ECOLOGY OF THE KANGAROO ISLAND WALLABY, *Macropus eugenii* (Desmarest), IN FLINDERS CHASE NATIONAL PARK, KANGAROO ISLAND.

by

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SUMMARY

The Kangaroo Island Wallaby (*Macropus eugenii*) was once quite common on the mainland of South Australia but due to habitat destruction and the introduction of alien competitors and predators it is now abundant only on Kangaroo Island, where it is considered to be a pastoral pest.

The presence of a large undisturbed population in Flinders Chase National Park, provided an ideal situation for a study of the population ecology of this species. Furthermore, such a study would also provide the basic biological data on which a management plan could be based.

In order to gain some understanding of the factors influencing the size of a natural population of wallabies, studies were made on their home-range and movement patterns, population size and structure, water metabolism and some aspects of reproduction.

The foraging area of a single population was determined by night-time observations and with the aid of radio-transmitters. The radio-tracking information showed that the wallabies in this population had well defined home-ranges which overlapped with each other. The size of the population fluctuated seasonally and annually. At around October - November each year there was an increase in the size of the population due to young animals leaving the pouch. This was followed by a decline in numbers over the late summer and early winter. A much higher mortality occurred in 1978 than in the previous years. A similar die-off has been reported for the winter of 1968. In both years the heavy mortality was preceded by a long, dry summer.

To ascertain which age-groups suffered the heaviest mortality it was necessary to establish the age of each animal captured. Tooth eruption in a number of animals of known age was studied in the laboratory and a standard curve relating age to stage of molar eruption was established. Animals in the field could then be accurately aged by reference to this graph. Young animals just out of the pouch suffered the highest mortality, particularly over summer, while the old animals also had a high mortality. However, in 1978 all age-groups were affected equally.

Both the radio-tracking data and the recapture records indicated that immigration and emigration were not significantly affecting the size of the population. Thus the number of animals was determined by the combined influences of natality and mortality.

The Kangaroo Island Wallaby has a seasonal breeding pattern with most young being born in late January and early February. The breeding pattern of females is controlled by seasonal changes in photoperiod. The presence of females in breeding condition appears to induce the increase in size of the accessory reproductive organs and rise in plasma testosterone levels observed in the males. This may act through pheromones. Fecundity was high in all years while mortality of pouch young was significant only in 1978.

During the summer months the grass on the main feeding area dried off and the wallabies were moving over greater distances than in winter, probably searching for better quality food. It was at this time, and in early winter, that the greatest mortality occurred while those animals which did survive were often in poor condition. Studies on their water metabolism in the field showed that although they were conserving water over summer, as indicated by low water turnovers and urine volumes, they were not suffering from dehydration. Although the causes of mortality would be quite complex a major factor seems to be a shortage of good quality food in late summer and early winter. This means that at the beginning of winter when there are increased metabolic demands due to the low temperatures and wet conditions the animals are in poor condition. Furthermore, heavy infestations of gastro-intestinal parasites at this time would also decrease their chance of surviving. The weather obviously has a major influence via the food supply and physical conditions in early winter.

DECLARATION

This thesis contains no material previously submitted by me for the award of any other degree or diploma in any University. To the best of my knowledge it contains no material previously published or written by another person except where due reference is made in the text of the thesis.

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1.0 INTRODUCTION

1.1 GENERAL INTRODUCTION

The environmental changes brought about by european settlement, together with the introduction of alien competitors and predators, has had drastic effects on the native fauna of Australia.

While the mammals seem to have been among those most adversely affected by the environmental changes, it appears that some species may actually have increased in number. For example population numbers of the euro (*Macropus robustus*) increased in the Pilbara district of Western Australia because overgrazing by domestic stock allowed their natural food plant (*Triodia spp.*) to spread (Brown and Main, 1967; Ealey, 1967a). Increased availability of water from man-made stock watering points has also allowed an extension of their range. Similarly, the red kangaroo (*Megaleia rufa*) has increased in abundance in some parts of its range (Frith, 1964; Newsome, 1965a). In the Upper Richmond and Clarence Rivers district of New South Wales, Calaby (1966) found that a varied and abundant native mammal fauna existed even though the area had a long history of european settlement. The main factor responsible for this richness appeared to be the considerable habitat diversity, due to the topography and climate, and the existence of state forests. Some alterations to the habitat through partial clearing for beef-cattle grazing has improved the quality of the available food plants for several species of macropods. However, in areas where complete clearing for dairying purposes has occurred there has been a decrease in the numbers of all species.

Despite these examples most species of native mammals have either declined in numbers or become extinct (Marlow, 1958; Ride, 1970). Within the Macropodidae the most seriously affected were the smaller species (Calaby, 1971). For example, in western New South Wales a combination of overgrazing by domestic stock, an increase in the number of rabbits and a severe drought caused extinction of species of *Bettongia, Lagorchestes* and *Onychogalea* (Calaby, 1971).

The Kangaroo Island Wallaby, or Tammar, *Macropus eugenii*, is another of the smaller members of the Macropodidae whose range has been considerably reduced in recent times. The first description and observations of an Australian marsupial were made on this species by the Dutch navigator, Francisco Pelsaert, after his ship the Batavia was wrecked on Houtman's Abrolhos in 1629. However, the species was not actually scientifically described until the early nineteenth century when a French expedition under Nicolas Baudin collected wallabies from L'Ile Eugene (now known as St. Peter Island) in Nuyts' Archipelago, South Australia. The type specimen was given the name *Kangarus eugenii* (Desmarest, 1817). This species was once quite common on the South Australian mainland, particularly in coastal scrub and parts of the Mt. Lofty Ranges (Finlayson, 1927). With european settlement much of their habitat was destroyed, and predators such as the fox (*Vulpes vulpes*) were introduced, so that they were thought to have become extinct on the mainland of South Australia by 1930. Then in 1969 a female carrying a pouch young was captured in mallee scrub near Cleve on Eyre Peninsula (Aitken, 1970) and in 1970 a young male was caught in the same area (P.F. Aitken, pers. comm.). Thus hopes were strengthened that a viable population still exists on the mainland. The population on St. Peter Island is now extinct while a colony on Flinders Island, in the Investigator Group, has been severely reduced in numbers since about 1964 (Calaby, 1971) and it is doubtful that it has survived (P.F. Aitken, pers. comm.). Some animals still live on Greenly Island although these were introduced there from Kangaroo Island (Mitchell and Behrndt, 1949). In Western Australia the tammar is still found on the mainland in the south-west of the state and on several offshore islands, namely Middle and North Twin Peaks in the Recherche Archipelago, Garden, East and West Wallabi Islands in Houtman's Abrolhos (Calaby, 1971). The one remaining area where this species is still abundant is on Kangaroo Island, South Australia, where it is considered to be a pastoral pest.

