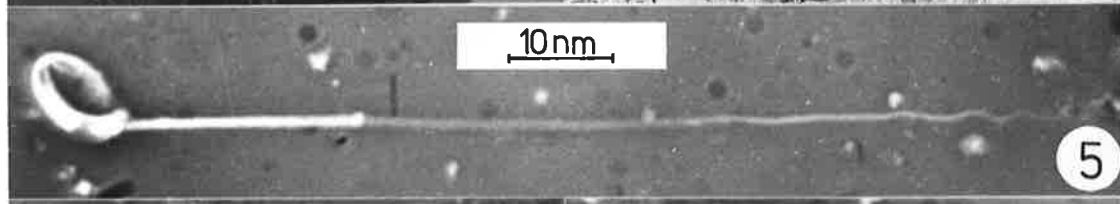
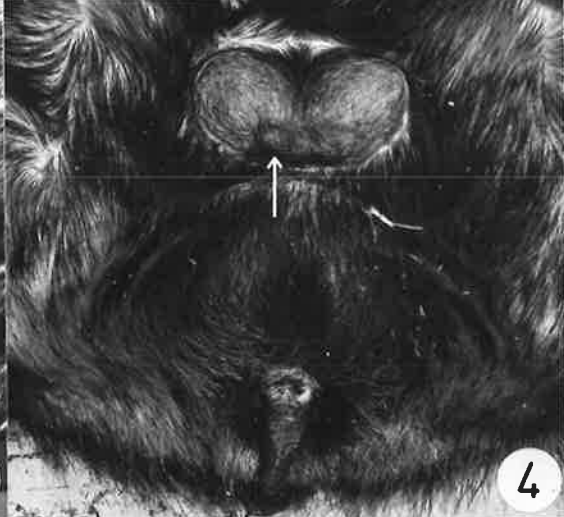
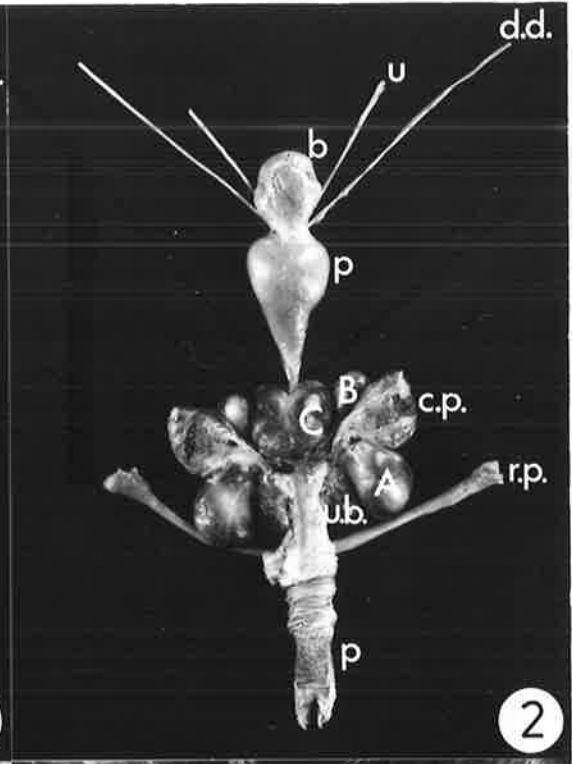
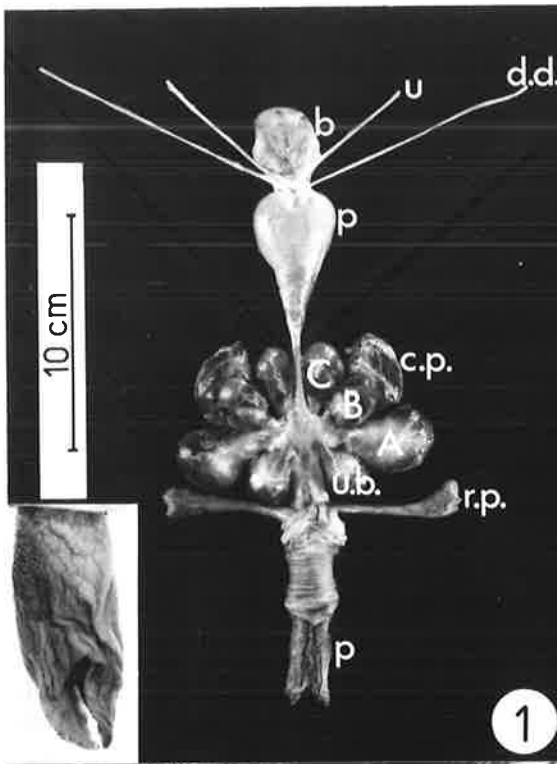


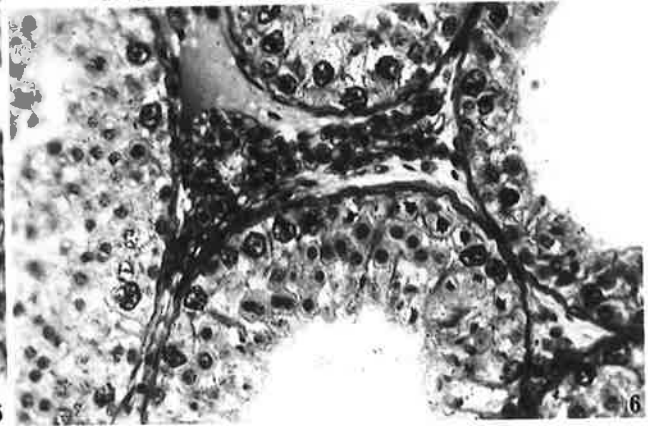
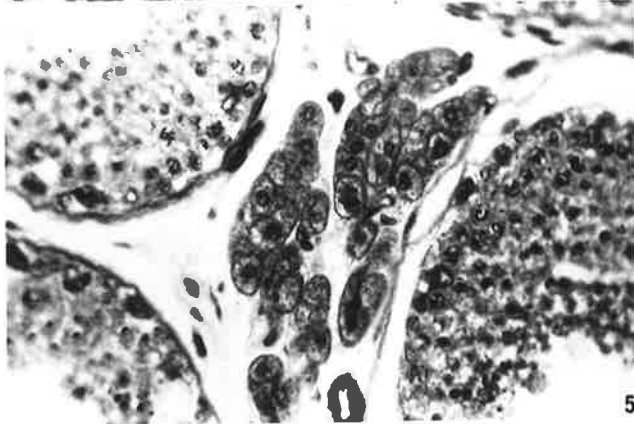
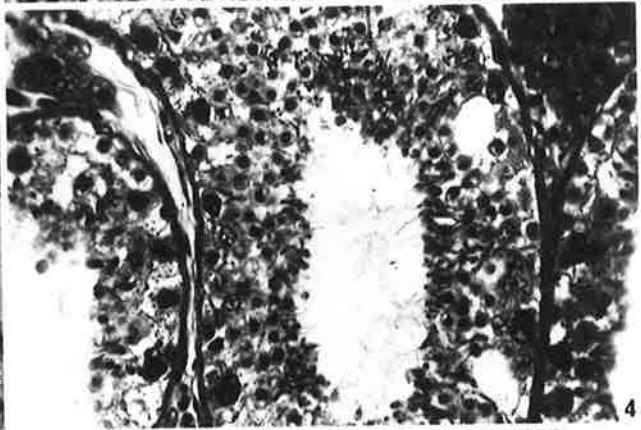
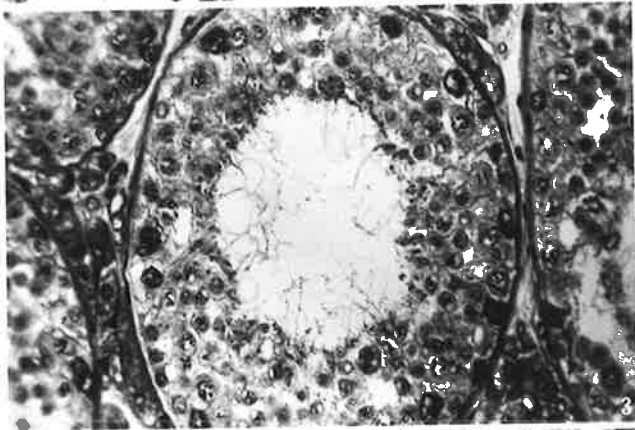
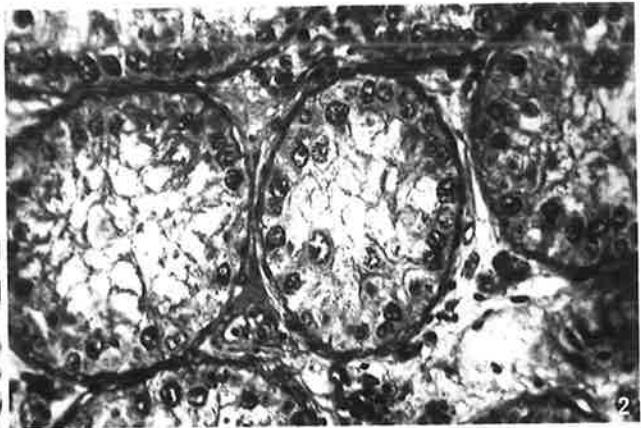
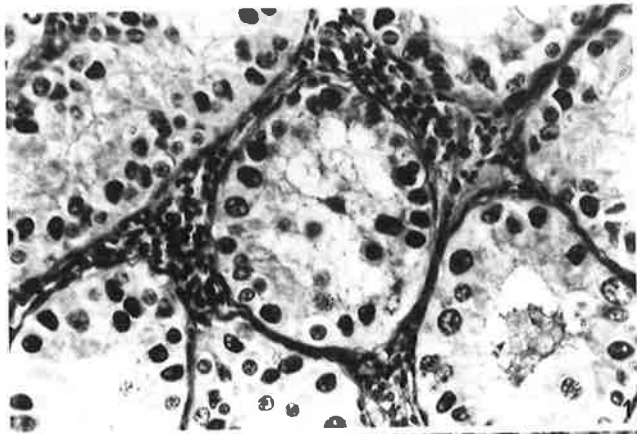
Figure 4.2 Photomicrographs of sections of testes of wombats in various reproductive states. × 400.

Plate 1. Juvenile wombat, sexually immature.

2. Adult wombat, January 1978 after 14 months of drought. Note similarity with Plate 1.

3-5. Adult wombats in breeding condition, August and September 1978.

6. Adult wombat, October 1977. Drought had inhibited reproduction. Note small size of Leydig cells and incomplete spermatogenesis.



nucleus occupied 1/3 to 1/2 of the cell. In contrast, when wombats were in the non-breeding state, shrinkage of the cytoplasm of Leydig cells was apparent, while the nucleus was small and pyknotic (Plates 1-6, Figure 4.2).

4.2.1.2 Prostate

The prostate was tapered in the carrot-like shape which is common in marsupials (Plates 1,2, Figure 4.1). The ureter and ductus deferens entered at the proximal end. The distal portion of the prostate was greyish in colour and on sectioning, the pigmentation could be seen to extend through the depth of the tissue. This pigmentation was not apparent in the prostates of immature animals. On histological examination, the prostate consisted of three distinct segments, the divisions running transversely as in a number of Australian marsupials (Rodger & Hughes 1973) and in the American opossum *Didelphis virginiana* (Chase 1939). In line with the terminology of Rodger & Hughes (1973), these segments were named anterior, central and posterior portions of the prostate. The division between the central and posterior segments was easily seen since it coincided with the junction of the pigmented and non-pigmented portions of the prostate. But the division between the anterior and central segments could not be identified so readily, and in general it coincided with the greatest diameter of the prostate. In adult animals the anterior, central and posterior segments represented 40 per cent, 40 per cent and 20 per cent respectively, of the total mass of the prostate.

The prostate was enclosed in a connective tissue capsule with

outer circular and inner longitudinal layers of smooth muscle, beneath the capsule. The glandular tissue was on the luminal surface beneath the smooth muscle. It consisted of branched tubular glands from which the collecting ducts generally ran anteriorly before entering the urethra. The glands were lined by a simple epithelium, the height of which varied in the different segments. In the anterior segment, the cells were columnar with basally located nuclei and the glandular lumen was relatively narrow. This contrasted with the central segment where the epithelium was more cuboidal and the glandular lumen was large. The posterior segment was histologically similar to the central segment, but it had a somewhat narrower lumen. So-called 'prostatic bodies' (Rodger & Hughes 1973) occurred in the glandular lumen of all segments but were particularly evident in the posterior segment.

4.2.1.3 Cowper's glands

Three pairs of glands were identified, and distinguished from the urethral bulbs and the crura penis. They were designated Cowper's glands A, B and C (Plates 1,2, Figure 4.1). The bulbar Cowper's A and B glands were located dorsal to the urethra; the glands of the C pair were ventral, more elongated and joined to each other by connective tissue along the medial border. Each gland was surrounded by striated muscle passing over the hemisphere opposite the entry of the duct into the urethra. In freshly dissected specimens this muscle showed spontaneous contractions. All three pairs of Cowper's glands contained long, branching, wide-lumen tubular glands. The glandular tissue was surrounded by a coat of connective

tissue and an outer layer of skeletal muscle. Histologically, Cowper's A and B glands were almost identical. Their epithelia were composed of cuboidal cells in which the nuclei appeared to occupy the major portion of the cell column. The lumina of these glands were filled with eosinophilic colloidal material. Cowper's C gland was quite distinct from A and B. It was lined with larger mucoid epithelial cells, which contained pale-staining nuclei and supra-nuclear cytoplasm. No obvious luminal contents were observed.

4.2.1.4 Penis

The total length of the extended penis was about 10 cm but the penis was held in an S-bend by the retractor penis muscles. The glans penis was bifurcated for about 1.5 cm at its distal end. In this region the epithelium was thrown into longitudinal folds, both on the exterior surface and on the opposing surfaces of the bifurcation, as described in other marsupials (Biggers 1966). A series of backward-facing spines surrounded the penis for about 2 cm proximal to the point of bifurcation (Plate 1, Figure 4.1).

4.2.1.5 Spermatozoa

The morphology of spermatozoa recovered from the urine, and examined in smears stained with nigrosin and eosin, is shown in Plates 5-7, Figure 4.1. The shape of the head was comparable with that observed in the common wombat (Hughes 1965), but the extent of the recurvature was variable. In some spermatozoa the head formed a half circle while in others a complete circle was observed. When viewed from the dorsal or ventral aspect it could be seen that the tip of the acrosome was displaced to one side of the longitudinal axis of the sperm. The dimensions of the

spermatozoa were: head 9 μm , midpiece 19 μm and total tail 80 μm . These measurements are similar to those of the common wombat (Hughes 1965) spermatozoa.

4.2.1.6 Organ weights

The average weight of a testis in adult animals was 6 g. The weight of the accessory organs from different animals was very variable, but a good correlation was found between the weight of the different glands within any one animal. This is demonstrated by the plots of the weights of Cowper's glands against prostate (Figure 4.3). A correlation was also observed between the weight of the urethral bulb (which consists of erectile tissue) and that of the prostate.

4.2.2 Chemical constituents of the accessory glands of the male wombat

Brooks et al. (1978) reported the results of chromatographic analyses of extracts of wombat accessory sex glands. Some of these chemical constituents were quantified in the extracts and the results are shown in Table 4.1.

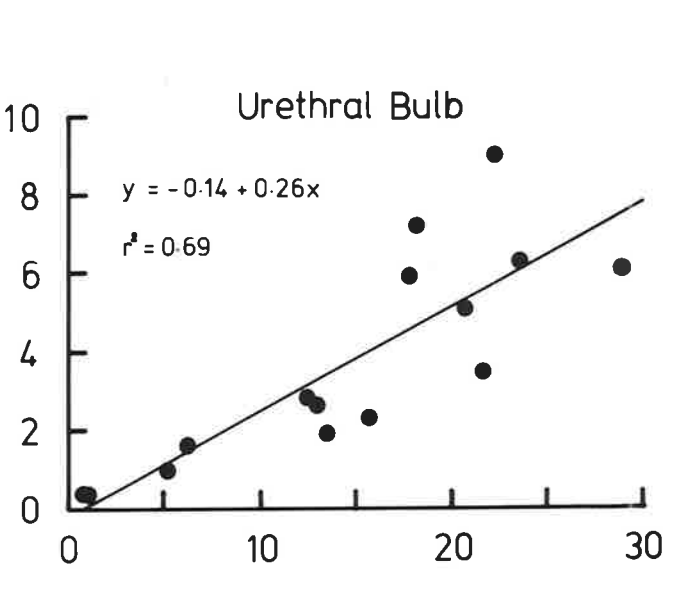
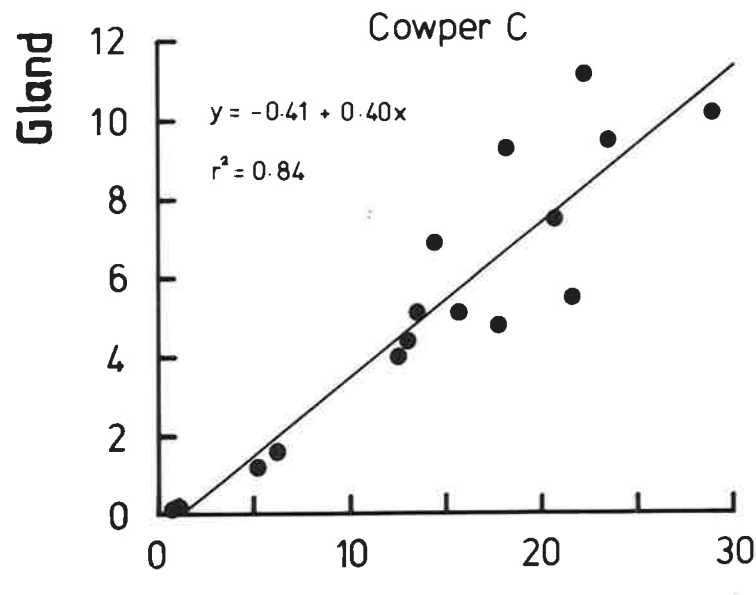
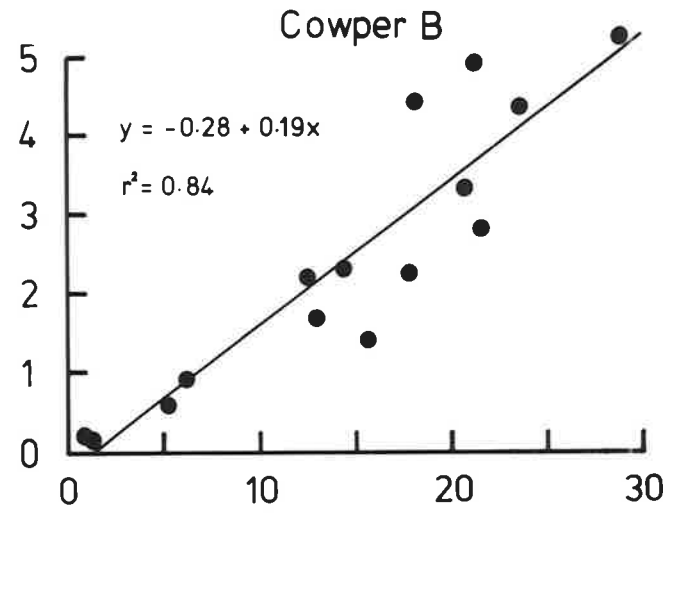
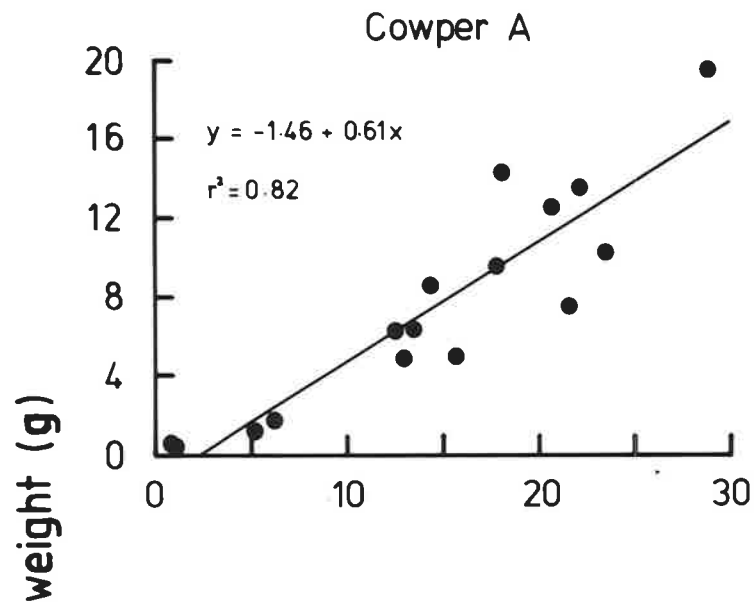
In the prostate, sorbitol was located in the anterior part, and fructose in the central segment. Glucose and N-acetylhexosamine were found in both central and posterior segments of the prostate. Cowper's C gland contained some glucose and fructose and a considerable amount of sialic acid. This gland and the posterior prostate contained the highest concentration of orcinol and anthrone-reactive carbohydrate. High concentrations of glycogen were found in the posterior prostate and Cowper's B and C glands. Citric acid was identified as a major chemical constituent of Cowper's A gland. *In vitro* mixing of secretions of each of the prostates (except the

Table 4.1

Chemical	Units	Anterior prostate	Central prostate	Posterior prostate	Cowper's A	Cowper's B	Cowper's C
Glucose	$\mu \text{ mol g}^{-1}$	0.88±0.19 (4)	3.50±0.48 (5)	4.76±1.13 (5)	1.23±0.33 (3)	2.15±0.75 (2)	6.36±0.78 (3)
Fructose	$\mu \text{ mol g}^{-1}$	0.87±0.30 (4)	5.53±1.26 (5)	1.19±0.23 (5)	0.22±0.05 (3)	0.26±0.05 (2)	0.81±0.17 (3)
Sorbitol	$\mu \text{ mol g}^{-1}$	2.95±0.68 (4)	0.06±0.03 (3)	0 (3)	0.09±0.09 (2)	0 (2)	0 (2)
N-acetylhexosamine	$\mu \text{ mol g}^{-1}$	0.43±0.05 (4)	1.28±0.20 (5)	2.68±0.69 (5)	0.17±0.09 (3)	0.58±0.07 (2)	1.05±0.30 (3)
Glucose-6-phosphate	$\mu \text{ mol g}^{-1}$	0.46±0.16 (4)	0.37±0.04 (4)	0.97±0.27 (4)	0.42±0.01 (2)	0.84±0.08 (2)	0.93±0.38 (2)
Total sialic acid	$\mu \text{ mol g}^{-1}$	0.62±0.19 (2)	1.00±0.14 (4)	1.31±0.13 (4)	0.48±0.18 (4)	1.53±0.78 (3)	20.0±3.9 (4)
Glycogen	mg g^{-1}	0.16±0.06 (2)	0.29±0.06 (2)	7.34±1.00 (2)	0.42±0.24 (2)	3.86±0.87 (2)	2.09±0.52 (4)
Orcinol-reactive carbohydrate	mg g^{-1}	1.83±0.03 (2)	3.59±0.26 (3)	11.4±0.65 (3)	1.50±0.18 (3)	6.86±0.50 (2)	13.4±0.8 (3)
Anthrone-reactive carbohydrate	mg g^{-1}	0.95±0.10 (2)	2.95±0.30 (3)	11.3±0.8 (3)	1.31±0.33 (3)	5.05±0.30 (2)	9.27±0.54 (3)
Citric acid	$\mu \text{ mol g}^{-1}$	3.13±1.82 (3)	3.02±1.46 (4)	1.88±0.83 (4)	22.8±2.4 (4)	2.76±0.94 (4)	2.71±0.99 (4)

Table 4.1 Chemical composition of the male accessory glands of reproduction in the hairy-nosed wombat. Mean values \pm S.E., with the number of glands assayed shown in parentheses.

Figure 4.3 Relation between the weight of various components of the male reproductive system of the hairy-nosed wombat, *Lasiorhinus latifrons*. The weight of the prostate gland has been used as the reference. Against this have been plotted the weights of the three glands designated as Cowper's A, B and C and also the urethral bulb (which consists of erectile tissue). Cowper's A, B, C and the urethral bulb exist as paired structures (see Figure 4.1) and each point represents the average weight of one of the pair. Regression lines were fitted by least squares analysis and the equation is shown for each line.



Prostate weight (g)

secretion of the posterior prostate) alone, with a mixture of the secretions of all the Cowper's glands resulted in coagulation and solidification of the mixture when heated at 37°C for 2-3 min. Mixing together the secretions of the Cowper's glands, or of the segments of the prostate did not result in coagulation.

4.2.3 Variation in the reproductive tract and plasma hormone concentrations of the male wombat

Samples were collected during the 3 breeding seasons and 2 non-breeding seasons.

In the July-December 1977 breeding season infertility (as demonstrated by an increased percentage of aspermatogenic males) was observed. Evidence to be presented in the following chapter supports the idea that the infertility could be attributed to drought, which occurred from December 1976 to April 1978. It was associated with a significant decrease in the weights of testis and accessory sex glands. The concentrations of the chemical constituents of the accessory glands fell, together with concentrations of FSH, LH and androgen in plasma (Tables 4.2,4.3).

Elevated concentrations of FSH, LH and androgen did not occur in 1977, when no reproduction was observed (see Chapter 5). The data from December 1976 suggest a decline in testis weight, hormone concentrations and size of accessory glands at the end of a period of breeding even though no infertility was apparent. Presumably the size of the accessory glands in October 1977 is below that which would be observed in the non-breeding season of a non-drought year.

Average prostate weight declined from 19.1g in October 1976 to 9.3g in June - August 1977; when no reproduction was observed in the following months the average prostate weight declined to 4.3g in October - November 1977. Presumably the weight of the gland would not fall below about 9-10g if further reproductive activity occurred at the end of the non-breeding period.

Table 4.2

Measurement	Units	Period					F ^a
		Oct 76	Dec 76	June 77 - Aug 77*	Oct 77 - Nov 77*	Aug 78	
n		10	6	14	7	3	
Testis weight	g	8.5 ±0.6	7.1 ±0.5	6.2 ±0.5	4.6 ±0.9	10.9 ±2.0	F4,31 = 6.6 ^a
Plasma androgen	ng ml ⁻¹	3.50 ±1.60	0.10 ±0.02	0.28 ±0.09	0.11 ±0.02	7.00 ±3.80	F4,33 = 5.2 ^a
Plasma FSH	ng ml ⁻¹	298 ±52	13 ±7	31 ±14	22 ±11	288 ±34	F4,38 = 19.2 ^a
Plasma LH	ng ml ⁻¹	0.50 ±0.10	0.10 ±0.00	0.20 ±0.05	0.10 ±0.05	0.80 ±0.10	F4,31 = 16.3 ^a
Aspermatogenetic	per cent	0	0	36	56	0	-

a P < 0.01 Analysis of variance. * Months of drought.

Table 4.2 Variation in testis weight, per cent aspermatogenetic males and plasma hormone concentrations of wombats caught on pastoral properties over 2 years. Mean values ± S.E.

Table 4.3

Measurement	Units	Period					F ^a
		Oct 76	Dec 76	June 77 - Aug 77*	Oct 77 - Nov 77*	Aug 78	
n		10	2	12	7	3	
Prostate weight	g	19.1 ±1.6	15.1 (17.8-12.5)	9.3 ±1.1	4.3 ±0.9	28.7 ±5.3	F4,29 = 21.17 ^a
Cowper's A weight	g	10.6 ±1.9	7.4 (5.6-9.1)	5.2 ±0.6	2.8 ±0.9	17.3 ±3.9	F4,25 = 10.78 ^a
Cowper's C weight	g	7.7 ±1.0	-	2.1 ±0.2	1.3 ±0.3	9.4 ±2.0	F3,24 = 29.56 ^a
Prostatic glycogen	mg g ⁻¹ wet wt.	9.8 ±1.2	5.8 (4.9-6.7)	4.4 ±0.9	2.7 ±0.4	-	F3,20 = 8.37 ^a
Prostatic fructose	μ mol g ⁻¹ wet wt.	5.8 ±1.0	3.6 (2.7-4.5)	4.4 ±1.3	0.9 ±0.2	11.5 ±3.0	F4,26 = 5.49 ^a
Cowper's A citric acid	μ mol g ⁻¹ wet wt.	22.9 ±3.6	38.5 (29.1-47.3)	13.6 ±3.1	15.1 ±6.8	-	F3,23 = 2.96
Cowper's C sialic acid	μ mol g ⁻¹ wet wt.	22.3 ±2.9	-	7.2 ±0.9	8.2 ±2.1	-	F2,22 = 21.24 ^a

a P < 0.01 Analysis of variance. * Months of drought.

Table 4.3 Variation in weights, and concentrations of the main chemical constituents of the accessory sex glands of male wombats caught on pastoral properties over 2 years. Mean values ± S.E.

4.2.4 Morphology of the reproductive tract of the female wombat

Reproductive tracts were obtained from juvenile, pregnant, lactating and anoestrous wombats. The gross appearance of typical reproductive tracts are shown in Plates 1-4, Figure 4.4 and is similar to that described for *Vombatus ursinus* by MacKenzie & Owen (1919). Results of morphological measurements made on the reproductive tracts are shown in Table 4.4.

4.2.4.1 Ovary

The ovaries are oval to rectangular structures flattened on their dorsal aspect, but convexly bent on their ventral surfaces. The surfaces of the ovaries show many convolutions that are particularly prominent in sexually immature wombats in which the ovaries have not been altered by a corpus luteum.

The corpus luteum of the wombat is a prominent yellow to pink structure, densely vascularized (Plate 4, Figure 4.4). In 3 lactating animals (with young 2-3 months of age) the corpus luteum (albicans) was of similar size to that of pregnant animals, but brown to grey in colour. A number of these non-functional (see later) corpora lutea (albicantia) were found in the ovaries of sexually mature wombats, but usually only one functional corpus luteum was present after ovulation.

Translucent graafian follicles were abundant on the surfaces of the ovaries of pregnant and also of some lactating wombats, the largest being nearly 1.0 cm in diameter (Table 4.4).

The largest ovaries were those of animals that had ovulated shortly before death, and the smallest ovaries were those of anoestrous and juvenile wombats.

Figure 4.4 The female reproductive tract of *Lasiorchinus latifrons*.

Plate 1. Female reproductive tract, ventral view.

2. Female reproductive tract, dorsal view.

3. Reproductive tract of an anoestrous wombat, ventral view.

4. Reproductive tract of wombat with prominent corpus luteum on left ovary, ventral view.

Abbreviations: O ovary; CL corpus luteum; GF graafian follicles;
U uterus; MV median vagina; LV lateral vagina;
B bladder; UGS urogenital sinus; UGSG urogenital
sinus glands; R rectum.

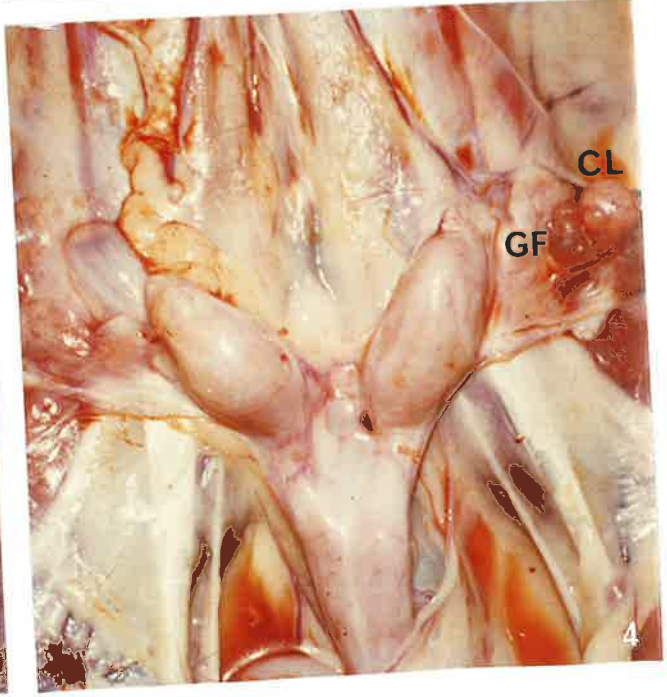
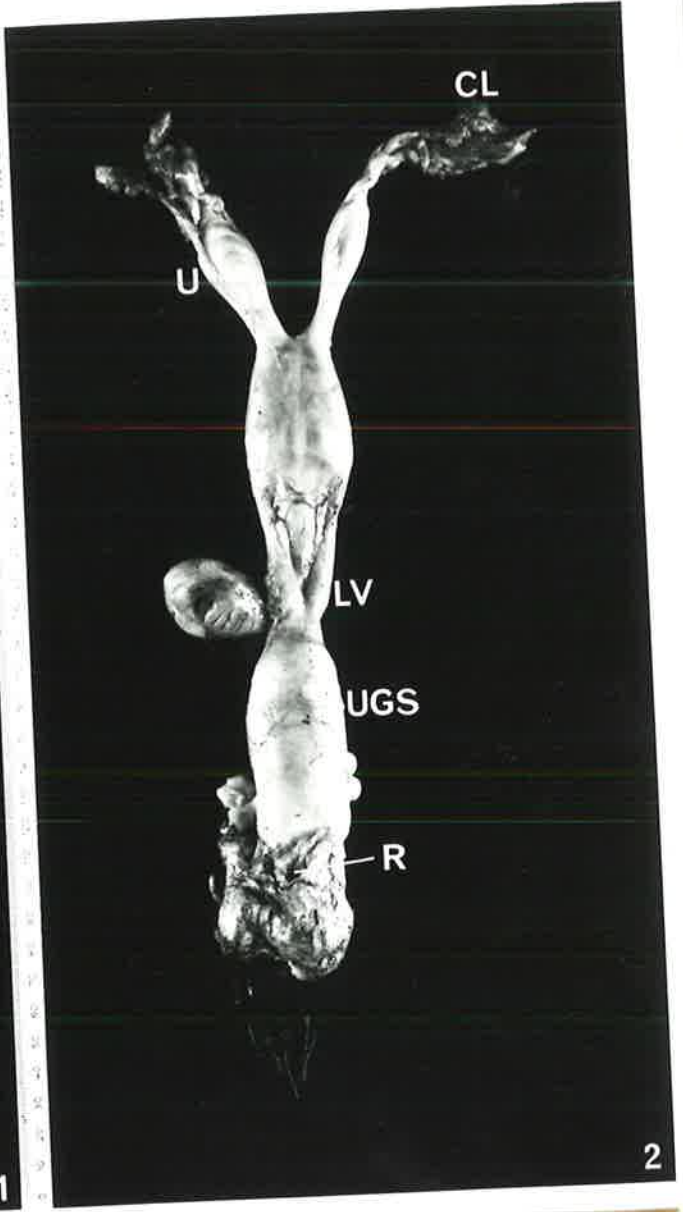
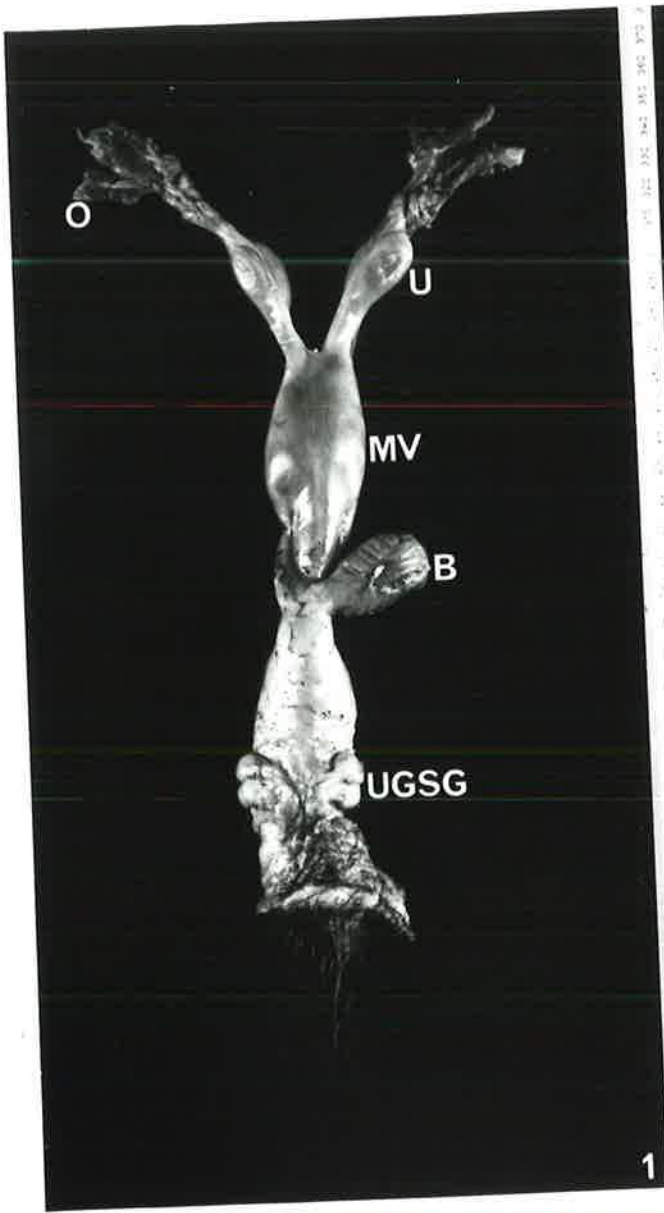