To minimize any further effects of clearing and grazing on the distribution and abundance of macropods, management plans must be formulated. Before this can be achieved field studies on habitat selection, general ecology, social organization and physiology are needed. However, at the present time little is known about the basic biology of most species.

The only species of macropods that have been studied in any detail in the field are the red kangaroo, the euro and the quokka (*Setonix brachyurus*). Studies on the red kangaroo and the euro were initiated because of their economic importance (Ealey, 1967a; Frith and Calaby, 1969) but they have also provided data which is of interest to the population biologist. On the other hand, research on the quokka was aimed at elucidating the factors controlling population size after a large die-off of quokkas on Rottnest Island was observed in the summer of 1954 (Waring, 1956). Other studies which have been more limited in extent, but which have nevertheless provided useful information, are those on the Eastern Grey Kangaroo (*Macropus giganteus*), the Whiptail Wallaby (*M. parryi*) and the Parma Wallaby (*M. parma*), (Caughley, 1964; Kirkpatrick, 1965a, 1966, 1967; Kaufmann, 1974; Maynes, 1974, 1977).

Both the red kangaroo and the euro are well adapted to living in the arid zone but have developed different physiological and behavioural mechanisms to cope with this environment. Research into their abundance and the factors influencing population size have indicated these differing patterns of adaptation.

Densities of red kangaroos have been measured by Frith (1964) in the Riverina district and in north-western New South Wales, by Newsome (1965a) in central Australia, and by Bailey (1971) in far western New South Wales. These workers all observed great changes in the density of animals in their study areas over relatively short time periods. They believed these changes could be attributed to the effects of either a drought, movements, or professional shooters. Frith (1964) concluded that shooting was probably the main factor for the decline that he observed as neither natural mortality nor movements could account for it. Newsome (1965b) found that red kangaroos were quite mobile resulting in congregations of animals in areas where green food persisted. However, after rain these animals dispersed widely. Thus, Newsome (1965a) thought that the numbers of red kangaroos on his study area depended on the availability of green herbage and shelter. Bailey (1971) showed that a variety of movement patterns could occur. Some animals were essentially sedentary, while others exhibited a marked mobility. Among the mobile animals neither sex nor any age group predominated. The decline in density that Bailey (1971) observed appeared to be due to a combination of the three factors; natural mortality due to drought, movement of animals out of the area and an increased harvesting programme by professional shooters.

In contrast to the red kangaroo the euro is sedentary and occupies a permanent home range that contains shelter, food and occasionally, water (Ealey, 1967b). However, during a long drought it has been observed that as the protein content of their food declines there is a fall in body weight and haemoglobin levels (Ealey and Main, 1967). Because they do not disperse to obtain better quality food many die of starvation.

Studies on the euro have indicated that they do have a low nitrogen requirement (Brown and Main, 1967; Brown, 1969). Work on the red kangaroo seems to indicate that they require a better quality diet, although some conflicting results have been obtained. Foot and Romberg (1965) found that juvenile red kangaroos were better adapted to make use of poor quality forage than sheep. McIntosh (1966) and Forbes and Tribe (1970), using mature animals, showed the red kangaroo was inferior to sheep in retaining nitrogen and utilizing poor quality roughage when placed on a low nitrogen diet. However, differences in the diets could account for the discrepancy in results. The poor quality diet given by McIntosh (1966) was lower in crude fibre and higher in soluble carbohydrate than that of Foot and Romberg (1965). Forbes and Tribe (1970) concluded that the red kangaroo may either have a higher nitrogen requirement than the euro, or their results may have been due to an inadequate energy intake while on the poor quality diet. In an experiment where euros, sheep and red kangaroos were compared, Hume (1974) found that the red kangaroo was less efficient than the euro and sheep in retaining nitrogen and sulphur, and in digesting fibre, when fed poor quality roughage. Hence, red kangaroos compensate for this by being highly selective in their feeding (Newsome, 1965b; Griffiths and Barker, 1966) while the euro is able to survive on plants low in nitrogen, except during extended droughts (Ealey and Main, 1967).

Field studies on reproduction in these macropods indicates that many females enter anoestrus during drought and that many pouch young die (Ealey, 1963; Newsome, 1964a,b). Frith and Sharman (1964) and Newsome (1965c) showed that a reduced food supply resulted in a high mortality of pouch young and young at foot in red kangaroos probably caused by a failure of lactation.

On Rottnest Island, Western Australia the quokka has been studied in two areas which differ mainly in the availability of water. In the Lakes area water is present all year round while on the West End there is no free water available during summer. The population on the West End appears to be isolated from the rest of the island as they do not migrate from there at any time of the year (Dunnet, 1962). Holsworth (1964) studied the population on the West End and suggested that changes in their pattern of reproduction tended to stabilize the population in a density-dependent manner. Following a population decline around 90% of females would breed, but when the population was increasing the birth-rate decreased until less than 50% of the females were reproducing. However, the harsh conditions over summer also exerted an effect as a high mortality occurred each year around the end of the dry summer period. Thus, much of the research on this species has attempted to determine the physiological changes that take place during summer and the factors which cause them.

Quokkas show a pronounced seasonal cycle in physical condition. They are in peak condition at the end of spring but then there is a steady decline in weight over the summer. If the summer is prolonged a large proportion of the population dies. Shield (1959) found that there was a pronounced anaemia associated with the decline in condition. He also found a difference between the West End and Lakes area populations. Those on the West End appeared in better condition in spring but had lower body weights and a more pronounced anaemia at the end of summer. From the work of Barker (1961a,b) it appeared that copper deficiency may be associated with the seasonal anaemia but it is not the main factor responsible. In a later study, Shield (1971) found that a decrease in blood volume in autumn was due to a decrease in red cell volume. Barker, Glover, Jacobsen and Kakulas (1974) subsequently showed that reduction in red cell diameter, haemoglobin levels and haematocrit occurred from spring to autumn.

Storr (1964) examined the diet of the quokka and found that nitrogen levels in their food declined over summer. However, not enough information was available on the nitrogen requirements of the quokka to say whether plant nitrogen was inadequate during summer. Barker, Glover, Jacobsen and Kakulas (1974) attempted to reproduce the anaemia suffered by field animals by placing two groups of captive quokkas on a low nitrogen diet, one group having water *ad lib.* and the other group on a restricted water intake. Although a partial anaemia developed, the experiment did not continue long enough because adverse weather conditions killed the experimental animals. However, from their data they theorized that animals living in the vicinity of the Lakes area suffered from an absolute nitrogen shortage while those on the West End suffered from an inadequate water intake and a shortage of nitrogen.

It is apparent from these studies that the size of macropod populations is regulated by environmental conditions which control the abundance and quality of food plants. The behavioural and physiological characteristics of the individual species show the extent to which they have adapted to their environment.