Table 4.4

Measurement	Units	Reproductive state			
		Recently ovulated	Lactating	Anoestrous	Sexually immature
n		9	3	12	7
Mean ovary weight	g	1.34 ±0.23	0.75 ±0.22	0.32 ±0.06	0.29 ±0.06
Corpus luteum weight	g	0.56 ±0.13	0.37 [†] ±0.07	-	-
Corpora albicantia diameter	mm	2-7	2-7	1.5-6	-
Number of corpora albicantia		1-4	1-3	0-3	0
Mean uterus weight	g	5.54 ±0.82	2.00 ±0.35	0.81 ±0.12	0.28 ±0.04
Mean urogenital sinus gland weight	g	2.07 ±0.28	1.98 ±0.47	0.51 ±0.07	0.15 ±0.02
Number of graafian follicles		0-8	0-5	0	0
Largest follicle size	mm	2.5-9.0	2.4-4.5	0.3	1.2
Plasma progesterone	ng ml ⁻¹	1.42* ±0.32	< 0.2	< 0.2	< 0.2

[†] Corpus luteum of preceding pregnancy. * n = 5.

Table 4.4 Morphological characteristics of the reproductive tract, and plasma progesterone concentrations of female wombats in different reproductive states. Mean values ± S.E.

Histologically, the ovaries resembled those described by O'Donoghue (1914, 1916) for *Vombatus ursinus*.

The luteal cells of a typical corpus luteum were large and polyhedral in shape with a centrally located nucleus. The cytoplasm of these cells appeared finely granulated. In contrast these cells in the corpus albicans were smaller and showed signs of degeneration since their nuclei were pyknotic (Plates 1,2, Figure 4.5). Apart from corpora lutea or corpora albicantia a prominent histological feature of ovaries was the presence of much interstitial tissue some of which appeared to be luteinized. In ovaries of juvenile and adult wombats two types of structured interstitial tissue were evident and both often contained a degenerate oocyte. In one type the cells were relatively large, the nuclei occupying approximately 40-50 per cent of the cells. In the other type, nuclei occupied up to 90 per cent of the smaller cells and as a result this type of interstitial tissue appeared darker in sections (Plates 4,5, Figure 4.5).

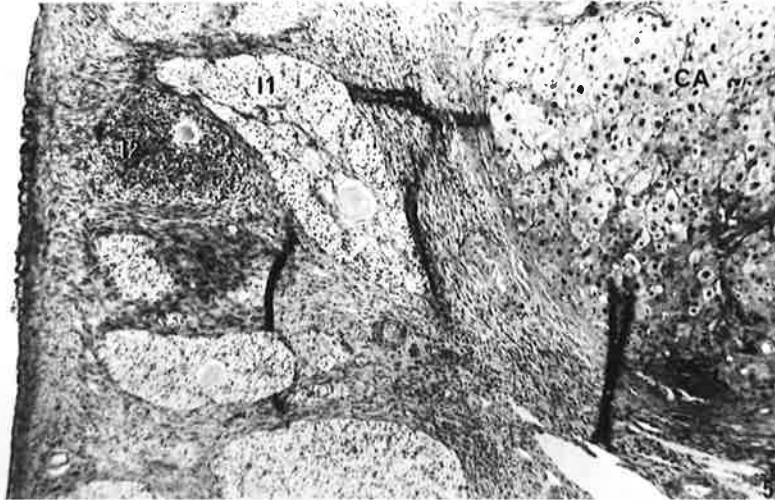
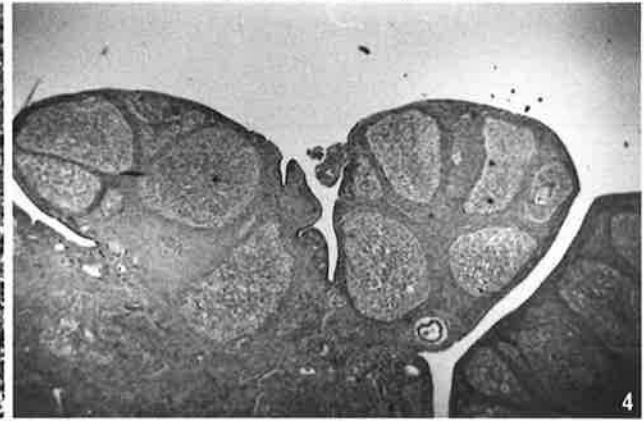
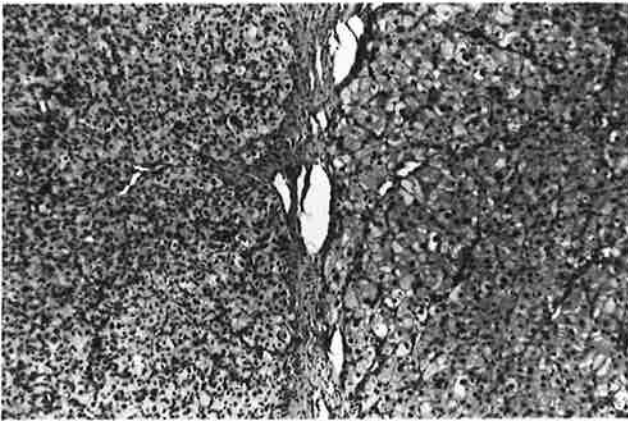
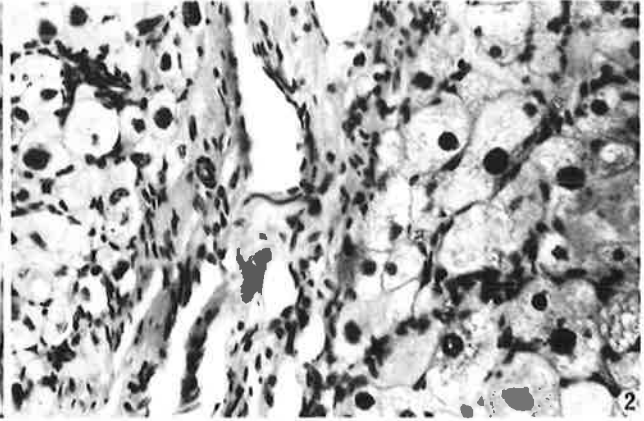
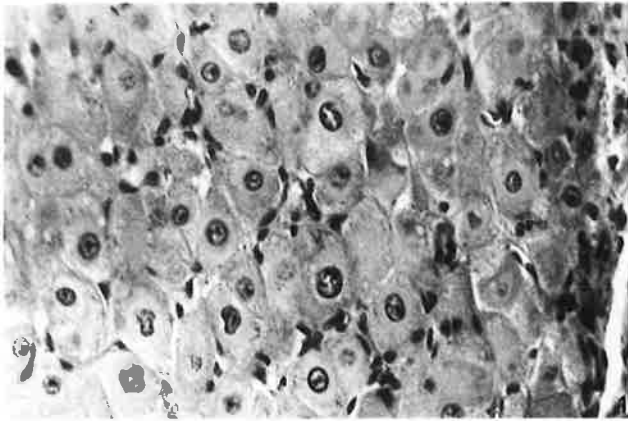
4.2.4.2 Uterus

Uteri were well-defined oval structures in pregnant and lactating wombats, but were of similar size to fallopian tubes in anoestrous and juvenile animals. Endometrial uterine glands of anoestrous wombats were of small size, the lumina narrow or closed and the nuclei of cuboidal epithelia occupied much of the cells. The cells of glands from uteri in the luteal phase were much larger, and columnar in type, while lumina were prominent. Uteri were smaller in lactating wombats and a much smaller amount of endometrium was evident (Table 4.4).

Figure 4.5 Photomicrographs of the ovary of *Lasiorhinus latifrons*.

Plate 1. Corpus luteum. × 400.

2. Two corpora albicantia separated by connective tissue. × 400.
3. Corpora albicantia shown in Figure 2. × 100.
4. Section through the surface of the ovary of a sexually immature wombat. Note the abundant interstitial tissue and convoluted surface of the ovary. × 40.
5. Section through surface of the ovary to illustrate the two types of interstitial tissue (11 & 12) described in the text. Note the degenerate oocytes associated with both types. A corpus albicans can be seen on the right. × 100.



4.2.4.3 Vaginae and urogenital sinus

Uteri open into the median vagina or vaginal cul-de-sac. Proximally, a well-defined septum extending for up to half the length of the median vagina separated the orifices of the two uteri and lateral vagina of each side. The median vagina of adult wombats opened into the urogenital sinus just above the opening of the bladder into this chamber. In juvenile wombats the median vagina did not connect with the urogenital sinus.

The greatly expanded nature of the median vagina of the reproductive tract shown in Plates 1,2, Figure 4.4 was due to the presence of a large quantity of coagulated semen and vaginal secretions.

Of particular interest in regard to the urogenital sinus were two pairs of glands (named urogenital sinus glands) with ducts opening into the sinus approximately 4-5 cm distal to the cloaca. They secreted a green viscous fluid into the urogenital sinus and were of greatest size in wombats with a functional corpus luteum (Table 4.4).

4.2.4.4 Marsupium

Many qualitative differences were observed among the pouches of wombats in the various reproductive conditions. Anoestrous and juvenile wombats had shallow, dry pouches with small teats and poorly developed sphincter muscles. Conversely, reproductively active females has moist, deep pouches, with one teat elongated. Sphincter muscles were well developed.

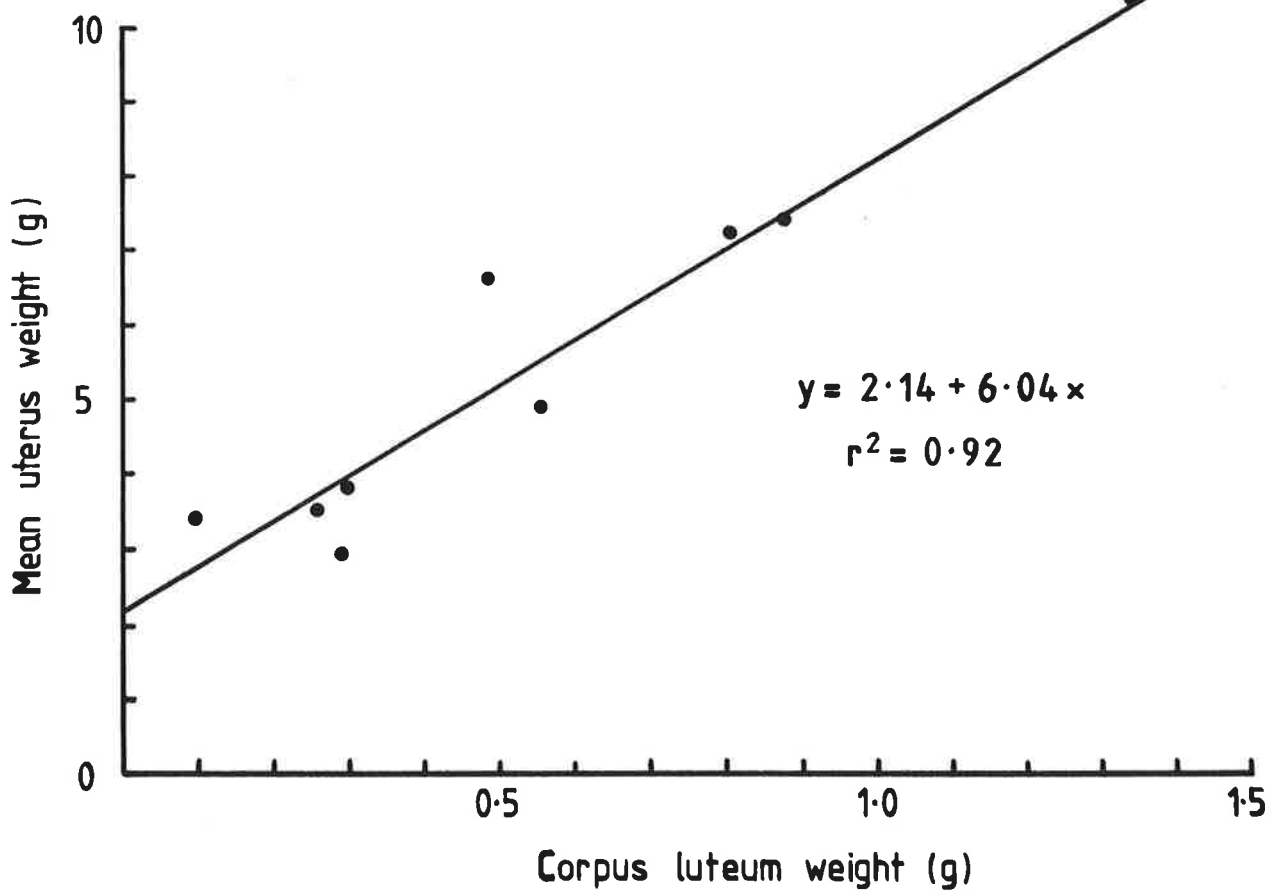
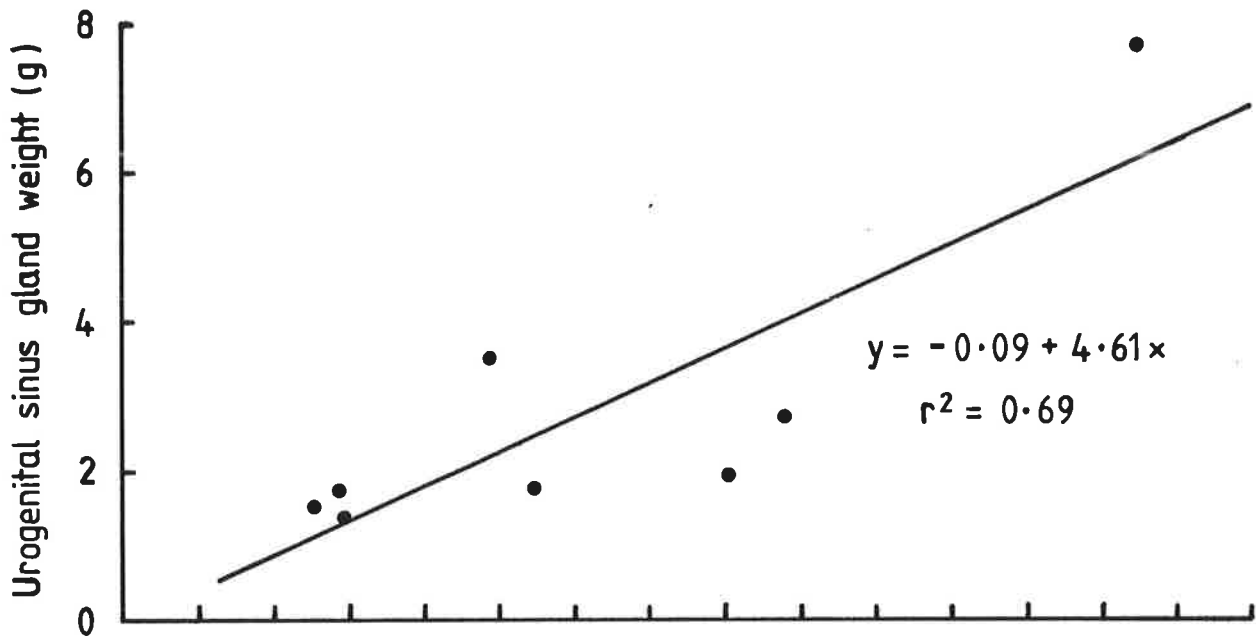
4.2.4.5 Functional considerations

From the limited material available it is not possible to say a great deal about the physiological control of reproduction in female wombats.

Plasma progestins were measured in animals with a corpus luteum but were not detectable in plasma of lactating, anoestrous or juvenile wombats even if well-defined corpora albicantia were present (Table 4.4). In animals with a functional corpus luteum (secreting progestins) there was a good correlation between the weight of the corpus luteum and the mean weight of the two uteri (Figure 4.6). Of interest was a similar correlation between the weight of the corpus luteum and the mean weight of the pairs of urogenital sinus glands (Figure 4.6).

In captivity female wombats are polyoestrous and will return to oestrus after weaning or loss of pouch-young. One piece of evidence from the field suggests this may be the case in the wild. The young of 5 wombats (estimated ages 5-90 days) were removed from their mothers' teats in October 1978. Two of these females were subsequently recaptured in December 1978 and 1 had a new-born young in the pouch. It was approximately 55 days between removal of the first young and birth of the second. Given the reported gestation period of 21 days, this leaves 34 days for follicular growth and ovulation, a period of time within the range of oestrous cycles of captive wombats. There was no evidence to suggest that post-partum ovulation occurs in *Lasiorchinus* since lactating females had regressed reproductive tracts and no corpora lutea were observed in the ovaries of these females. Crowcroft & Soderlund (1977)

Figure 4.6 Relationships between the weights of the urogenital sinus glands (average weight of the 2 pairs) and uterus and the weight of the corpus luteum. Regression lines were fitted by least squares analysis and the equation is shown for each line.



did not report post-partum oestrus or copulation in their successfully breeding captive wombats.

Plugs of coagulated semen were found in the urogenital sinus and median vagina of 2 females. In both these animals (the corpus luteum depicted the corpus luteum although evident was relatively small, weighed 0.1g), in Plates 1,2, Figure 4.4. Copulation presumably had occurred within 4-5 days since in captivity it is known that copulatory plugs are expelled 4-5 days after mating.

Uteri were dissected, but only one embryo visible to the naked eye was found. It was 5 mm long, and the corpus luteum on the corresponding ovary was the largest found in this study. The smallest pouch-young found was 19 mm in length.

The appearance of the reproductive tract of the female wombat in the different seasons of the study are discussed in detail in the following chapter, but like male wombats there was no reproductive activity (pregnancy, lactation or oestrus) when drought occurred in the breeding season. Two females in October 1977 had a few small graafian follicles (2-3 mm diameter) in their ovaries but none had ovulated.

4.3 Discussion

The gross anatomy and histology of the accessory sex glands of the male wombat are similar to those described for other marsupials (Rodger & Hughes 1973). The range of chemical compounds detected in these glands overlapped with the many well-known constituents of the semen of eutherian mammals (Mann 1964, Rodger 1976).

Unlike many other marsupials where N-acetylglucosamine is

reported to be the main prostatic sugar (Rodger & White 1976) the wombat showed high concentrations of fructose, but relatively low concentrations of N-acetylglucosamine.

Rodger (1976) divided marsupials into two groups on the basis of the biochemistry of their accessory sex glands. In one group, the Macropodidae, Phalangeridae and Peramelidae, N-acetylglucosamine was the major prostatic sugar while the other group comprising Dasyuridae and Didelphidae, showed little of this compound but large amounts of glycogen. The wombat must be considered a separate group again since there are high concentrations of both fructose and glycogen in its prostate, which distinguishes it from other marsupials.

Rodger (1978) stated that in the Marsupialia, coagulation of semen occurs only in the Macropodidae, but it is apparent from this study that coagulation occurs in the semen of *Lasiorchinus* and further, it is dependent on adequate mixing of the secretions of the prostate and Cowper's glands. This was consistent with Rodger's (1978) arguments relating coagulation of semen to a patent median vagina, since this was the condition found in adult female wombats also.

Seasonal studies on the reproductive tract of the male wombat revealed a marked variation in the size of the testis and accessory sex glands together with marked changes in concentrations of reproductive hormones in plasma. The data presented show that a decline in organ size and concentrations of hormones occurs at the end of a breeding season, and further decline occurs if drought inhibits reproduction. Presumably the concentrations of FSH, LH

and androgen fall below a certain level, then spermatogenesis ceases, as observed in 1977. Infertility is an obvious result of the cessation of spermatogenesis, but it is reasonable to assume that the reproductive potential of male wombats would also be curtailed as a result of a marked decrease in size of accessory sex glands. Drought conditions appear to inhibit the pituitary-gonadal axis in male wombats, but because of the fossorial and nocturnal habits of wombats it is unlikely that heat inhibits spermatogenesis as it does in red kangaroos (Newsome 1973).

Peak reproductive condition of male wombats as determined by hormone concentrations and organ sizes, coincided with times at which female wombats ovulated, suggesting that reproductive activity of male wombats is determined by that of females or that the same environmental factors influence both sexes. Accompanying the seasonal reproductive cycle of many other marsupials are seasonal changes in the size of testes or accessory sex glands or both. Examples include the brushtail possum (Gilmore 1969), Bennett's wallaby *Macropus rufogriseus fruticus* (Catt 1977) and the tammar wallaby (Inns 1978).

The size and function of the accessory sex glands are determined by the concentrations of plasma androgens in eutherian mammals (Mann 1964, Gustafson & Shemesh 1976). The seasonal data presented here suggest that this is true of *Lasiorchinus* also.

In the brushtail possum, Cook et al. (1978) have shown that there is a positive correlation between concentrations of serum testosterone and the weight of the prostate gland. Similar observations have been made by Carrick & Cox (1977). The

concentrations of plasma androgen measured in the wombat were similar to values reported for macropods (Lincoln 1978) and the brushtail possum (Cook et al. 1978).

Of particular physiological interest is an apparent difference between the wombat and the tammar wallaby, in the seasonal pattern of FSH concentrations. A study by Catling & Sutherland (1980) has shown that LH and androgen (but not FSH) fluctuate seasonally in this wallaby whereas all three hormones fluctuated seasonally in the wombat. It is also known that testis weight does not vary seasonally in the wallaby, but there are marked changes in weight of the prostate gland (Inns 1978). Such comparative data suggest that maintenance of the weight of testes is dependent primarily on FSH concentrations in these marsupials.

The appearance of ovaries obtained from wombats in different reproductive states was consistent with well-known patterns of ovulation, corpus luteum development and uterine development, in marsupials (Hughes et al. 1965, Tyndale-Biscoe 1973, Tyndale-Biscoe et al. 1974) particularly other families than macropods.

The corpus luteum formed after ovulation reached a very large size (up to 17 mm diameter and 1.0 g in weight) yet at this stage of its development the length of one embryo was 5 mm. This corresponded to the largest corpus luteum found by O'Donoghue (1914) in a pregnant *Vombatus ursinus* where the embryo was 9 mm in length. In two cases he also noted that when the embryo was larger (15.5 mm and 17.5 mm) the corpus luteum was slightly smaller (11.8 mm and 14.3 mm respectively) suggesting a decline

in corpus luteum size during later stages of gestation. Further, he observed the corpus luteum to be smaller again after birth, a pattern found in this study for *Lasiiorhinus*.

The close relationship between the size of the corpus luteum and mean weight of the uteri, and the fact that progestins were not detected in the plasma of animals without a corpus luteum, suggests that in keeping with other marsupial and eutherian mammals, the corpus luteum secretes progestins which influence the secretory activity of the uteri (and hence their weight). Further, it is highly likely that the many corpora albicantia found in ovaries of mature wombats do not secrete significant amounts of progestins, which is in keeping with their histological appearance.

The anatomical fate of the corpus luteum in marsupials is varied, and ranges from complete degeneration in some macropods (Tyndale-Biscoe 1973) and the common ringtail possum (Hughes et al. 1965) to complete retention in the mountain possum *Trichosurus caninus* (Smith & How 1973). The wombat is intermediate with the corpus luteum slowly decreasing in size over many years.

The limited physiological interpretation that can be placed on the data suggests that the wombat has a reproductive pattern similar to that of the brushtail possum. As in the possum, uteri of pregnant animals reach a very large size and concentrations of plasma progestins are higher than in macropods that have been studied (Tyndale-Biscoe et al. 1974).

There is no evidence from this study or in the literature that post-partum oestrus occurs in wombats. Graafian follicles

were prominent in the 3 lactating females examined, and were also noticed by O'Donoghue (1914) in *Vombatus ursinus*, but no corpus luteum was observed. O'Donoghue described the corpus luteum of lactating *Vombatus* as being similar to the corpus luteum of pregnant animals. Ovaries of lactating wombats were not sectioned for histological examination in this study, but undetectable concentrations of progestins and involution of uteri suggest that functional activity of the corpus luteum is lost after birth.

The qualitative differences in the pouches of pregnant compared with anoestrous wombats can probably be attributed to the influence of reproductive hormones on this structure. Bolliger (1942) found that dry shallow pouches changed into moist, deep structures when gonadotrophin obtained from the urine of pregnant humans was injected into the brushtail possum.

Of practical value in determining the reproductive state of female wombats was the relationship between the sizes of the corpus luteum and the urogenital sinus glands. In animals with a large corpus luteum and in those that had recently given birth, the secretion of these glands was easily expressed into the urogenital sinus. These glands have not been described by other authors except for the mention in Parker and Haswell's 'Textbook of Zoology' where they were referred to as 'rectal glands'. Such accessory sex glands in female mammals are perhaps unusual and to my knowledge have not been described for other marsupials. Their functional significance is unknown, but they may be associated with successful parturition, since they increase in size throughout pregnancy.

In summary, it is clear that several anatomical and physiological features of the reproductive biology of wombats are useful for determining the reproductive state of males and females. They include concentrations of hormones in plasma of both sexes and the gross appearance of the pouch and urogenital sinus in females. Spermatogenesis can be accurately assessed by histological examination of sections of testicular tissue obtained by biopsy.

There is much evidence to suggest that the reproductive cycle of male wombats is controlled in the typical mammalian manner, but the physiology of its seasonal reproductive pattern is clearly dependent on environmental conditions. Whether development of follicles, ovulation, oestrus and lactation occur appears to be dependent upon aspects of environment also.

These conclusions are based on the observations that

- 1) the seasonal patterns of high concentrations of gonadotrophins associated with high concentrations of androgens is consistent with gonadotrophin stimulation of androgen release
- 2) The association between high concentrations of androgens and large accessory sex glands is consistent with the latter being 'androgen dependent'
- 3) The sustained low concentrations of androgens and gonadotrophins associated with cessation of spermatogenesis is consistent with the spermatogenic process being dependent on those hormones
- 4) Failure of wombats to breed during drought was associated with diminished gonadotrophin and androgen secretion.

CHAPTER 5

PATTERNS AND FREQUENCY OF REPRODUCTION OF WOMBATS

5.1 Introduction

A major determinant of growth and survival of a population is the frequency at which new individuals are recruited to it.

There is much evidence in the literature to suggest that the frequency of reproduction is influenced by environmental circumstances both in the short-term and in an evolutionary sense (see Chapter 1). As such, depending on habitat, variation in reproductive frequency can be broad, ranging from consistent production of young, one or more times each year, to highly irregular reproductive events. An animal may reproduce once (semelparity) or many times (iteroparity) in its life.

Theoretical models of reproductive patterns are usually based on ideas that the frequency of reproduction represents part of adaptations enabling maximum genetic reproduction. Apparently submaximal phenotypic reproduction may be entirely consistent with maximal reproduction of genes. Lack (1966) was the first to propose such ideas for birds and recently there have been examples from the mammals in the literature (see Barash 1974).

Patterns—largely temporal variations in frequency of reproduction—represent the accommodations individuals make to the environment, and are the result of the integration of many external and internal forces acting on an animal. Such forces include lifespan, seasonal conditions and nutritional status.

In general, if resources available to mother and young are highly seasonal in abundance reproduction will tend to be seasonal. If the availability of resources is unpredictable, a situation often found in deserts, different^{and} often episodic patterns of reproduction

may be more appropriate, allowing maximum advantage to be taken of the resources when they are available.

To understand the way in which environmental forces influence patterns of reproduction it is necessary to recognize those resources which are the most important to a species.

There are various patterns of reproduction in desert marsupials ranging from continuous reproduction in red kangaroos (if environmental conditions are suitable) to seasonal reproduction in grey kangaroos inhabiting arid regions (see Chapter 1). Attempts to fit observed reproductive patterns to popular theories of population dynamics, such as r and K-selection, have been apparently successful in some cases (Richardson 1975). But the great variety of reproductive patterns of marsupials as a whole (Sharman et al. 1966) means that consideration of differences in species' habitats rather than typing ecosystems will be more useful to an understanding of why particular reproductive patterns evolved in a species.

Predictably, little is known of the reproductive patterns of wombats. McIlroy (1973) observed that *Vombatus ursinus*, near Canberra, bred in the latter half of the year. His records, however, contain too few cases to make definite statements about the effects of environment on reproduction although he noted that particular females did not produce young in some years.

Wells (1973) noted from his records of capture that small hairy-nosed wombats were found in spring and summer, but a detailed analysis of these records was not made. His records have been analysed and used to supplement data collected in this study.

5.2 Results

5.2.1 Birth and pouch life

Twenty-nine pouch young were examined: 19 females and 10 males ($\chi^2_1 = 2.79$, $P > 0.05$, sex ratio not significantly different from 1:1). The number of births per month is shown in Figure 5.1. The earliest births occurred in winter with a peak in numbers in early spring. Young wombats were carried in the pouch for 6 to 9 months; females rarely carried the young of the previous year beyond late winter (August) or early spring (September, Figure 5.2). The size of young is shown in Figure 5.3. Observation of 2 lactating females suggests that once young attain a body length of 30-40 cm they leave the pouch permanently, but remain in the burrow when the mother emerges to graze. Within 1 to 2 months of leaving the pouch these young wombats emerged from the burrow. Initially they did not accompany the mother when she moved away from the warren to graze, but they did so after a few weeks. The average weight of young caught at this time was 1.8 kg and their body lengths were 40-50 cm; all bore wear-facets on their teeth.

Observations of a young wombat from the time it first emerged from the burrow in July until it was permanently independent of the mother indicated that it was weaned in September when approximately 1 year old. At 16-18 months, wombats were about 70 cm long and, at 10-15 kg in weight, were approximately half the weight of an adult.

Growth rates were highly variable following weaning. In years of good pasture growth young wombats grew rapidly as from April 1975 when they grew from 10-15 kg to over 20 kg by February 1976, and attained lengths of 80 cm. In years of poor pasture

Figure 5.1 The number of wombats born in each month of the year. The months of births of the 29 wombats were estimated by extrapolation from the rate of growth of the pouch-young in captivity.

9

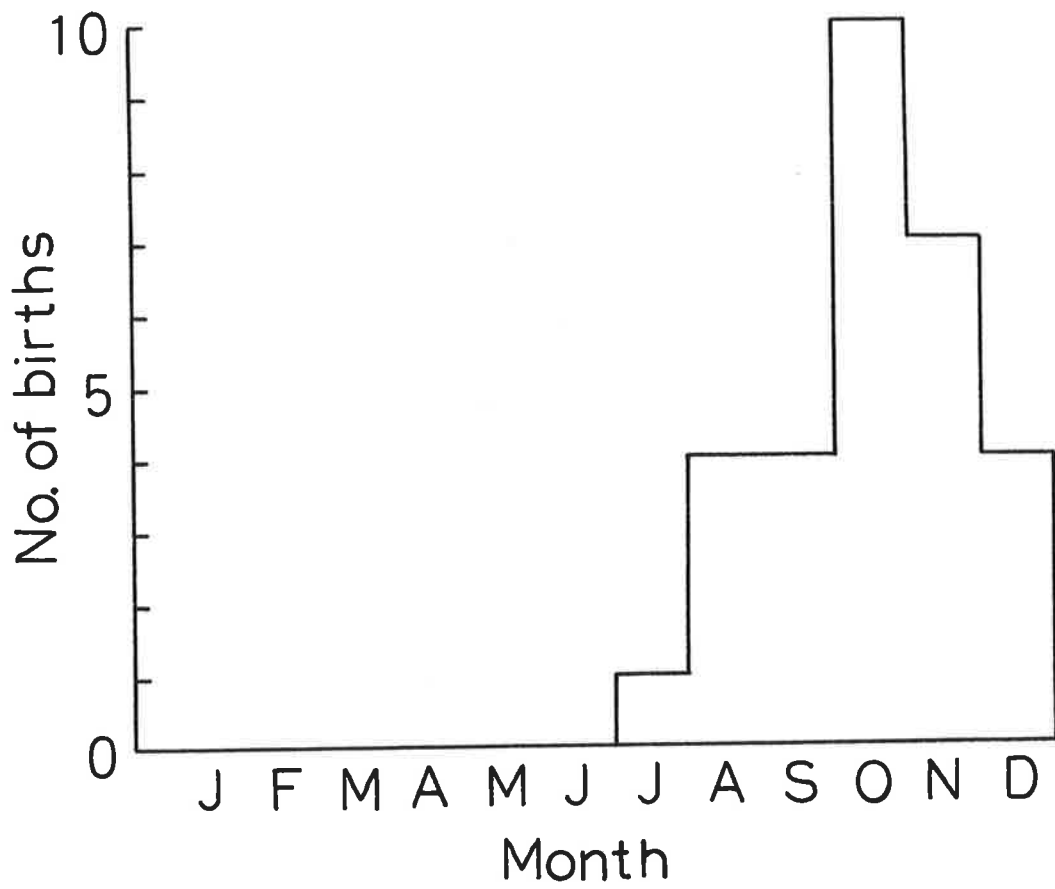


Figure 5.2 The months during which 3 wombats inhabiting the same warrens carried young in their pouches.