1.2 THE PRESENT STUDY

In 1975 when the present study began some information was available on the physiology of captive Kangaroo

Island Wallabies. This included work on nitrogen metabolism (Barker, 1968; Lintern and Barker, 1969; Barker, Lintern and Murphy, 1970; Lintern-Moore, 1973a,b), thermoregulation (Dawson, Denny and Hulbert, 1969), and thyroid function (Setchell, 1974). In addition, a considerable amount was known about the reproductive physiology of female wallabies, reviewed by Tyndale-Biscoe, Hearn and Renfree (1974). The only work done in the field has been an assessment of the nitrogen status of the wallaby at different times of the year (Barker, 1971). A programme of ear-tagging was carried out in conjunction with this study in Flinders Chase National Park, Kangaroo Island, and resulted in a large pool of individually marked animals (Andrewartha and Barker, 1969). The data obtained from this marking programme has been used in the present study to estimate population numbers from 1966 to 1969.

The large undisturbed population of wallabies at Flinders Chase National Park provides an ideal situation for a study of the field biology of the Kangaroo Island Wallaby. I chose to work on the population dynamics of this animal for a number of reasons. Firstly, the wallaby was accessible, abundant and relatively easy to catch. Moreover, specimens could be obtained from nearby farms, for the reproductive study, without disturbing the protected population. Secondly, there was a lack of detailed information on the population biology of macropods as a group. Thirdly, the species was regarded as a pastoral pest and information on their biology was required before effective management plans could be formulated.

The core of my study of the Kangaroo Island Wallaby has been the estimation of population size using the mark/recapture method. This required ear-tagging a large number of animals in one particular part of Flinders Chase National Park during 17 catching trips made at approximately two-monthly intervals. In addition, at the time of capture, animals were examined for their stage of tooth eruption. This data was then compared with that obtained from captive animals of known age, such that the age structure and survival rates of the field population could be calculated.

Migration is another factor which is important in determining population size. To take this into account, information on the movements and home-ranges of several wallabies has been obtained at different times of the year using radio-transmitters. Other aspects of the biology of the Kangaroo Island Wallaby which were investigated in this study include water metabolism in the field, onset of sexual maturity and seasonal changes in the male reproductive tract.

1.3 THE STUDY AREA

1.3.1 Location

Kangaroo Island is situated approximately 130 Km south-west of Adelaide, across the mouth of Gulf St. Vincent. The island is 145 Km long, east to west, and 55 Km wide at the widest point, and the total land area is approximately 3890 Km^2.

The western two-thirds of Kangaroo Island is covered by a high plain or plateau capped by an ironstone or lateritic crust while the southern and western coasts are backed by calcareous aeolinite dune-systems. The plateau has been cut by rivers and streams along its northern and southern margins. The eastern end of the island is low lying and more fertile. For this reason it has proved more suitable for intensive agriculture and much of it is now cleared. The first official settlement took place at this end of the island in 1836, although before this time the island was frequented by whalers and sealers.

Flinders Chase National Park occupies most of the western end of the island with an area of 570 Km^2. The study area was located in the vicinity of the original Rocky River Homestead and the present Park Ranger's Headquarters in Flinders Chase (Figure 1.1).

1.3.2 Climate

The climate of Kangaroo Island is typically Mediterranean with mesothermal temperatures and a pronounced concentration of rainfall in the winter months (Bauer, 1959). Rainfall and temperature data were obtained from the Adelaide Bureau of Meteorology.

The mean annual rainfall recorded at the Rocky River station in Flinders Chase for the years 1965 - 1978 was 806 mm. Mean monthly total rainfalls over these years is shown in Figure 1.2 while monthly rainfalls for the period of study are presented in Table 1.1. The total rainfall over the summer months (December - March) are shown in Table 1.2.

The effect of rainfall, temperature and evaporation on promotion of plant growth shows that rainfall is effective for about 6.5 months over most of the island (Burrows, 1979) so that the growing season begins, on average, in the second week of April and ends around the third week of October.

The mean maximum and minimum temperatures for each month of the year (from 1965 - 1978) at Parndana are shown in Figure 1.3 and the extreme maximum temperatures for 1975 - 1978 are presented in Table 1.3. Parndana is situated in the centre of the island approximately 50 Km from Flinders Chase.

1.3.3 Vegetation

The vegetation is comprised of a thick sclerophyllous cover 2 - 10 m in height and dominated by *Eucalypts*, many of which exhibit the mallee form, with *Acacias*, *Melaleucas* and *Banksias* forming much of the shrub layer.

On the study area the dominant trees are *Eucalyptus diversifolia* and *E. obliqua* while the shrub layer consists of *Acacia retinodes*, *A. armata*, *Melaleuca lanceolata*, *Hakea rostrata*, *Banksia marginata* and *B. ornata* with occasional *Xanthorrhoea tateana*. The ground cover within the scrub contained such plants as *Isopogon ceratophyllus*, *Epacris impressa*, *Leptospermum juniperinum*, *Lasiopetalum schulzenii* and *Hibbertia sericea*.

On the cleared area surrounding the Rocky River homestead the southern corner was covered by Bracken Fern, *Pteridium esculentum*, while the rest of the area consisted of a mixture of introduced and native grasses, small annuals and bryophytes. The plants on the cleared area are subject to heavy grazing pressure from Grey Kangaroos (*Macropus fuliginosus fuliginosus*) and Cape Barren Geese (*Cereopsis novaehollandiae*) as well as the wallabies. The height of this ground cover is kept to around 2 - 3 cm throughout the year by the continuous grazing.

The affect of the seasonal distribution of rainfall on the plant cover of the cleared area is shown in Figures 1.4 and 1.5. The photographs were taken in summer (Figure 1.4) and in winter (Figure 1.5). During summer the vegetation dries out, the annuals disappear and patches of bare ground appear. In winter the pasture appears quite lush.

A list of the plants identified on the study area is presented in Appendix I.

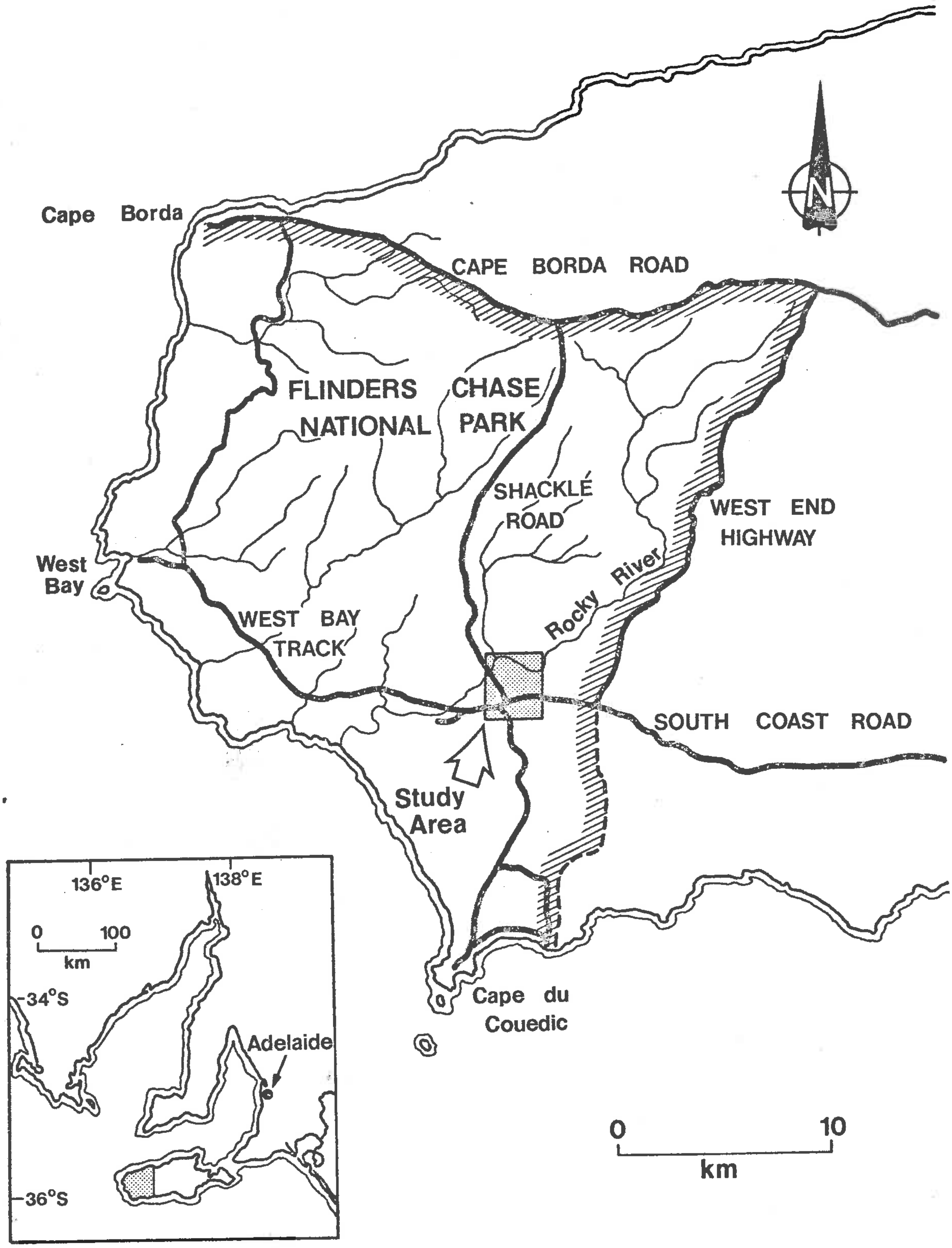


Figure 1.1 Location of the Study Area in Flinders Chase National Park, Kangaroo Island.