F4

FD

FT

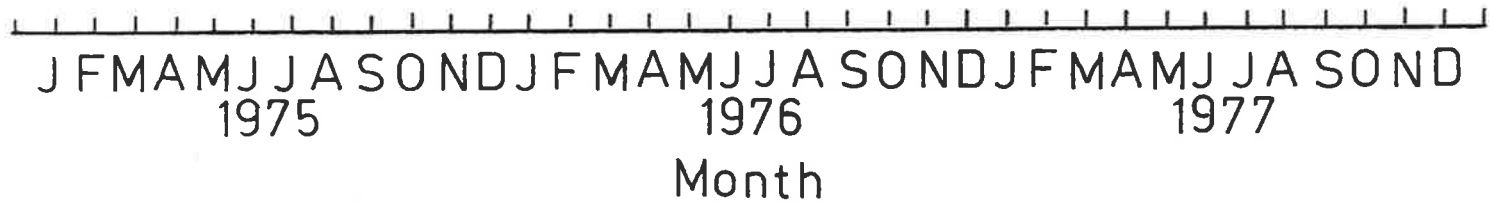
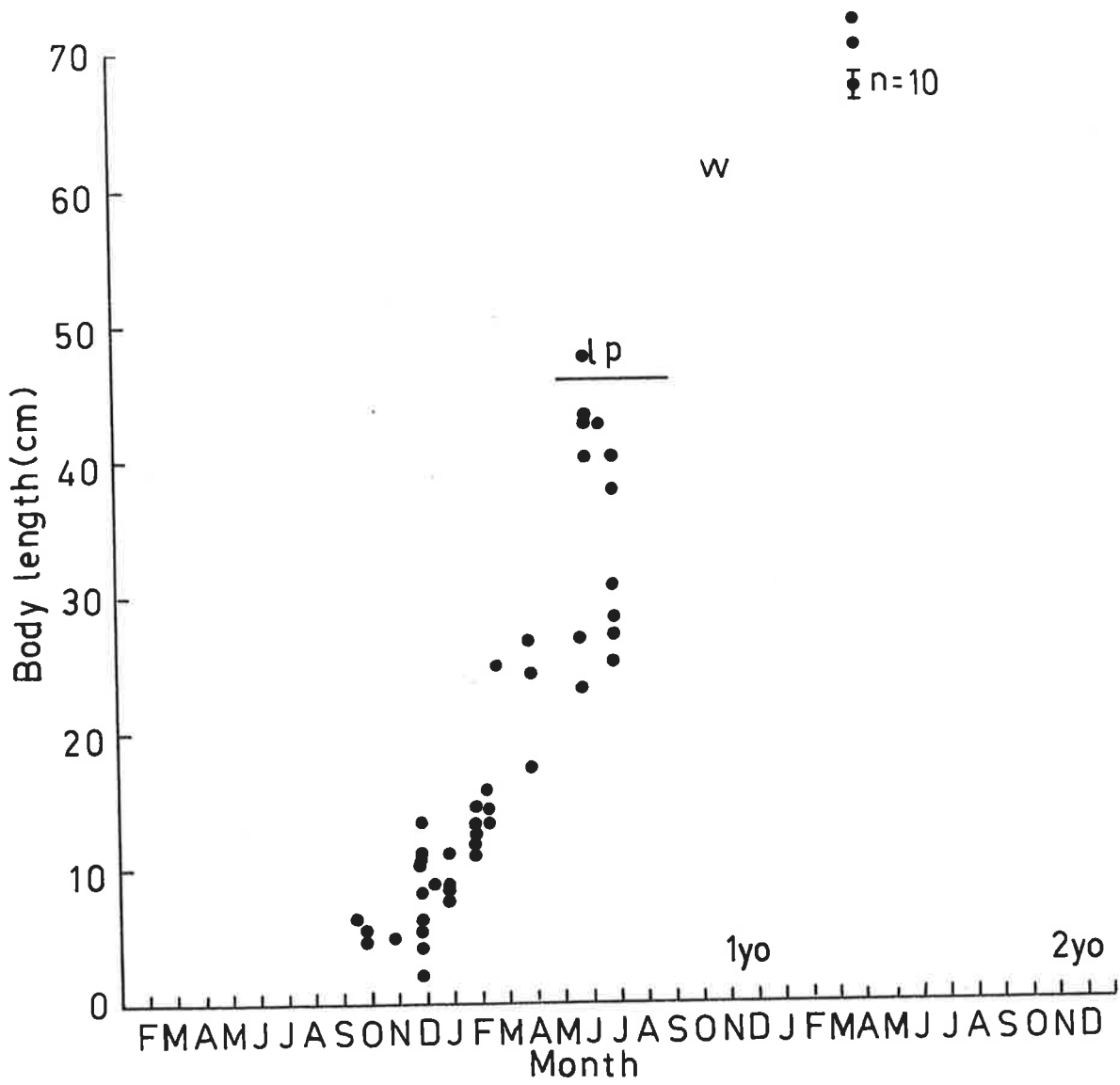


Figure 5.3 The body lengths of young wombats caught in particular months of the year.

Abbreviations: lp leaves pouch; w weaned.

The horizontal line below lp refers to the months during which wombats leave their mothers' pouches.

The vertical line and bars adjacent to n=10 is a measure of the standard error (\pm SE) of the 10 lengths.



growth such as 1969-70, 3 juveniles (average weight 13 kg) caught in March had failed to increase their body weights by the following January.

5.2.2 Ovulation

Observations made on the occurrence of ovulation are shown in Table 5.1. Of 14 adult females shot in October 1976, 10 had a corpus luteum in one ovary and an enlarged uterus in the luteal condition, indicating recent ovulation. The ovaries of 10 wombats examined in June and August 1977 showed no signs of recent ovulation or follicular development. Among 11 wombats examined in October and November 1977, 3 had small (1-3 mm diameter) graafian follicles but none had recently ovulated. In July and August 1978 all the wombats examined had recently ovulated. Reproduction occurred in 3 out of 4 wombats occupying the same warrens on the conservation park from 1975 to 1977; 2 bred in 3 successive years (Figure 5.2). Thus ovulation varied in time from year to year, but took place between July and October in the years 1976 and 1978.

5.2.3 Spermatogenesis

The main body of data on male reproduction is included in Chapter 4. Spermatogenesis may be continuous under 'optimal' conditions both in the wild and in captivity (Brooks et al 1978). All adult males shot in October and December 1976 showed evidence of spermatogenesis whereas during the drought year 1977 the proportion of aspermatogenetic adult males increased. All males shot in August and September 1978 were producing spermatozoa. Biopsies of testes from animals caught on the conservation park

Table 5.1

Period	No. adult females examined	No. adult females breeding	Per cent breeding	Criteria*	Wt. of breeding females kg (\pm SD)	Wt. of non-breeding females kg (\pm SD)
October 1976	14	10	71	CL	24.5 \pm 1.9	24.9 \pm 1.5
December 1976	11	3	27	CL PY	27.9 \pm 1.7	25.9 \pm 2.2
June-Aug 1977	10	1**	10	PY L	-	22.1 \pm 2.9
Oct-Feb 1977/78	13	0	0	CL PY	-	24.5 \pm 3.2
Aug-Sept 1978	3	3	100	CL PY	25.5 \pm 1.3	-

* CL, corpus luteum; ** observed but not captured; PY, pouch young; L, lactating.

Table 5.1 Frequency of reproduction of wombats inhabiting pastoral properties.

Table 5.2

	Period									
	Oct 76	Jan 77	April 77	July 77	Oct 77	Jan 78	April 78	July 78	Oct 78	
No sperm	0	0	0	1	3	5	4	1	0	
Few sperm	0	1	0	1	3	2	2	3	0	
Many sperm	6	3	10	8	0	1	0	3	3	
Per cent aspermatogetic males	0	0	0	10	50	63	67	14	0	

Table 5.2 Spermatogenesis in male wombats inhabiting the conservation park.

indicated a similar pattern (Table 5.2) although males did not become aspermatogenetic until October 1977. Testis, prostate and other accessory sex glands were largest in animals shot in October 1976 and in August-September 1978 (see Chapter 4) which coincided with the times of ovulation in females. These glands were reduced in size in December 1976 and remained small throughout 1977 (see Tables 4.2, 4.3).

5.2.4 Development of sexual maturity

The ovaries of mature females may contain up to 4 or 5 corpora albicantia usually of different sizes. The ovaries of 7 juvenile (1 year) and sub-adult (2-3 years) wombats of body length less than 80 cm did not contain corpora albicantia, or corpora lutea in October 1976 when 70 per cent of the adult females examined had ovulated.

Juvenile and sub-adult male wombats did not have spermatozoa in their testes. Sub-adult wombats of greater length than 74 cm and with testis weight greater than 3-5 g had spermatocytes present in seminiferous tubules with well-formed lumina although complete spermatogenesis was not in progress. One sub-adult wombat (body length 78 cm) examined in December 1976 had a testis of 6.5 g, and was producing spermatozoa.

The testes of juvenile wombats (less than 70 cm long) were less than 2.5 g in weight, and the small seminiferous tubules without lumina contained only spermatogonia. It appears that spermatogenesis commences when a young male wombat is a little over 2 years of age. However, the accessory sex glands of sub-adult wombats were smaller than those of adults examined at the same time

(the mean prostate weight of 2 sub-adult wombats in October 1976 and September 1978 was 11.7 g, relative to 23.9 g in adults), suggesting that these wombats were not as sexually well-developed as adult males.

Drought may be associated with delayed sexual maturation also, since there was no evidence that spermatogenesis had started in a few sub-adult wombats which were at least 2 years old in 1977 (a year of drought).

5.2.5 Frequency of reproduction

Although wombats appear to have a highly seasonal breeding period, reproduction may not occur every year (Tables 5.1, 5.3). Failure to reproduce appears to be due to both death of pouch-young and failure to ovulate. In October 1976; 71 per cent of adult females examined in one paddock had ovulated. By December 1976 only 3 of 11 females (27 per cent) in another paddock nearby carried small pouch-young. Two other females examined at this time had a large corpus albicans from the previous ovulation in about October and a reproductive tract similar in size to that of females with pouch-young, indicating that they had ovulated and that one, with an enlarged teat, had carried a pouch-young which had presumably died. These results for December 1976 gave an ovulation frequency of 45 per cent among wombats occupying this paddock.

Of 10 adult females examined in June and August 1977 when they were expected to have pouch-young or to be lactating, only 1 carried a pouch-young. In the period October 1977 to February 1978 none of the ovaries of 13 female wombats examined showed signs of

Table 5.3

	Year							
	December-July							
	1969-70	1970-71	1971-72	1974-75	1975-76	1976-77	1977-78	1978*
No. adult females examined	5	15	23	4	8	14	11	7
No. adult females with pouch young	1	0	15	2	6	6	0	6
Percentage of females with pouch young	20	0	65	50	75	43	0	86
Plant growth index (PGI) (previous July-Dec.)	2.6	1.8	2.3	3.6	2.8	2.1	1.4	3.6
Percentage deviation of PGI from average	-1	-33	-12	+37	+6	-23	-48	+37

* Oct-Dec

Table 5.3 Percentage of female wombats with pouch-young examined on the conservation park from 1970-78, together with an index of plant growth.

recent ovulation although in October, 3 wombats had a few small (1-3 mm diameter) graafian follicles in the ovaries.

In the years 1971-1978 the proportion of wombats on the conservation park (an area grazed by sheep until July 1971) carrying pouch-young at the expected time, was highly variable ranging from 0-90 per cent (Table 5.3) Despite the occasional small sample, it is clear that in some years such as 1970-71, and 1977-78 none of the wombats had pouch-young, while in other years (1971-72, 1975-76, October-December 1978) the proportion of wombats with young was high.

Thus, although the seasonal pattern of wombat reproduction is stable the frequency of reproduction is erratic.

5.2.6 Body weight and body condition

Among wombats examined in 1976 and 1978 there was no significant difference (t test) between the weight of female wombats that had ovulated and those that had not. Similarly, there was no difference between female wombats that ovulated in 1976 and 1978, and those that had not ovulated in 1977 (Table 5.1). The mean body weight of the wombats examined was near the average of the species (Crowcroft 1967) and a large proportion carried some reserves of peritoneal, mesenteric and subcutaneous fat.

5.2.7 Rainfall, pasture growth and fecundity

Rainfall and pasture growth is seasonal in the Blanche Town region (Trumble 1948, Wells 1973) , with most of the effective rain falling in the winter and spring months (see Appendix 1). The estimated drought frequency is as high as 70 per cent (Trumble 1948). The data presented in Table 5.3 have been plotted graphically

in Figure 5.4 to illustrate the relationship between the plant growth index during the breeding season and the percentage of female wombats with young in the following year. It is apparent that the 2 parameters are related, possibly in a sigmoidal fashion. When the plant growth index was depressed more than 20 per cent below average, a small proportion of females carried young. A depression of the index between 30 per cent and 50 per cent was associated with the failure of most females to ovulate, as in 1977 (Tables 5.1, 5.3)

A relationship between food and reproduction is further indicated by yearly variation in the estimated mean birth dates (Figure 5.5). Despite possible errors in measurement of the lengths of pouch-young and variation in growth rates, it is apparent that when rainfall and associated pasture growth occurred early in the season (July-August 1978) ovulation and births also occurred early. When rainfall and pasture growth occurred later in the season (October 1976) reproduction was late also.

The availability of food is often influenced by the presence of competing herbivores and this may have affected wombat reproduction. Wombats examined in October 1976 were caught in one paddock of a pastoral property where sheep had been absent for the previous 3-4 months. In this paddock an ovulation frequency of 70 per cent was observed. Wombats caught in December 1976 were taken from the same property, but in a paddock where sheep and wombats grazed together, and the ovulation frequency was 45 per cent. Similarly the small proportion of female wombats with young on the conservation park in 1970-71 may have been, in part, the result of

Figure 5.4 The relationship between the percentage of wombats with pouch-young in the months December-July and the mean plant growth index for the previous July-December. Open circles, sample size less than 7.

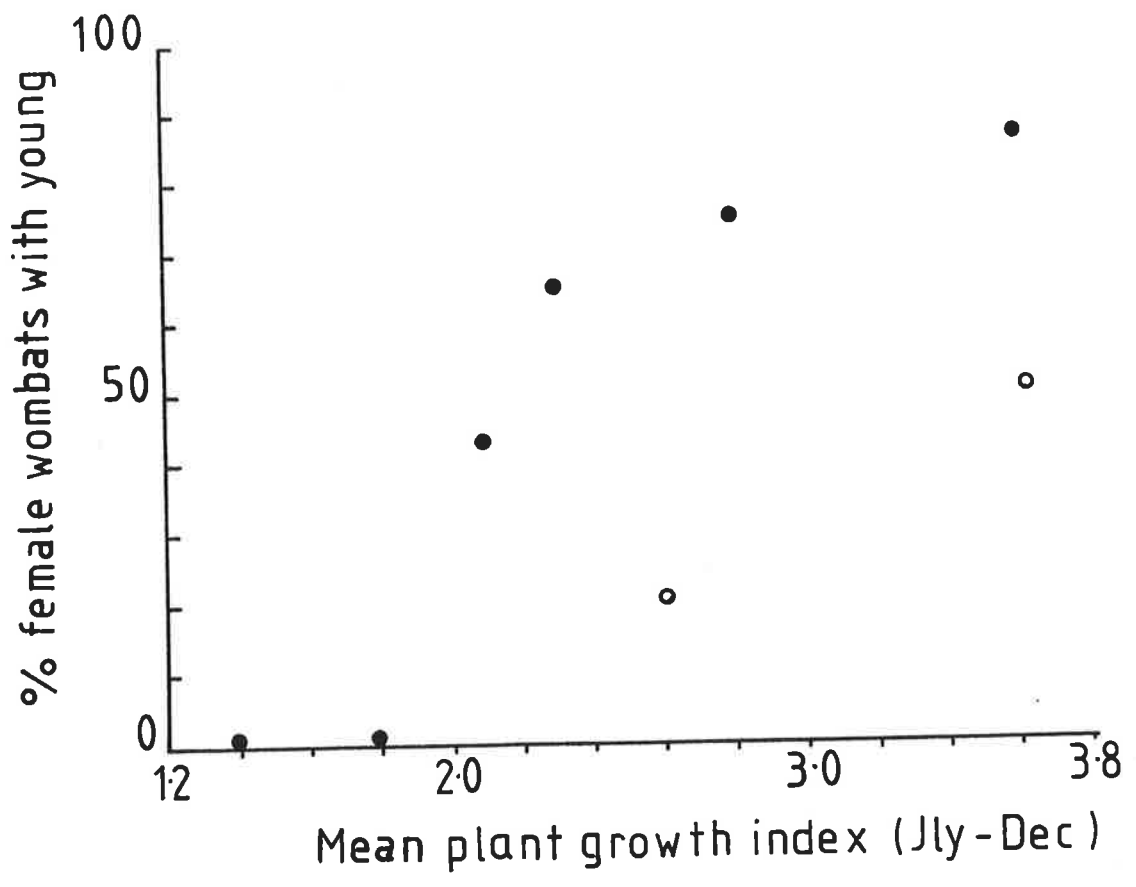

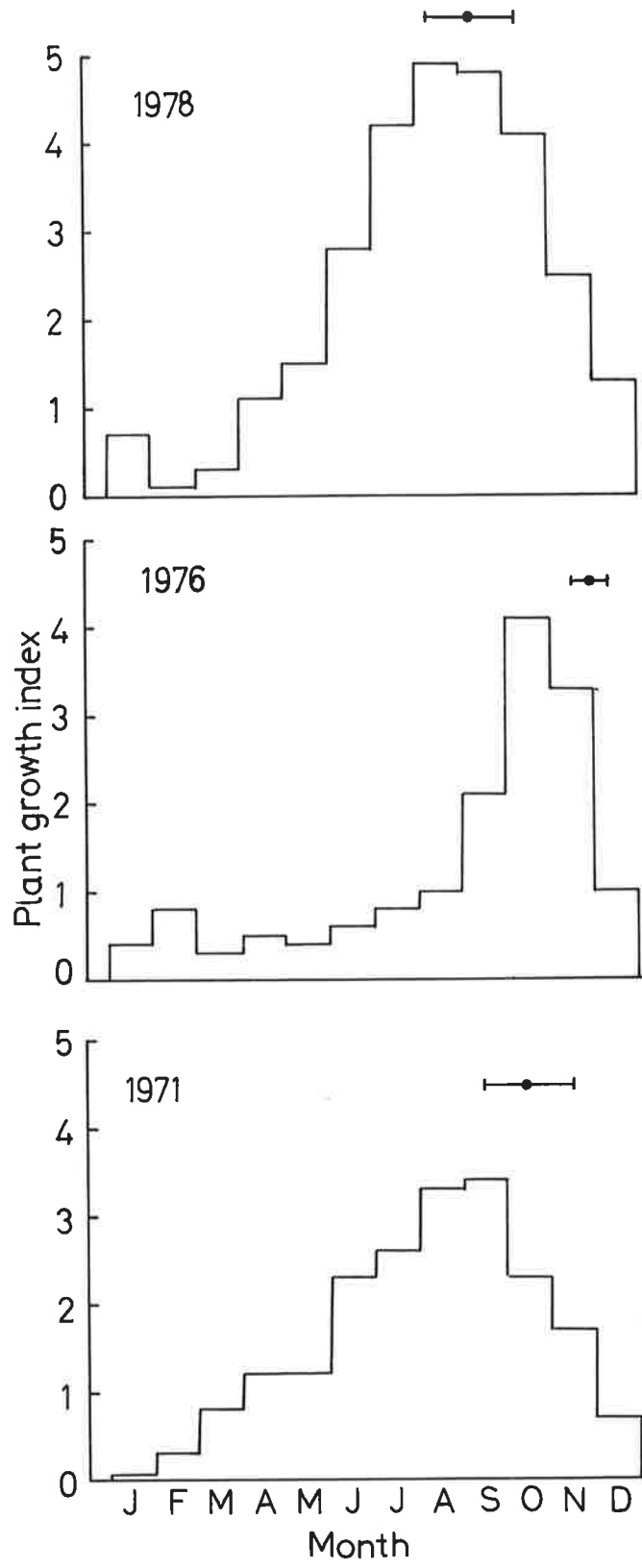


Figure 5.5 The estimated mean (\pm SD) date of birth () of wombats in each of the years 1976, 1977 and 1978 and the value of the plant growth index for each month of those years.