Figure 1.2

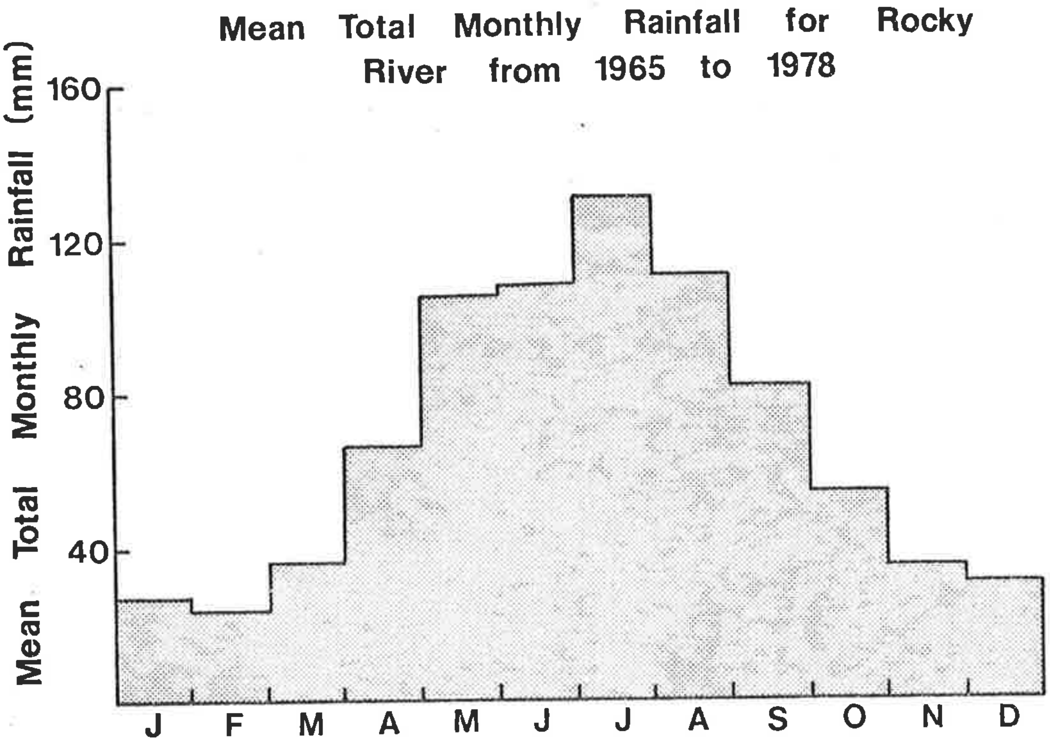


Figure 1.3

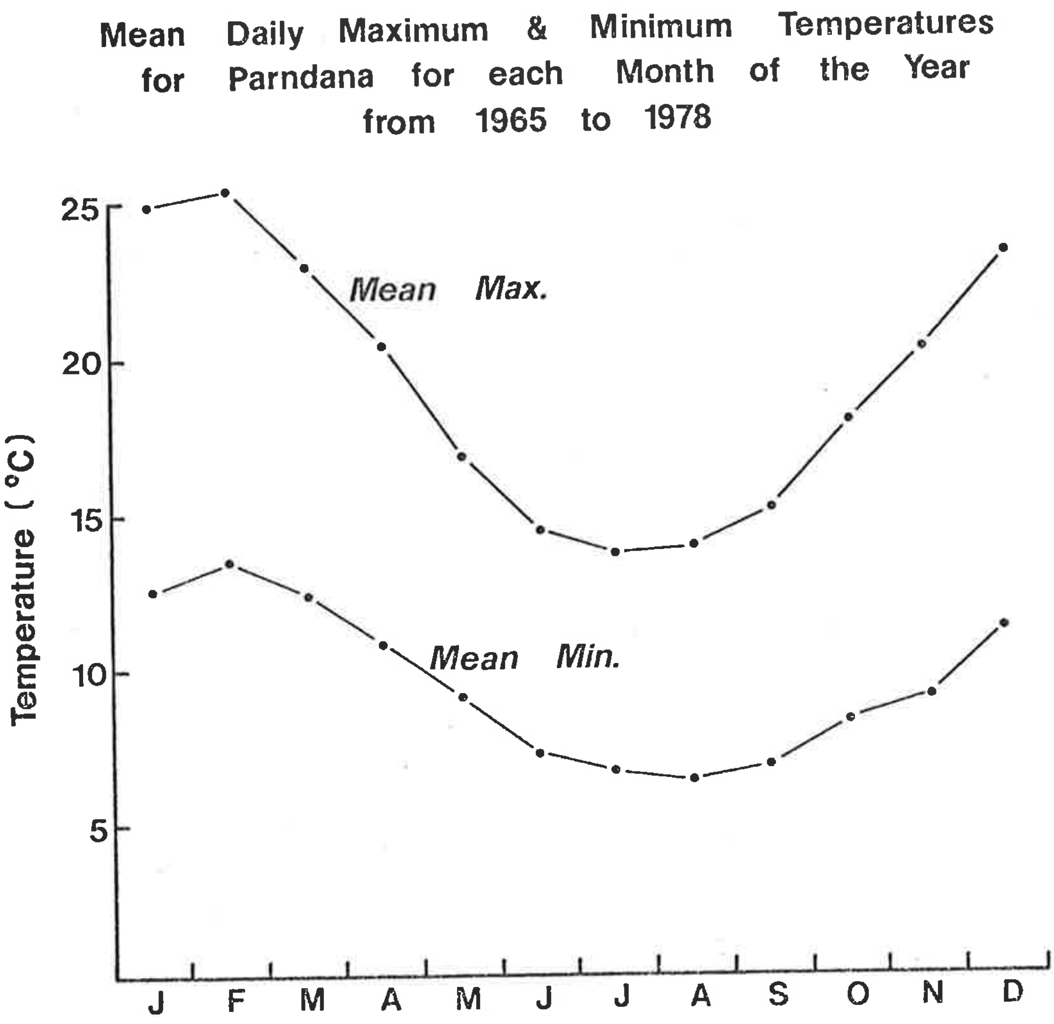


TABLE 1.1

RAINFALL (MM) AT ROCKY RIVER, FLINDERS CHASE

Year	J	F	M	A	M	J	J	A	S	O	N	D	Total
1975	34	4	68	31	106	82	152	79	66	126	35	6	789
1976	35	49	3	41	62	171	78	100	64	84	37	22	746
1977	44	13	40	38	137	92	72	54	76	14	97	13	690
1978	5	8	16	14	75	227	188	75	129	35	24	14	810

TABLE 1.2

RAINFALL DURING SUMMER MONTHS (DECEMBER - MARCH)

December 1975 - March 1976	93
December 1976 - March 1977	119
December 1977 - March 1978	42

TABLE 1.3

EXTREME MAXIMUM TEMPERATURES (PARNDANA)

(^{o}C)

Year	J	F	M	A	M	J	J	A	S	O	N	D
1975	36.3	39.8	31.3	29.9	25.2	16.9	22.2	17.2	18.7	25.3	29.9	40.4
1976	39.2	34.2	33.9	28.9	20.4	17.2	17.2	18.0	19.7	24.0	30.9	41.3
1977	40.8	40.9	34.6	25.2	22.8	16.2	18.7	22.2	24.1	32.4	35.2	36.9
1978	38.8	34.6	36.2	30.3	24.5	16.7	17.7	19.4	19.6	26.9	33.0	35.3

Figure 1.4 The Main Study Area in Summer

Figure 1.5 The Main Study Area in Winter

2.0 GENERAL METHODS

2.1 CAPTURE OF WALLABIES IN THE FIELD

Fence-traps (Andrewartha and Barker, 1969) were built in a number of locations using 1 m high wire-netting and star droppers. The design of these traps is shown in Figure 2.1. From October 1976 onwards the wings of the two traps on the main study area were extended during each catching trip with nylon nets (3 cm mesh, 20 m x 2 m). The nets were supported by wooden stakes driven into the ground.

After dark wallabies emerged from the scrub to feed on the main study area. They had access to this area through small holes in the fence and these were blocked off before catching commenced. The operators then attempted to drive the animals slowly along the fence line and into one of the traps. Once they were within the main yard of the trap, the gate was closed. The animals were then caught with hand nets and placed individually into sacks.

At least two people were needed for catching operations. Head torches provided sufficient light while leaving both hands free for handling wallabies.

After three to four drives, when no more wallabies could be caught, those animals which had been captured were transported back to the field station.

2.2 EXAMINATION OF ANIMALS IN THE FIELD

After capture, all animals were ear-tagged with individually numbered monel metal ear tags (Fingerling tags No. F3, Salt Lake Stamp Co., Salt Lake City, Utah). Initially, all animals were tagged in the right ear but later they were tagged in both ears to obtain an estimate of tag