the presence of sheep at a density of 4 ha^{-1} . In the summer of 1971 available dry matter was limited to 18 g m^{-2} whereas in the following year it was $60\text{--}180 \text{ g m}^{-2}$ (Wells 1973).

While the body condition of wombats at the time of ovulation did not seem to be important in influencing reproduction it is likely that any effects of food on body condition would be observed later. Thus in December 1976 there was a significant difference (t test $P < 0.01$) between the weight of 5 females that had ovulated (28.1 ± 1.6) and those that had not previously ovulated in October ($n = 6$, mean weight 25.0 ± 1.5) even though 2 of those that had ovulated did not have pouch-young. This difference may be the result of the earlier poor supply of food for some of the wombats and its influence on the probability of ovulation occurring.

5.3 Discussion

A seasonal pattern of reproduction is an adaptation favouring survival of young following weaning which has evolved in many species of mammals (Sadleir 1969). The breeding pattern of *Lasiorchinus latifrons* in the arid to semi-arid environment of Blanche Town allows females not only to wean young in late winter and early spring (a period of potentially good supplies of water, energy and protein) but also to carry small rather than large pouch-young through summer when water is scarce. Reproduction in *Lasiorchinus latifrons*, like the rabbit in Australia (Poole 1960), appears to be both seasonal and opportunistic, as evidenced by failure to develop or maintain reproductive condition in some years. Hormonal studies (see Chapter 4) suggest that depressed gonadotrophin secretion and inadequate gonadal function contribute to this failure.

These data also suggest that the reproductive condition of males may be influenced by that of the females, or that environmental factors affect the reproductive condition of both sexes simultaneously.

Anoestrus due to poor nutritional status has been reported in another marsupial, the red kangaroo (Myers et al. 1976, Newsome 1977b) and in eutherian mammals such as red deer, *Cervus elaphus* (Mitchell et al. 1976). In each case females weigh significantly more and are in better condition when breeding than when in a non-breeding state. Data presented in Table 5.1 indicate that body condition, as measured by weight, is unlikely to be an important factor in the failure of wombats to ovulate. Detailed biochemical, haematological and trace-element studies (see Chapter 6) have shown that, except for copper, wombats were not deficient in trace elements or vitamins in breeding and non-breeding years. Data presented in Figures 5.4 and 5.5 suggest that periods of wombat breeding were closely associated with new growth of pasture. Since, however, ovulation and reproduction occurred in wombats before the nutritional effects (showing as body weight) of fresh pasture growth were detectable, it appears that fresh pasture per se provides a stimulus for the development of the reproductive condition.

Samples of stomach contents taken from wombats at times of ovulation in breeding years yielded high concentrations of organic matter which contained little fibre while the reverse was true for samples taken at the same time in non-breeding years (see Table 6.5). This evidence suggests that it is both quality and quantity of pasture which influence the onset of reproduction. A similar

situation is reported in the rabbit in Australia (Myers & Bults 1977). The fact that some minor follicle development occurred in October-November 1977 but females did not ovulate, suggests that other factors influence the seasonal periodicity of reproductive activity. The period when mating and ovulation occur is one of increasing daylength and temperature, and they could play a fundamental role in initiating pituitary-gonadal activity. The absence of births outside the period July to December also supports this idea. Evolutionary factors selecting for the seasonal pattern have been discussed at the beginning of this section. In 1975 and 1976 a pair of wombats maintained under good nutritional conditions in captivity copulated at intervals of 20-35 days, most frequently in the months July to January, but not at all in April or May, suggesting that a diminution of reproductive activity or a seasonal anoestrus occurs between January and July. The selective disadvantages to both mother and young of mating and giving birth outside the months July to December have been discussed. The overall pattern of wombat reproduction in the areas of study can be defined as one of opportunism within a fixed breeding season.

In captivity the hairy-nosed wombat is polyoestrous and will return to oestrus after weaning or loss of young (Crowcroft & Soderlund 1977). This may occur in the wild also since after the pouch-young of 5 wombats were removed in October 1978, 1 of the 2 females recaptured in December had a new-born young in the pouch, showing that some females will breed again after the loss of young. It is unlikely, however, that wombats would lose young unless

environmental conditions were harsh and in that case breeding would not be expected.

Other forms of reproductive failure may also occur in the population since one animal that had ovulated in 1978 did not have a foetus in the uterus despite the corpus luteum being of large size.

Any species in which food is a major determinant of reproduction and fecundity, is likely to be affected by competition with other animals for that food. On the conservation park from January-July 1977 when adequate dry-matter was available (Figure 5.6), 6 of 14 (43 per cent) adult females had young, whereas on pastoral properties, devoid of ground cover, only 1 of 10 (10 per cent) carried young in the same period. Interestingly, Newsome (1965) noted that at the end of a drought in central Australia, 16 per cent of female kangaroos remained in breeding condition in areas where cattle grazed, compared to 27 per cent in areas free from competition with cattle.

The population of wombats inhabiting the Blanche Town region is relatively small, so given the estimated drought frequency of 70 per cent in the region, the observations on the frequency of reproduction arouse some concern. The apparent disparity in the sex-ratio of pouch-young in favour of females would enable populations of wombats to be maintained and increased, but this would be of little significance if the effect of environmental conditions and agricultural practice were to reduce the frequency of ovulation and increase mortality of young significantly. Aitken's (1971) interesting observations on the relative abundance

Figure 5.6 The amount of pasture on one pastoral property (right of the fence) relative to the amount on the conservation park in August 1977.



of wombats and rabbits and his hypothesis of a reciprocal relationship between the numbers of them may well indicate the long-term effects of competition between wombats and other herbivores for food.

In summary, it appears that wombats in the Blanche Town region have a well-defined breeding season from about July to December. But reproduction is also opportunistic and the wombats do not breed when they experience drought in the mating period. It seems likely, that the growth of new pasture is the stimulus which initiates the development of the active reproductive condition. Competition with sheep for food probably reduces wombat fecundity.

CHAPTER 6

ADAPTATIONS, SURVIVAL AND DISEASES

- THE RESPONSE OF WOMBATS TO DROUGHT

6.1 Introduction

The ability of a desert animal to survive drought is determined by the efficiency of its behavioural and physiological adaptations. Droughts, characterized by a decreasing supply of food and water, pose severe stresses for desert animals.

In general, dehydration, starvation or both probably cause the death of many desert mammals that fail to survive drought. The duration of drought will determine the patterns of mortality. Those animals possessing adaptations enabling maintenance, or minimal loss of body 'condition' and nutritional status, and those that maintain adequate function of their physiological systems, will survive in times of drought, depending on its duration.

Body 'condition' refers to the weight of an animal and the proportion of that weight which represents nutrient reserves - as a drought continues and nutritional requirements are not met those reserves are used in maintaining basic body functions. When reserves are exhausted other tissue such as bone and muscle are used until there is not enough cellular material to maintain life (Young & Scrimshaw 1971).

Inevitably, in the terminal stages of starvation due to lack of food an animal will appear severely 'wasted' and at death body weight is well below that of an animal in normal 'condition'. The rate of loss of body weight, and the body weight at death are useful measurements that can be used quantitatively to compare the drought hardiness of desert mammals.

The availability of water will also influence patterns of mortality, but acute dehydration should not cause the deaths of

mammals adapted to desert habitats. Chronic dehydration and its effects on intake of food will interact to cause death (Barker 1974 on quokkas) but probably less weight is lost in this situation compared with a situation of starvation alone.

Starvation can result from an inadequate total intake of food, or specific nutritional requirements such as that for protein or trace elements may not be met even though there is no lack of energy in the food.

In the field situation it is not possible to determine an animal's precise nutritional requirements for trace elements, protein, energy and water, but useful comparisons can be made if samples of tissues, blood and food are collected over the range of environmental conditions experienced by the animals. It is sometimes useful to compare the 'condition' and nutritional status of healthy, captive animals with that of their wild counterparts.

In order to assess the health of individual animals it is necessary, in addition to making morphological measurements, to ascertain the functional status of the major physiological systems within the animal's body. Biochemical, haematological and trace element measurements can give a guide to the functional status of the cardiovascular, respiratory, urinary and hepatic systems (Tietz 1976). Often, many of these measurements are associated with intake of food and nutritional status. Anaemia and hypoproteinaemia due to inadequate protein intake are documented for some Australian marsupials (Ealey & Main 1967, Barker et al. 1974). More complex biochemical interactions, ultimately determined by inadequate intake of even one trace element, can have profound effects on the

health of individuals. In many species one such interaction is the effect of copper in mobilising stores of iron from the liver for haemoglobin synthesis (Underwood 1977).

It is useful, therefore, also to examine the quantity and quality of the food that is available to an animal during a drought. Problems of an animal's selectivity can be overcome if food samples taken from the stomach are used. This technique has been widely applied, particularly in studies of eutherian mammals such as rabbits (Myers & Bults 1977) and red deer (Staines & Crisp 1978), but some marsupials (Ealey & Main 1967) have been studied also.

In some domestic mammals it has been verified experimentally that intake of food and measurements of gain in live weight can be predicted from a knowledge of the chemical composition of the diet selected (Siebert & Hunter 1977). Changes in the quality of the food have been correlated with changes in health, productivity and survival of wild mammals also (Klein 1965, Myers & Bults 1977, Sinclair 1977).

Starvation or inadequate nutrition may not be the only cause of death during drought since disease may also play a role. Again, clinical biochemistry (liver enzymes) haematology (leucocyte counts) and histological studies can help in the assessment of the nature of any disease present and its effect on functions of the body. Cheal et al. (1976) made this approach to *Antechinus stuartii* (although not during drought).

There have been a few studies of herbivorous desert marsupials relating the quality and quantity of their food to measures of their health, productivity and survival. The studies on quokkas have been

reviewed in Chapter 1. Storr (1968) estimated dry matter intake in macropod marsupials by measuring changes in body weight at different times of the year. Main (1971) reviewed the role of many aspects of nutrition in influencing the well-being of macropod marsupials. Little is known of the ability of wombats to survive drought. The only studies relevant to this question have been made by Wells (1973). He measured water, nitrogen and fibre content of pasture near wombat warrens, but this approach does not take into account the selectivity of the animals. He also measured body weight, total body water and water turnover of wombats he caught over 2 years.

6.2 Results

6.2.1 Morphological measurements (Table 6.1)

There was significant seasonal variation in body weight and the 'condition' index but not in body length, gut weight or fat index. Since there was a positive linear correlation between body weight and length ($r = 0.69$ $P < 0.01$) the lack of variation in mean body lengths of the samples of wombats obtained indicates that variation in weight was due to variation in body solids or water or both. Further evidence to support this idea is the seasonal pattern of weight change of particular wombats inhabiting the conservation park (Figure 6.1).

The lowest body weights occurred in November 1977 and February 1978 after approximately 12-14 months of drought; weight loss was about 20 per cent of pre-drought weight. Expressing body weight as a fraction of the weight-for-length of captive wombats in good condition also indicates a decline in body 'condition' as drought continued. This pattern was not shown clearly in the fat index but the lowest

Table 6.1

Measurement	Units	Period								F ^a
		Dec 76	June 77*	Aug 77*	Oct 77*	Nov 77*	Feb 78*	Aug 78	Nov 78	
n		13	12	10	14	4	4	5	2	
Body weight	kg	26.4 ±0.6	22.4 ±1.2	23.6 ±0.8	25.1 ±0.8	22.7 ±2.2	21.2 ±1.0	25.2 ±0.7	27.4	F7,56 = 2.98 ^a
Gut weight	kg	-	5.0 ±0.5	5.9 ±0.2	6.3 ±0.3	6.1 ±0.6	5.3 ±0.3	4.9 ±0.1	5.4	F6,42 = 1.95
Body length	cm	86.4 ±0.9	86.3 ±0.7	87.4 ±0.4	87.7 ±1.0	88.3 ±1.9	86.0 ±1.4	88.6 ±0.7	91.5	F7,56 = 1.26
Fat index	0-5	-	2.3 ±0.5	2.0 ±0.3	2.3 ±0.3	1.8 ±0.7	0.9 ±0.5	1.8 ±0.4	2.3	F6,42 = 0.73
Condition index	See 'Methods'	0.94 ±0.01	0.79 ±0.03	0.82 ±0.02	0.86 ±0.01	0.76 ±0.05	0.76 ±0.03	0.85 ±0.01	0.86	F7,56 = 6.25 ^a

a P < 0.01 Analysis of variance. * Months of drought.

Table 6.1 Variation in morphological characteristics of *Lasiorhinus latifrons*. Mean values ± S.E.

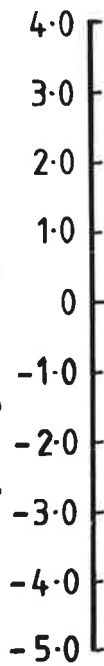
These animals were killed on pastoral properties.

Figure 6.1 Variation during 1976-78 in mean body weight of wombats (\pm S.E.) and mean change in body weight of particular wombats (\pm S.E.) inhabiting the conservation park together with monthly plant growth index values for the period.

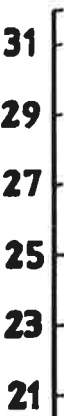
Plant growth index



Body weight change (Kg)



Body weight (Kg)



J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1976 1977 1978

mean fat index was observed in February 1978.

On two occasions during the study severely emaciated adult wombats were found alive. One was shot for examination in June 1977. He weighed 13.0 kg (approximately half the average body weight of adults), no fat reserves were visible and his gut was virtually empty, weighing only 1.0 kg. Another mature wombat of similar size and condition (approximately 14 kg in weight) was found on the conservation park during the daytime. It was caught and placed in a cage with food and water but died some hours later. One wombat (approximately 26 kg in weight) taken into captivity after receiving a head injury which partly paralysed it, was euthanized about 6 weeks after capture when it weighed 13 kg. It neither ate nor drank in that time.

6.2.2 Blood biochemistry (Table 6.2)

There was no significant seasonal variation in plasma electrolytes, except for chloride which was elevated in November 1977 and February 1978. Similar elevations of urea in February 1978 and plasma concentration of creatinine (suggesting a decreased glomerular filtration rate) took place.

No significant variations in concentrations of plasma protein or cholesterol were observed, but the lowest values occurred in August 1978, a period of increased availability of water. The low values may reflect some expansion of plasma volume.

Plasma glucose was lowest in February 1978, but it was not possible to discern a pattern in the significant variations observed. All values were within the ranges found in captive wombats (Gaughwin & Judson 1980, Appendix 2) and it is unlikely that wombats

Table 6.2

Measurement	Units	Period						F ^{a,b}
		June 77*	Oct 77*	Nov 77*	Feb 78*	Aug 78	Nov 78	
n	.	10	12	4	4	5	2	
Sodium	m mol l ⁻¹	141 ±4	144 ±2	144 ±1	145 ±1	139 ±2	143	F5,31 = 0.46
Potassium	m mol l ⁻¹	5.9 ±0.5	5.4 ±0.3	5.7 ±0.9	5.0 ±0.5	5.4 ±0.5	5.5	F5,31 = 0.37
Chloride	m mol l ⁻¹	101 ±3	101 ±1	108 ±1	107 ±1	97 ±1	99	F5,31 = 2.67 ^b
Glucose	m mol l ⁻¹	6.6 ±0.6	6.2 ±0.3	7.5 ±0.6	5.0 ±0.3	7.3 ±0.4	8.2	F5,31 = 2.70 ^b
Urea	m mol l ⁻¹	13.5 ±0.8	12.7 ±0.2	11.5 ±0.4	15.4 ±0.8	12.6 ±1.7	9.4	F5,31 = 2.99 ^b
Creatinine	m mol l ⁻¹	0.15 ±0.01	0.16 ±0.01	0.20 ±0.03	0.19 ±0.02	0.13 ±0.01	0.17	F5,31 = 3.75 ^a
Protein	g l ⁻¹	70 ±4	71 ±2	70 ±3	69 ±1	63 ±2	76	F5,31 = 1.00
Cholesterol	m mol l ⁻¹	2.9 ±0.2	3.2 ±0.1	2.8 ±0.1	2.8 ±0.2	2.5 ±0.2	3.1	F5,31 = 1.39
Aspartate transaminase	U l ⁻¹	85 ±21	67 ±7	71 ±31	53 ±16	159 ±51	42	F5, 31 = 2.2

a P < 0.01, b P < 0.05 Analysis of variance. * Months of drought.