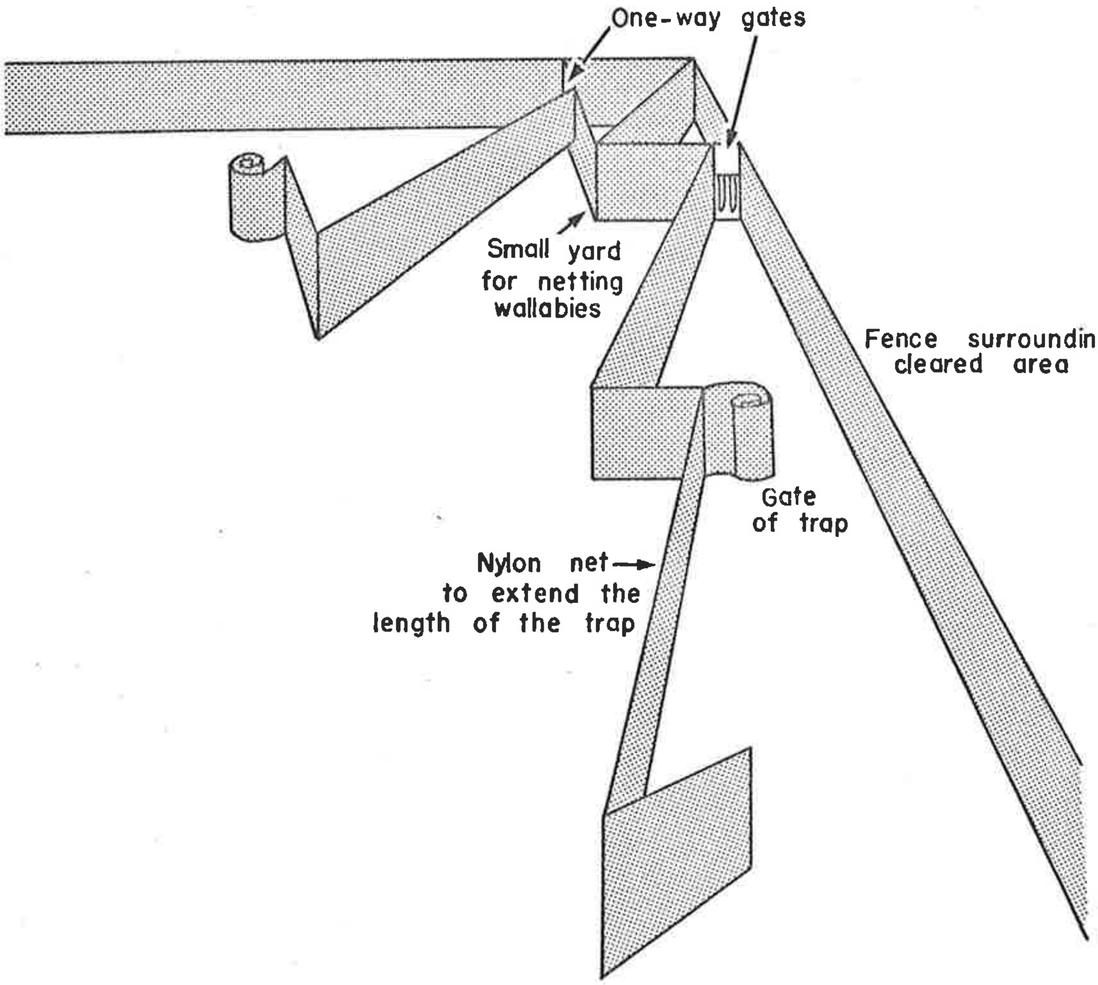


Figure 2.1 Design of the fence-trap used in one corner of the Main Study Area for capturing wallabies.

loss.

A number of observations were recorded from each animal examined, these being: sex; body weight; pes length; stage of tooth eruption; condition of pouch; presence of pouch young; sex of pouch young; pes, hind leg and head length of pouch young; the teat to which the pouch young was attached; and the general condition of the animal.

2.3 TOOTH ERUPTION STUDIES OF KNOWN AGE ANIMALS

2.3.1 Animal Husbandry

Animals were housed in large concrete-floored yards, either partly or wholly roofed with corrugated iron. Cages measured 9.5 m x 6.7 m and housed 10 - 15 wallabies of mixed sex and ages. The floors were covered with straw.

Kangaroo pellets (William Charlick Ltd.) and water were always available. Lucerne hay was given every other day and fresh cabbages and carrots twice a week.

2.3.2 Age Determination

Age was determined by examining the sequence of eruption of premolars and molars of known age animals.

Nine adult females, with pouch young, were obtained from Kangaroo Island in August 1975. The pouch young were measured to obtain their date of birth and the first examination of their teeth took place in December.

Animals were placed in sacks with their heads just emerging from the opening while the hind legs were firmly held by one person. The other person both controlled the forelimbs and examined the teeth using an auroscope handle with a bent arm while the jaws were held open with a mouth gag.

2.4 TELEMETRY

2.4.1 Equipment

Three types of radio-transmitter were used during the study:

(a) The first transmitter was designed and made by Mr. N. Weste of the Electrical Engineering Department, University of Adelaide.

Transmitter: 147.5 MHz, 1 w, crystal controlled, FM modulated with 1 KHz tone for 30 secs. every 5 mins.. Antenna - "rubber duck" helix.

Receiver: Superheterodyne with 10 element yagi antenna.

This transmitter was used only once in December 1976 because of its size and weight. It was attached as a back-pack to a large male (Male 1). The movements of this animal were followed for three days and then the transmitter was removed.

(b) Eight transmitters were subsequently borrowed from the Division of Wildlife Research, C.S.I.R.O., Canberra. They were initially designed for use on dingos and were reduced in size to fit the wallabies.

Transmitter: operated in the U.H.F. band, 403.1 MHz with channels spaced 10 KHz apart with different pulse rates to identify individual animals. Power supply was 7 Mallory RM 640 cells in series. Transmitters were wrapped in parafilm and fibre-glass tape, coated with araldite and attached to small dog collars. Total weight of transmitter was 120 gm. Aerial was a helical monopole.

Receiver: a double conversion superheterodyne with a sensitivity of - 135 dbM. The antenna was a 4 element yagi with two directors and measured 39 x 39 cm. For locating animals in the field the antenna was hand held.

(c) The third type of transmitter used was obtained from the AVM Instrument Company, Champaign, Illinois, U.S.A. The equipment consisted of SB 2-IV crystal-controlled transmitters, a twelve channel model LA 12 portable receiver and a 4 element yagi antenna. Each transmitter was powered by one mercury battery (1.35 v) and the frequency range was from 150.710 to 150.993 MHz with different pulse rates for each transmitter. Transmitters weighed 40 gm and were attached to collars which also contained the antenna. The receiving antenna was mounted on a 4 m aluminium pole.

2.4.2 Location of animals in the Field

Location of animals was achieved by taking compass bearings along the direcion of maximum signal strength. By taking bearings from two or more points the position of each animal could be plotted on a map by triangulation. A number of fixed stations were used at various points around the study area.

A problem with this method of locating animals is that readings cannot be made at the different stations simultaneously. This would not affect the results significantly as the stations were only 300 - 900 m apart.

Initially measurements were taken at irregular intervals during the day while a normal collecting trip was in progress. Later, to obtain more accurate measurements of the wallabies home-range size, as well as their daily and seasonal movements, I took readings at approximately 4 hourly intervals over a period of 3 days, repeating this at different times of the year.

2.5 WATER METABOLISM

2.5.1 Estimation of Total Body Water and Water Turnover

Prior to field-work a laboratory experiment was performed on 5 captive wallabies (2 M, 3 F) to determine equilibration time for tritium (Table 2.1). The animals were injected intramuscularly with 0.5 ml of tritiated saline at a concentration of 100 µCi/ml. Blood samples of 2 ml were taken from the lateral tail vein at intervals of 2 hours over a period of 12 hours. Equilibration was achieved within 4 hours and the concentration of tritium in the blood remained relatively constant up to 10 hours.

TABLE 2.1

CONCENTRATION OF TOH (µCi/l) AT VARIOUS TIMES AFTER INJECTION

	Time After Injection (hrs.)					
Animal No.	2	4	6	8	10	12
M 1	12.9	12.1	12.0	11.9	11.9	12.0
M 2	11.8	11.4	11.3	11.2	11.4	10.7
F 3	14.7	13.9	13.8	13.4	13.8	13.4
F 4	16.7	16.1	16.1	16.0	16.0	16.0
F 5	14.1	13.6	13.6	12.7	13.2	13.1

In the field the following procedure was used. Wallabies were weighed to the nearest 100 g and given an intramuscular injection of tritiated saline, as described above. After allowing 8 - 9 hours for equilibration (overnight) a 2 ml blood sample was taken from either the tail vein or by cardiac puncture. The animals were then released in the scrub near the point of capture. Upon recapture, during the same trip, they were re-weighed and another blood sample collected. All blood samples were stored frozen.

Stored blood samples were sublimed to dryness (Vaughan and Boling, 1961) and 0.5 ml of the separated water was added to 10 ml of scintillation fluid. The scintillation fluid consisted of 80 g napthalene, 5 g PPO (2,5 diphenyloxazolyl), 375 ml dioxane, 375 ml toluene and 250 ml ethyl alcohol. Samples were counted for three periods of 10 minutes in a Packard Tricarb Scintillation Spectrometer (Model 3002), with a suitably diluted standard and a water blank.

The total body water (TBW) was determined for each animal from the initial sample, after equilibration.

$$\text{TBW (ml)} = \frac{\text{activity TOH injected } (\mu\text{Ci})}{\text{activity TOH initial sample } (\mu\text{Ci/ml})}$$

Water turnover rates were estimated by fitting an exponential curve to the data, plotting sample counts against time in days. The slope of the line was calculated from $\ln \frac{Ct}{Co}/t$, where Co is the activity at time 0, Ct is the activity at time t, and t is the time in days between samples. This fractional change per day was multiplied by the TBW (ml) to give the water turnover in ml/day.

2.5.2 Measurement of Body Fluid Compartments

Plasma volume (PV) was determined by the dilution of the dye T1824 (Evan's blue). This dye binds to albumin and circulates with it to allow estimation of the albumin space.

The extracellular volume (ECV) was determined using sodium thiocyanate.

Before collecting data from field animals an experiment was conducted to see whether a single sample technique could be used for estimating plasma and extracellular volumes.

Four wallabies (2 M, 2 F) were cannulated in the lateral tail vein using Terumo Surflo-st Winged Infusion Sets (21 G). The wallabies were anaesthetized with Ketalar (Ketamine hydrochloride) at 15 mg/kg. An initial blood sample of 5 ml was taken from each wallaby to obtain the plasma blank. At time zero 1.0 ml of sodium thiocyanate solution (70 mg/ml) was injected into a marginal ear vein. Fifteen minutes later 0.5 ml of Evan's blue solution (4 mg/ml) was also injected into an ear vein. Blood samples were taken at 20, 30, 45, 60 and 75 minutes after injection of the thiocyanate. Blood samples were placed in heparinized centrifuge tubes and spun for 20 minutes at 3000 rpm to obtain plasma.

Plasma volume could be estimated by measuring the optical density of plasma samples directly against the pre-injection blank in an Eel Spectrophotometer at 620 mμ. A dye disappearance curve was fitted by eye to readings obtained from all samples, except the first, and extrapolated to time of injection. Plasma volume was determined by comparison with a standard curve made by dilution of the Evan's blue solution. A small correction was made for the plasma obtained from the initial pre-injection sample.

The error involved in estimating plasma volume from a single sample taken at 5 minutes after injection of Evan's blue was 1.9±.9%.

To obtain measurements of extracellular volume the plasma samples were first treated with trichloroacetic acid to remove plasma proteins. Two ml of plasma was mixed with 5.5 ml of water and then 2.5 ml of 20% trichloroacetic acid was added relatively slowly. After thorough mixing they were allowed to stand for 10 minutes before being filtered. Equal volumes of the filtrate and a colour reagent were mixed and the optical density read immediately at 460mμ against the blank sample prepared in the same way. The colour reagent consists of 80 g ferric nitrate in 250 ml of 2N nitric acid made up to 500 ml with distilled water and then filtered.

Extracellular volume was determined by comparison with a standard curve in the same way as plasma volume.

For the ECV the error involved in using a single sample at 20 minutes after injection of the sodium thiocyanate was 4.6±2.4%.

Thus for measurements of plasma volume and extracellular volume in field animals it was decided that the single sample technique gave reliable results. An initial blood sample was collected by cardiac puncture for the pre-injection blank. Then 1.0 ml of thiocyanate was injected into an ear vein followed 15 minutes later by 0.5 ml of Evan's blue. At 20 minutes after the first injection another blood sample was obtained by cardiac puncture. This sample was used to calculate the plasma and extracellular fluid spaces.

2.5.3 Collection of Urine and Faeces

From January 1977 to May 1978 urine and faecal samples were collected from wallabies held for 12 hours in metabolism cages.

The metabolism cages were constructed from 2 cm square galvanized wire mesh and measured 60 cm^3. Cages were lined with hessian to prevent the wallabies from panicking and damaging themselves. Each cage was suspended over a fibre-glass collecting shute and urine/faeces separator, similar to that described by McIntosh (1966).

Urine drained into polythene jars containing a small quantity of toluene and faeces were collected into plastic bags.

The volume of urine and wet weight of faeces excreted over the 12 hours was recorded. Samples were then frozen for transport back to the laboratory.

Moisture content of the faeces was determined after drying samples for 24 hours at 105^{o}C.

Osmolality of urine samples was measured with a Knauer Osmometer. Sodium and potassium concentrations were determined by flame-photometry with an Eel Flame Photometer Mk. II.

2.5.4 Haematocrit

The total haematocrit value (red cells plus white cells and platelet layer) was determined from blood collected into heparinized micro-haematocrit tubes after pricking an ear vein. Samples were centrifuged for 20 minutes at 3000 rpm.

2.5.5 Plasma Protein

Plasma protein concentration was determined by refractive index on an Atago Refractometer using the plasma collected during measurements of haematocrit.

2.5.6 Plasma Concentration

Blood samples were collected by cardiac puncture and placed into heparinized (lithium heparin) centrifuge tubes. Plasma was collected after centrifugation at 3000 rpm for 20 minutes.

Osmolality and electrolyte concentrations were determined as for the urine samples.

3.0 AGE DETERMINATION

3.1 INTRODUCTION

The ability to determine the age of individuals is an essential part of any study of the population dynamics of a species. This information can then be used to construct life-tables for estimating survival rates.