Table 6.2 Variation in plasma biochemical constituents of *Lasiornhinus latifrons*. Mean values ± S.E.

were hypoglycaemic at any time.

The activity of aspartate transaminase was greatest in August 1978 and considerably higher than at other times, which may indicate the presence of some liver dysfunction in August 1978, in view also of the low concentrations of total plasma protein.

6.2.3 Haematology (Table 6.3)

Red cell count, haemoglobin and haematocrit value showed significant seasonal variations, the lowest values occurring in November 1977 and February 1978. Haemoglobin concentrations at these times, however (103 and 109 g l⁻¹ respectively) were not so low that the animals were anaemic. The red blood cell values may have been influenced by the wombats' nutritional status, body condition or both, since there was a positive linear correlation between the 'condition index' and haemoglobin concentration ($r = 0.45$ $P < 0.01$).

Total leucocyte count was relatively high when compared with other marsupials (Parsons et al. 1971), but this may be characteristic of the Vombatidae since Presidente (1978) found high numbers of leucocytes in the blood of *Vombatus ursinus*. A pattern was not apparent in the significant variation in numbers of leucocytes.

6.2.4 Trace elements and vitamins (Table 6.4)

Of all the measurements made, the greatest variation was found in trace elements. Plasma copper was lowest in November 1977 and highest in August 1978. Plasma zinc and serum vitamin B₁₂ concentrations showed little variation, but serum vitamin B₁₂ was slightly elevated in August 1978. The average concentration of blood selenium

Table 6.3

Measurement	Units	Period						F ^{a,b}
		Aug 77*	Oct 77*	Nov 77*	Feb 78*	Aug 78	Nov 78	
n		10	12	4	4	5	2	
Red cell count	Cells × 10 ¹² l ⁻¹	4.75 ±0.15	4.62 ±0.16	3.80 ±0.56	3.96 ±0.19	4.93 ±0.25	4.60	F5,31 = 2.74 ^b
Haemoglobin (Hb)	g l ⁻¹	132 ±4	125 ±5	103 ±17	108 ±6	129 ±5	120	F5,31 = 2.64 ^b
Haematocrit value	l l ⁻¹	0.406 ±0.015	0.389 ±0.013	0.321 ±0.053	0.320 ±0.019	0.395 ±0.015	0.384	F5,31 = 2.78 ^b
Leucocyte count	Cells × 10 ⁹ l ⁻¹	10.9 ±1.5	9.2 ±1.0	5.9 ±1.4	7.7 ±1.9	7.1 ±1.0	15.7	F5,31 = 2.63 ^b
Neutrophils	Cells × 10 ⁹ l ⁻¹	5.4 ±0.8	-	2.6 ±0.5	2.0 ±0.5	3.1 ±1.2	5.3	F4,20 = 3.64 ^a
Lymphocytes	Cells × 10 ⁹ l ⁻¹	5.0 ±0.8	-	2.8 ±0.8	5.0 ±2.4	3.8 ±0.6	9.8	F4,20 = 3.35 ^a
Eosinophils	Cells × 10 ⁹ l ⁻¹	0.6 ±0.2	-	0.4 ±0.2	0.7 ±0.4	0.2 ±0.1	0.2	F4,20 = 0.68

a P < 0.01, b P < 0.05 Analysis of variance. * Months of drought.

Table 6.3 Variation in haematological characteristics of *Lasiorhinus latifrons*. Mean values ± S.E.

Table 6.4

Measurement	Units	Period						F ^{a,b}
		Aug 77*	Oct 77*	Nov 77*	Feb 78*	Aug 78	Nov 78	
n		10	12	4	4	5	2	
Plasma copper	$\mu\text{ mol l}^{-1}$	6.0 ±0.6	6.0 ±0.3	4.0 ±0.5	6.0 ±0.3	11.4 ±1.0	8.5	F5,30 = 13.4 ^a
Plasma zinc	$\mu\text{ mol l}^{-1}$	18 ±1	17 ±1	16 ±1	19 ±1	16 ±1	15	F5,30 = 1.06
Serum vit. B ₁₂	$\mu\text{g l}^{-1}$	2.14 ±0.21	1.48 ±0.30	1.23 ±0.15	1.78 ±0.30	2.49 ±0.34	1.07	F5,29 = 2.17
Liver:								
selenium	$\mu\text{ mol kg}^{-1}$ dry wt.	32 ±2	31 ±1	45 ±5	47 ±2	22 ±1	20	F5,31 = 16.28 ^a
copper	$\mu\text{ mol kg}^{-1}$ dry wt.	0.33 ±0.02	0.25 ±0.01	0.26 ±0.02	0.92 ±0.25	0.21 ±0.01	0.21	F5,31 = 12.85 ^a
zinc	$\mu\text{ mol kg}^{-1}$ dry wt.	1.71 ±0.09	1.84 ±0.04	1.75 ±0.09	2.14 ±0.15	1.50 ±0.08	1.92	F5,30 = 4.50 ^a
manganese	$\mu\text{ mol kg}^{-1}$ dry wt.	0.21 ±0.01	0.19 ±0.01	0.17 ±0.01	0.17 ±0.01	0.23 ±0.03	0.16	F5,31 = 2.17
iron	$\mu\text{ mol kg}^{-1}$ dry wt.	29.8 ±2.6	25.3 ±1.4	30.9 ±1.9	47.5 ±7.3	4.59 ±0.67	5.96	F5,31 = 20.30 ^a
vit. A	IU g ⁻¹ wet wt.	455 ±125	269 ±41	334 ±136	406 ±62	251 ±22	288	F5,31 = 0.83

a P < 0.01, b P < 0.05 Analysis of variance. * Months of drought.

Table 6.4 Variation in trace element and vitamin concentrations of *Lasiorhinus latifrons*. Mean values ± S.E.

in 5 wild wombats was $6.50 \pm 0.38 \mu \text{mol l}^{-1}$ compared with 3.62 ± 0.48 in 8 captive wombats (Appendix 2). Liver selenium concentrations increased as drought conditions continued, but dropped markedly after rain had initiated pasture growth (August 1978). Similarly, liver concentrations of iron were from 5-10 times lower when good pasture was plentiful, compared with times of drought. Liver copper and zinc showed a similar though less dramatic pattern. Marked changes did not occur in liver manganese or vitamin A concentrations.

6.2.5 Chemical composition of stomach contents and faeces (Table 6.5)

Samples were obtained on 3 occasions during drought and once after rain had initiated pasture growth. The organic matter component of stomach contents remained low throughout the drought, but increased 17 per cent in August 1978. Nitrogen content did not show a similar pattern but it was consistent with the changes in plasma urea (Table 6.2). Measurement of cell-wall content on pooled samples indicated that the plant material consumed in August 1978 was significantly less fibrous than that obtained during drought. These data and gut weights (Table 6.1) indicated that wombats found some food during the drought, but it was of poor quality.

For most of the year wombat faeces were well stipated and faecal water decreased as drought conditions continued, particularly in the hot summer period from November to February. But in August 1978 the consumption of fresh grass with relatively high concentrations of organic matter and water, resulted in extremely moist faeces, some failing to stipate. Unlike the nitrogen of the food in the stomach, faecal nitrogen showed significant variation, and was

Table 6.5

Measurement	Units	Period				F ^{a,b}
		Oct 77*	Nov 77*	Feb 78*	Aug 78	
n		12	3	4	5	
Stomach contents:						
organic matter	g dg ⁻¹ dry matter	73.2 ±1.4	72.3 ±3.1	70.4 ±1.1	82.2 ±1.8	F3,20 = 6.48 ^a
nitrogen	g dg ⁻¹ organic matter	3.4 ±0.2	2.7 ±0.5	3.3 ±0.2	3.1 ±0.2	F3,20 = 0.83
cell wall content [†]	g dg ⁻¹ organic matter	65.5	79.1	78.0	47.1	-
Faeces:						
moisture	Per cent wet weight	60.3 ±1.7	47.9 ±3.5	52.2 ±1.8	74.8 ±1.5	F3,21 = 22.3 ^a
nitrogen	g dg ⁻¹ organic matter	2.90 ±0.05	2.24 ±0.14	2.22 ±0.11	3.05 ±0.15	F3,21 = 17.6 ^a
organic matter	g dg ⁻¹ dry matter	63.5 ±2.3	62.0 ±2.5	64.2 ±1.2	70.3 ±0.8	F3,21 = 1.82

a P < 0.01, b P < 0.05 Analysis of variance. * Months of drought. † samples pooled for analysis.

Table 6.5 Variation in chemical composition of stomach contents and faeces of *Lasiorhinus latifrons*.
Mean values ± S.E.

low at the end of the drought, but became 37 per cent higher after the drought had broken. The high water content of food consumed in August 1978 may have contributed to lower gut weights at this time. It is likely that the time food particles remained in the gut was reduced and indeed, the contents of the small intestine and colon were often watery liquid.

6.2.6 Parasites and diseases

Four species of internal parasites were found in the specimens examined. A cestode, *Progamotaenia festiva* (Beveridge 1976) was found in the bile ducts. This produced some portal fibrosis (Presidente & Beveridge 1978). Another cestode found in the duodenum was *Paramoniezia johnstoni* (Beveridge 1976). There were 2 species of nematodes in the colon *Macropostrongyloides lasiorhini* (Mawson 1955) and *Oesophagostomoides giltneri* (Beveridge 1978) the numbers of which varied from 1000-4000 in 6 specimens examined in June 1977. The numbers of *Macropostrongyloides lasiorhini* were low and less than 100. None of the gastrointestinal tract parasites appeared to produce any pathological effects.

Histopathological investigations (P.J.A. Presidente personal communication) revealed the presence of intestinal coccidiosis resulting in mild and diffuse chronic enteritis, though there was no significant inflammation of the intestinal mucosa. The lungs of the wombats contained a fungal spore similar to *Emmonsia* species (R. Mason & M. Gaughwin unpublished observations) but there was little evidence of significant pathology associated with the infection.

Fleas (*Echidnophaga* species, Dunnet & Mardon 1974) and lice

(*Booplia* species, von Kéler 1971) were the main ectoparasites found on the specimens examined.

6.3 Discussion

From the isolated examples of adult wombats found alive but emaciated it appears likely that under conditions of chronic starvation wombats can sustain a body weight loss of at least 50 per cent before they die. Clearly, the wombats examined in this study during a drought of 13 months duration maintained a good reserve of body nutrients. The average weight of wombats at the end of drought probably indicates that no significant mortality of adults occurred. Body weight and condition dropped most rapidly when the effects of heat and drought in summer combined to decrease the availability of food and water in the period January-June 1977.

The initial weight loss in the drought period January-June represented a 15 per cent weight loss in 6 months, with a total loss for the year of 20 per cent. Comparative figures for other herbivorous marsupials given in Chapter 1 show the wombat to be relatively hardy in times of drought. Very few wombats examined had no reserves of visible body fat. What is perhaps more surprising is that they lost so little weight in the face of almost complete removal of pasture by sheep. Adult body weights remained near the average of 25 kg found for a large sample of wombats examined by Crowcroft (1967). There were few differences between body weights of wombats caught on the conservation park and those caught on pastoral properties nearby, indicating little difference in the nutritional status of the two populations. Throughout the drought it was impractical to measure the amount of dry matter on the pastoral properties because of the

sparseness of vegetation. This was estimated to be less than 20 g m^{-2} as compared with $60\text{-}100 \text{ g m}^{-2}$ on the conservation park (Wells 1973).

It appears likely that modification of behaviour enabled wombats inhabiting pastoral properties to obtain enough food to minimize loss of body condition. This was highlighted by comparing the behaviour of wombats inhabiting the conservation park with that of wombats inhabiting pastoral properties. Wombats observed during the day on the conservation park seldom grazed, but lay on the mounds of their burrows, whereas the majority of wombats that were observed on pastoral properties were up to 600 m from their burrows grazing intensely. Because of wombats' intolerance of heat (Wells 1978) such behaviour could only occur in winter and spring, when the ambient temperature is, on average, less than $28\text{-}30^{\circ}\text{C}$. It is likely therefore, that the declines in body weight and 'condition' of wombats in the period January-June 1977 and October-February 1977-78 were due to both a decline in quantity and quality of food and to the inability of wombats to graze during the day at these times.

It is generally recognized that body weight, fat reserves and measures of 'condition' are good indicators of the health and well-being of mammals (Bamford 1970, Main 1971, Mitchell et al. 1976, Martin 1977):

Loss of body weight can be due to loss of water, fat reserves and some other tissue. Wells (1973) found that wombats at Blanche Town lost weight over the regular summer drought and part of this loss was due to a loss of body solids. It is interesting to note

that for a given body length the difference in weight between a fat and a lean wombat may be of the order of 3-5 kg. The greatest body weight of a fat (fat index 2.4) 86 cm long wombat was 25.0 kg, while the greatest weights of lean (fat index less than 0.5) 86 cm long wombats were 20.4 and 22.4 kg.

Like populations of rabbits in semi-arid regions (Myers & Bults 1977) it appears likely that the quantity and quality of food available to the wombats at Blanche Town determine their body weight and 'condition'. The close relationship between the plant growth index and the pattern of changes in body weight of wombats inhabiting the conservation park support this hypothesis, as do the results of analyses of stomach contents and faeces of wombats on pastoral properties.

While wombats appeared to be able to obtain enough food so that gut weight remained near average, the quality of this food was demonstrably poorer during drought being highly fibrous and of low organic matter content. Relatively high concentrations of inorganic matter in food samples obtained at this time indicated that some soil was consumed also.

Nitrogen of food in the stomach probably showed little variation because of the high concentrations of plasma urea which would diffuse readily into the stomach, possibly obscuring any real differences between samples. Faecal nitrogen may be a more useful measurement - it was high when wombats gained weight even during drought when it was 2.9 g dg^{-1} organic matter in October 1977 and 3.05 g dg^{-1} in August 1978, but low when weight loss occurred (2.2 g dg^{-1} in November 1977).

Myers & Bults (1977) found that except when rabbits consumed diets very low in protein, the nitrogen content of the faeces was indicative of the quality of food ingested. Stanley Price (1977) noted the difficulties she experienced in interpreting values of the concentrations of nitrogen in the rumen of the hartebeest *Alcelaphus buselaphus cokei*, but she found faecal nitrogen to be a useful measure of dry matter intake. The values obtained in this study for measures of the quality of food consumed in October 1977 are probably close to the values that would be observed when wombats maintain, or marginally gain body weight (see Table 6.1). This is so because even though the period June-October 1977 was part of the drought, some weight gain occurred.

Associated with changes in body 'condition' and quality of food were changes in a number of physiological and biochemical measurements. Haematological and biochemical measurements of the type made in this study have often been used by wildlife biologists to assess the well-being and nutritional status of wild populations of mammals such as possums (Barnett et al. 1979), quokkas (Barker et al. 1974), the euro (Ealey & Main 1967) and other macropods (Main 1971). In particular, these studies illustrate the usefulness of haemoglobin as a measure of health and well-being. The haematological results of this study are also in agreement with those ideas. Low red cell counts, low haemoglobin concentrations and haematocrit values occurred toward the end of the drought when body condition was lowest and food had been scarce and of poor quality over the previous few months. In the quokka, Barker et al. (1974) experimentally demonstrated that a low nitrogen diet was enough to induce body weight

loss and the development of anaemia. Slight anaemia was correlated with a fall in the nitrogen content of forage ingested by euros (Ealey & Main 1967). It is likely that a similar situation applies to the wombats in this study.

Correlative studies of the type used in this work cannot provide verification or falsification of hypotheses, but the measurement of many selected body constituents can offer some insight into the variety and nature of the determinants of health and 'condition'. For example, the correlation found between plasma copper and haemoglobin ($r = 0.60$ $P < 0.01$) during drought suggests some involvement of copper in the slight anaemia observed at the end of drought. The greater concentrations of haemoglobin and plasma copper of captive wombats (Appendix 2) is also consistent with this hypothesis (Gaughwin & Judson 1980). Low liver concentrations of copper, characteristic of other marsupials (Beck 1956), the small variation in values, and lack of correlation between concentrations of liver and plasma copper all suggest a restricted ability of *Lasiorphinus* to store copper in the liver. Plasma copper would then tend to reflect availability of dietary copper. Indeed, concentrations of plasma copper rose dramatically after rain had induced new growth of pasture.

It is interesting to speculate further that liver iron concentrations were also part of these interactions. Liver iron dropped five fold when plasma copper rose. It is known that in many mammals copper plays a role in mobilising iron from the liver (Underwood 1977). It is possible that vitamin B₁₂ was involved also since there was a significant correlation between the concentration

of serum vitamin B₁₂ and haemoglobin ($r = 0.68$ all samples, $r = 0.58$ for drought samples $P < 0.01$). Newsome (1975) found no difference between drought years and good seasons in serum vitamin B₁₂ or blood haemoglobin concentrations of red kangaroos, but he did not report the body weights of the animals on which measurements were made.

Serum vitamin B₁₂ concentrations of wild wombats were similar to those of captive wombats (Gaughwin 1980, Appendix 2) and within the range of domestic species (Gardiner 1977), the quokka (Barker 1974) and red kangaroo (Newsome 1975). Vitamin A concentrations were highly variable but showed no significant seasonal variation and it is reasonable to assume that liver stores were adequate. In a number of species blood selenium is correlated with liver reserves of selenium and is responsive to dietary intake (Underwood 1977). Presumably the greater concentrations of blood and liver selenium in wild wombats compared with captive wombats (see Appendix 2) reflects the intake of food which for the wild wombats contained some soil, especially during the drought. Liver selenium concentrations were high when compared with cattle and sheep (Underwood 1977) or with two species of marsupial, the red-necked wallaby *Macropus rufogriseus* and the red-bellied pademelon *Thylogale billardieri* with values of 4.15-17.3 $\mu\text{mol kg}^{-1}$ dry liver; but the greater barred bandicoot *Perameles gunnii* with values of 28-46 $\mu\text{mol kg}^{-1}$ dry liver (Munday 1978) reached concentrations of the order of *Lasiorchinus*.

The biochemical studies indicated that the drought probably had little effect on plasma volume of wombats. The data suggesting a lowered glomerular filtration rate during November 1977 and

February 1978 are consistent with the changes in faecal water and may in part explain the low water turnover of wombats in dry periods (Wells 1973).

There was no evidence to suggest that the portal fibrosis caused by *Progamotaenia festiva* significantly affected liver function. Although diseases and parasites probably contributed in some way to the poor condition of the animals during drought it is unlikely that the effects were significant because body condition improved when there was more food of good quality, despite the presence of parasites.

In summary, it appears that wombats are able to minimize loss of tissue and to maintain functions adequately for at least 12 months of drought. Like many other mammals inhabiting arid and semi-arid regions the well-being of individuals is largely determined by the availability of food and water. Some increase in foraging occurred when there was competition for food by sheep. But there was a remarkable lack of change in physiology or nutrient status during the year of drought.

CHAPTER 7

DISCUSSION AND CONCLUSIONS

7.1 Introduction

Some resolution of the question of whether the patterns of social behaviour, reproduction and health observed in wombats have adaptive value in an arid environment has emerged from the findings reported in Chapters 3-6.

The studies of Wells (1973, 1978) provide strong evidence that the low physiological rates of water use, and metabolism of energy and protein in hairy-nosed wombats allow their survival in their dry, hot and unproductive habitat. He supported his evidence with reference to the extensive literature on the benefits to desert mammals of low metabolic rate, water turnover and nitrogen requirements, and avoidance of heat (Schmidt-Nielsen 1972).

It is difficult to avoid the conclusion (using the criteria of Macfarlane (1978)) that these wombats have evolved in arid conditions and that many aspects of their basic physiology are adaptations allowing conservation of energy and water.

These functions raise the possibility that the behaviour and the population biology of the species are part of the same adaptation.

7.2 Resources and social behaviour

The social behaviour of wombats is remarkably simple although there is some complexity in overall organisation of a social structure. The limited ethogram could, in part be explained by the morphology of the animals. The rhinoceros, *Ceratotherium simum*, is a similar bulky, slow animal with an ethogram like that of wombats in many respects (Owen-Smith 1975). In both, movement patterns toward or away from conspecifics make up much of the behaviour. But the absence of close-quarter behaviour (which is common in social eutherians and even other

marsupials) suggests that the wombat is essentially solitary.

The social adaptations of desert herbivores to arid conditions have not been of major interest to ethologists. There are solitary, as well as highly social desert herbivores, with gradations between these extremes (Estes 1974).

It seems unlikely that desert environments select for only a few types of social structure, as is seen in the great diversity of social structures among rodents in the Kalahari desert (Nel 1975). The level at which adaptation for survival is important must primarily be that of energy and water turnover of the individual. If as a result of the adaptive use of these resources they survive and reproduce then it may not matter whether they occur in a solitary or a gregarious social system. The levels of sociality may then be adaptations to other aspects of life such as avoidance of predators, or fossorial and nocturnal living. It is not possible to say whether the limited ethogram, precise social relationships and overall social structure observed in *Lasionrhinus* are genetically based adaptations to an arid environment. They may well be, but other explanations are possible.

The important question is whether the responses of wombats to depletion of resources (short and long-term) are enhanced by behavioural mechanisms. Data on activity patterns suggest that wombats alter their periods of activity to correspond with times when ambient temperatures are within the species' thermoneutral zone and when relative humidity is high (Wells 1973, 1978). Wells postulated that such behaviour would result in considerable conservation of energy and water.

The data presented in Chapter 3 suggest that the same is true of social behaviour, and further, a possible physiological explanation for this is provided by the evidence given in Chapters 4, 5 and 6, which suggests that variation in the intensity of social behaviour is strongly associated with variation in reproductive status which is influenced by the pattern of rainfall and growth of pasture.

The short-term responses of animals to depletion of resources are generally, the use of mechanisms of conservation. Theoretical and actual evidence support this idea (Geist 1971, 1974a,b, Moen 1973, McFarland 1977). Maximizing food for females and reducing waste of energy in unnecessary social interactions, are two traits predicted to be the response of social animals to a depleted environment (Geist 1974 a,b, Geist & Petocz 1977). Both these predictions seem to hold for wombats. These traits may occur as a result of a change in social organisation, or as a result of changes in frequency of interactions within the same social organisation. The latter alternative seems to apply to *Lasiorchinus*.

Compared with males the basic social structure of female wombats reduces the potential number of social interactions in which they may be involved, and females are less likely to interact with males than males are with each other. Since female wombats are not territorial they can move over a greater area than males, which probably increases the quantity and variety of resources available to them.

The intensity of wombat social behaviour varied seasonally and correlated closely with the occurrence of mating. Outside the breeding season (July to December) at Blanche Town the frequency of

social interactions was relatively low. While the studies of social behaviour were made in years when reproduction did occur, it is reasonable to extrapolate the patterns of behaviour observed when female wombats were carrying young or were anoestrous, to times when no reproduction occurs because of drought (evidence for which was provided in Chapter 5). This is so because there is some evidence that a major part of wombat social behaviour is determined by the reproductive status of males, which is basically similar when drought occurs or when females carry young (see later). Thus when resources were depleted, the essential social organisation of the wombats did not change, but the actual frequency of social interactions decreased markedly. One effect of this would be a decrease in expenditure of energy above that required for maintenance.

7.3 The influence of reproduction on behaviour

Social interactions of wombats were determined largely by the behaviour of males because females interacted rarely and did not show 'addressor' behaviour patterns. A few studies reported in the literature have demonstrated that the social life of male mammals is largely influenced by whether or not they are in breeding condition (Lincoln et al. 1970, Jewell 1977). Only a few studies on wild mammals have experimentally verified the relationships between secretion of pituitary and gonadal hormones and social/sexual behaviour. Lincoln's study of red deer is now a classic example - rutting behaviour, including herding of a harem, territoriality, roaring and fighting do not occur if androgen production by the testes of the deer is inhibited (Lincoln et al. 1970).

The data presented in Chapter 4 show that maximal development of the accessory sex glands, and the highest concentrations of gonadotrophins and androgens in plasma of the wombats occurred in the breeding season, but declined toward the end of it, and there was no significant sexual development when drought occurred in the breeding season. These changes correlate closely with the observed patterns of increased social behaviour in the breeding season also.

Although experimental verification of the hypothesis that social behaviour of male wombats was determined largely by their reproductive status was beyond the scope of this study, the observations made at different times of the year suggest that it is correct.

Only part of the social structure of wombats could be explained in this way, since female reproductive status would also play a role. But as reported also, in Chapter 4, ovulation, the development of ovarian follicles and presumably, signals of oestrus released to the environment occurred at the same time as maximal development of the reproductive system of the male wombat. Thus synchronisation of the physiological patterns of both sexes would be likely to influence social structure. When females are anoestrous they are unattractive to males and are approached less by them.

Thus many of the dynamic aspects of wombat social structure can be explained on the basis of variation in the reproductive physiology of both sexes. Other questions arise on the causes of this variation in reproductive status, its nature and its part in the adaptation of wombats to an arid environment.

Two basic patterns of wombat reproduction were apparent from this study. First, reproduction is seasonal, matings and births occur

in the latter half of the year. Second, reproduction does not occur at all if drought conditions prevail during the breeding season, so that there is a link between rainfall and reproduction. In the Blanche Town region rain falls mainly in winter and there is a resultant growth of pasture (Trumble 1948, Wells 1973 and Appendix 1) but there is also a high frequency of drought (70 per cent). The adaptive significance of both these patterns is clear. The seasonal pattern of reproduction is consistent with much of the evidence in the literature relating the time at which young are weaned to the abundance of food (Sadleir 1969). By definition, drought is associated with a decreased amount of food. The lack of reproduction during drought, particularly that due to physiological inhibition, can be regarded as a mechanism by which young are not produced in years when they are unlikely to survive. In this way resources already depleted are not wasted on young unlikely to reach adulthood. In one year of this study (1976) when ovulation, mating and some births occurred, subsequent drought was associated with the death of pouch-young (Chapter 5).

The observed patterns of reproduction in wombats were also consistent with the theoretical models of reproduction in irregular environments discussed in Chapter 1. Longevity and iteroparity are consistent with a potentially high juvenile mortality (Wilbur et al. 1974) while the highly irregular reproduction keyed to occasional years of good food supply is consistent with Holgate's (1967) predictions of reproductive patterns expected in harsh erratic environments. Wombats cannot be considered to occupy a position on the r-K continuum of Pianka (1970) but show irregular fluctuations in manifestations of r or K characteristics in their population biology.

If the iteroparous pattern of reproduction of wombats is to be a success in terms of reproduction of genes then longevity of adults is essential. This can occur in the arid zone if somatic and behavioural adaptations enable individuals to survive when food and water supplies fail during drought. Attention was given to this question in Chapter 6.

7.4 Survival in drought

The results of various measurements used to assess body condition and functional status of the wombat showed that a drought of 13-15 months duration had little significant effect on the health of most individuals. Specific deficiencies in some minerals such as copper, and evidence of anaemia were observed, but generally the minor loss of body weight that occurred suggested that little adult mortality would be caused by a drought of this length. It was remarkable that health was maintained on pastoral properties where pasture removal by sheep and rabbits was so severe that no significant ground-cover was present. Under natural conditions adult wombats could probably survive droughts of at least 2 years duration. One of the basic conditions for an iteroparous pattern of reproduction thus appears to be satisfied for hairy-nosed wombats. Whether it is successful in terms of the maintenance of specific gene pools depends on the frequency and duration of droughts in the average life of a wombat.

7.5 Conclusions

It appears that the population biology of wombats is largely influenced by one or two important features of the environment. There is much evidence in this thesis (Chapters 3, 5 and 6) to

support the idea that it is food which largely determines the life-habits of the wombat. Further, evidence in Chapter 6 suggests that it is the quality and quantity of food available to the wombats which determines whether reproduction occurs, whether body condition improves or declines and whether social behaviour changes. For example, food consumed by wombats when reproduction occurred, was relatively high in organic matter, protein and water while the converse was true when there was no reproduction. The abundance and availability of this food of good quality is known to be determined by the relationship between rainfall and water loss (largely evaporation) from the ecosystem (Trumble 1948, Specht 1972, Noy-Meir 1973, Wells 1973) measured here as the plant growth index (Specht 1972).

The life-history of the wombat appears to be centered on a basic set of somatic and behavioural adaptations, and variation in life-history traits about these adaptations seem to be associated with the unpredictable variation in rainfall. Availability of food of good quality seems to be the thread linking the physiological with the behavioural processes described in this thesis. It is at both a gross and fine level that the lifestyle of the wombat is sensitive to and determined by this feature of the environment. At a gross level it was observed that reproduction did not occur during drought, but at a fine level variation in the initiation of reproductive events was determined quite precisely by the time at which enough rain fell to cause growth of lush pasture. This was late in some years such as 1976 but early in others such as 1978.

A brief examination of the plant growth index values (Appendix 1) in relation to other aspects of the biology of wombats serves to illustrate the deterministic role of rainfall and pasture growth in

their lives.

Examples include:

(1) The broad peak of increased social activity during August to December 1975 (Figure 3.8), the low intermediate activity and the later occurrence of a large peak in October and November 1976; patterns which correlate closely with the plant growth index values for these years.

(2) The positive relationship between the plant growth index and the proportion of female wombats with young (Figure 5.4 and Table 5.3).

(3) Variation in estimated mean birth date which correlates closely with the time of onset of winter or spring rains (Figure 5.5).

(4) Variation in body weight and in changes in body weight which follow closely the plant growth index (Figure 6.1).

It is perhaps no coincidence that a sensitive system adjusting energy expenditure to its availability develops by linking the initial growth of pasture to reproductive events which in turn largely determine the intensity of social behaviour. The potential for efficient conservation of resources is the natural result of this.

A unique feature of wombats as relatively large desert animals, is their fossorial habit. This may be the trait ultimately responsible for the general patterns of biology described here. Once a fossorial life-style was adopted by wombats, then mobility and range would have decreased. This would mean that shortages of food and water would affect them more acutely than other desert herbivores such as the kangaroos which could possibly avoid severe droughts by moving to favourable areas. The selection pressures on *Lasiorchinus* should have

been very strong. The result of this appears to be the complex interaction of fixed and variable, somatic and behavioural adaptations which enable the animal to survive times of extreme shortages of food and water which drive away or kill sheep, kangaroos and rabbits. The breeding season is fixed by seasonal pasture growth and an optimum weaning period exists, but at the same time food supply varies unpredictably from year to year, and the patterns of socio-biology of the wombat are adjusted accordingly. This is achieved because features of the physical environment control the switching mechanisms within the wombat's brain which activate or inhibit the physiological systems important to the population biology.

In summary, the evidence in this thesis suggests that:

- (1) The ethogram, patterns of social relationships and variations in the intensity of social behaviour are part of adaptations which allow a relatively solitary animal to live in a group without expending too much energy in social behaviour.
- (2) Reproduction in hairy-nosed wombats is dependent upon food supplies that follow rainfall.
- (3) The development of reproductive condition determines the intensity of social behaviour.
- (4) The interactions of the reproductive and behavioural adaptations with somatic adaptations (largely low physiological rate functions) enable most wombats to survive during drought.

CHAPTER 8

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CHAPTER 9

APPENDICES

APPENDIX 1 Rainfall and plant growth index records.

Table A1

Year		Month											
		J	F	M	A	M	J	J	A	S	O	N	D
1975	R	14	5	17	9	14	3	27	17	50	66	13	18
	PGI	0.6	0.2	0.7	0.7	0.9	0.8	1.8	2.0	3.5	4.9	3.1	1.6
1976	R	8	20	4	9	3	8	6	8	36	69	27	2
	PGI	0.4	0.8	0.3	0.5	0.4	0.6	0.8	1.0	2.1	4.1	3.3	1.0
1977	R	6	0	5	4	15	8	3	3	21	19	43	13
	PGI	0.2	0	0.2	0.2	0.7	0.9	0.9	0.8	1.4	1.6	2.4	1.2
1978	R	16	2	8	25	20	43	48	30	35	30	21	4
	PGI	0.7	0.1	0.3	1.1	1.5	2.8	4.2	4.9	4.8	4.1	2.5	1.3
Average*	R	17	19	17	23	29	26	23	26	23	26	18	18
	PGI	0.7	0.8	0.8	1.2	1.9	2.5	2.9	3.4	3.3	3.1	2.0	1.2

* All years of records of Bureau of Meteorology.

Table A1 Monthly rainfall (mm) (R) and plant growth index (scale 0-10) (PGI) values for Blanche Town during period of study.

APPENDIX 2 Haematological and biochemical values of captive
wombats.

Table A2 Haematological values of *Lasiorhinus latifrons* maintained in captivity (Mean values \pm S.D.). Twelve measurements from 8 wombats.

Measurement	Units	Value
Red cell count	cells $\times 10^{12} l^{-1}$	5.68 \pm 0.57
Haemoglobin	g l^{-1}	140 \pm 12
Haematocrit value	l l^{-1}	0.433 \pm 0.040
Leucocyte count	cells $\times 10^9 l^{-1}$	14.3 \pm 2.5
Neutrophils	cells $\times 10^9 l^{-1}$	7.98 \pm 1.27
Lymphocytes	cells $\times 10^9 l^{-1}$	6.03 \pm 1.57
Eosinophils	cells $\times 10^9 l^{-1}$	0.27 \pm 0.22

Table A3 Biochemical, vitamin and trace element values of *Lasiornhinus latifrons* maintained in captivity (Mean values \pm S.D.). Twenty-nine measurements from 9 wombats.

Measurement*	Units	Value
Sodium	m mol l ⁻¹	140 \pm 2.6
Potassium	m mol l ⁻¹	4.2 \pm 0.4
Chloride	m mol l ⁻¹	100 \pm 2.2
Creatinine	m mol l ⁻¹	0.22 \pm 0.03
Glucose	m mol l ⁻¹	6.1 \pm 1.0
Urea	m mol l ⁻¹	7.7 \pm 1.5
Protein	g l ⁻¹	75 \pm 6
Aspartate transaminase	U l ⁻¹	32 \pm 10
Copper	μ mol l ⁻¹	11 \pm 3
Zinc	μ mol l ⁻¹	20 \pm 5
Blood selenium	μ mol l ⁻¹	3.62 \pm 0.48
Serum vitamin B ₁₂	ug l ⁻¹	1.4 \pm 0.5

* All measurements made on plasma unless otherwise indicated.