Many different techniques have been used in age determination of mammals. These include the degree of epiphyseal fusion (Washburn, 1946), weight of eyelens (Dudzinski and Mykytowycz, 1961), tooth eruption and wear (Severinghaus, 1949; Robinette, Jones, Rogers and Gashwiler, 1957), and annual growth rings in horns (Caughley, 1965; Geist, 1966) and teeth (Scheffer, 1950; Laws, 1952; Kingsmill, 1962; Low and Cowan, 1963; Pekelharing, 1970).

In the macropod marsupials age determination of the pouch young has been estimated from body measurements (Shield and Woolley, 1961; Sadleir, 1963; Sharman, Frith and Calaby, 1964; Murphy and Smith, 1970; Maynes, 1972). In older animals either the sequential eruption of the molars (Sharman, Frith and Calaby, 1964; Ealey, 1967c; Shield, 1968; Maynes, 1972) or the forward progression of the molar row along the jaw has been used (Kirkpatrick, 1964, 1965b; Sharman, Frith and Calaby, 1964; Dudzinski, Newsome, Merchant and Bolton, 1977).

In this chapter the growth curves obtained by Murphy and Smith (1970) for pouch young of captive Kangaroo Island Wallabies are compared with growth rates in field animals. The pattern of tooth eruption in animals older than one year is described and its usefulness for aging wallabies in the field is assessed.

3.2 METHODS AND TERMINOLOGY

3.2.1 Age Determination of Pouch Young

In order to assess the reliability of using the growth curves obtained by Murphy and Smith (1970) in determining the ages of pouch young in the field 19 young were measured at different times during the year in 1977 and 1978. The ages were determined from head, pes and leg lengths as described by Murphy and Smith (1970). The error involved was taken to be the difference between the actual number of days between two successive measurements and the estimated number of days.

3.2.2 Tooth Eruption

The tooth eruption sequence was observed in 23 animals (14 F, 9 M) of known age that were born in captivity, and a further 5 females that were of unknown age when first brought from Kangaroo Island. The teeth of the upper jaw only were examined at intervals of 2 - 6 months.

The notation used in recording the stage of eruption of molar teeth followed that of Sharman, Frith and Calaby (1964). Each stage is scored subjectively, three stages being recognized in live animals.

Notation	Position of Anterior Loph	Position of Posterior Loph
.2	Just emerged through gum	Below the gum
.3	Partly erupted	Just emerged through gum
.4	Fully erupted	Partly erupted

A fully erupted molar tooth was represented by an M followed by a capital Roman numeral. For a partly erupted molar this was represented by the number of the fully erupted tooth in front followed by the appropriate decimal notation for the stage of eruption of the partly emerged tooth.

3.2.3 Molar Index

The molar indices of the skulls of 19 animals (7 F, 12 M) were measured using the method established by Kirkpatrick (1964). The notation used followed that of Newsome, Merchant, Bolton and Dudzinski (1977). Ten stages in the progression of any molar past the anterior border of the orbits was recognized and given decimal notations accumulating in tenths.

3.2.4 Measurements of the Size of the Skull and Teeth

A series of measurements of both skulls and teeth were made on 69 crania (21 F, 48 M) from animals shot in the field as part of the reproductive study. The skull measurements were based on those described by Thomas (1888) and are defined in Appendix II. Measurements were made with a dial caliper reading to 0.05 mm and were recorded to the nearest 0.1 mm. The right side of the skull was used for unilateral measurements, and for measuring teeth, except where this side had been damaged.

3.3 RESULTS

3.3.1 Estimation of Age of Pouch Young in the Field

The error involved in using the growth curves of Murphy and Smith (1970) to age pouch young in the field are shown in Table 3.1. In 1977 only 2 animals had an error greater than 5 days while in 1978 all errors were underestimations and only one animal had an error that was less

TABLE 3.1 ERROR INVOLVED IN ESTIMATING THE AGE OF POUCH YOUNG IN THE FIELD FROM DATA ON CAPTIVE ANIMALS

Year	Sex of Pouch Young	First Age Estimation (days)	Second Age Estimation (days)	Estimated Number of days between measurements	Actual Number of days between measurements	Error (days)
	M	47	120	73	78	5
	M	77	153	76	79	3
	M	34	118	84	82	2
	M	75	156	81	77	4
1977	F	77	161	84	82	2
	F	64	137	73	84	11
	F	68	142	74	85	11
	F	72	159	87	89	2
	F	75	155	80	75	5
						Mean Error: 5.0 ± 3.6
	M	60	100	40	44	4
	M	62	139	77	104	27
	M	69	150	81	109	28
	M	55	143	88	106	18
1978	M	97	152	55	62	7
	F	63	136	73	101	28
	F	94	147	53	60	7
	F	66	93	27	42	15
	F	5	154	149	165	16
	F	111	162	51	60	9
						Mean Error: 15.9 ± 9.2

than 5 days. The differences between the two years suggests that nutrition of the mother is important to the growth of the pouch young.

3.3.2 Cranial Features and Dentition

The skull of *Macropus eugenii* is strongly built with short nasals, which are expanded in width at their posterior ends, a square inter-orbital region while the inter-temporal constriction is scarcely observable (Thomas, 1888; Wood Jones, 1924). They also possess a well developed external zygomatic shelf (Ride, 1957), (Figure 3.1).

A marked sexual dimorphism was observed in cranial measurements, except for nasal width in young animals (p^3dp^4 still present) and inter-orbital width in adults (p^4 present). Males were always larger than females (Tables 3.2 and 3.3).

The adult dental formula is:

$$I\ \frac{3}{1}\quad C\ \frac{0\text{-}1}{0}\quad PM\ \frac{1}{1}\quad M\ \frac{4}{4}$$

Molars are hypsodont and the cusps are joined by transverse ridges or lophs. A vestigial canine tooth is sometimes found in the upper jaw.

In juvenile animals two deciduous premolar teeth are present, a sectorial tooth (p^3) and a molariform tooth (dp^4). These are later replaced by a permanent, sectorial premolar (p^4). Because of the resemblance between p^3 and p^4, and dp^4 and MI, identification of these teeth is not always easy.

Tooth measurements show that there is no significant difference in anterior or posterior widths between p^3 and p^4 in females but p^4 is longer than p^3. However, in males, p^3 is significantly wider than p^4, and p^4 is longer than p^3

Figure 3.1

A. Ventral view of skull of a Kangaroo Island Wallaby showing the well developed external zygomatic shelf (zs).

B. Dorsal view of skull showing the short nasals (n) and the square inter-orbital region (io).

C. Teeth of a juvenile wallaby

p^3 = deciduous sectorial premolar

dp^4 = deciduous molariform tooth

MI and MII = first and second permanent molar teeth.

D. The permanent premolar (p^4) has just erupted on one side and has pushed out the deciduous molariform tooth (dp^4).

E. The permanent premolar (p^4) is fully erupted and has replaced both the deciduous molariform tooth (dp^4) and the deciduous sectorial premolar (p^3).

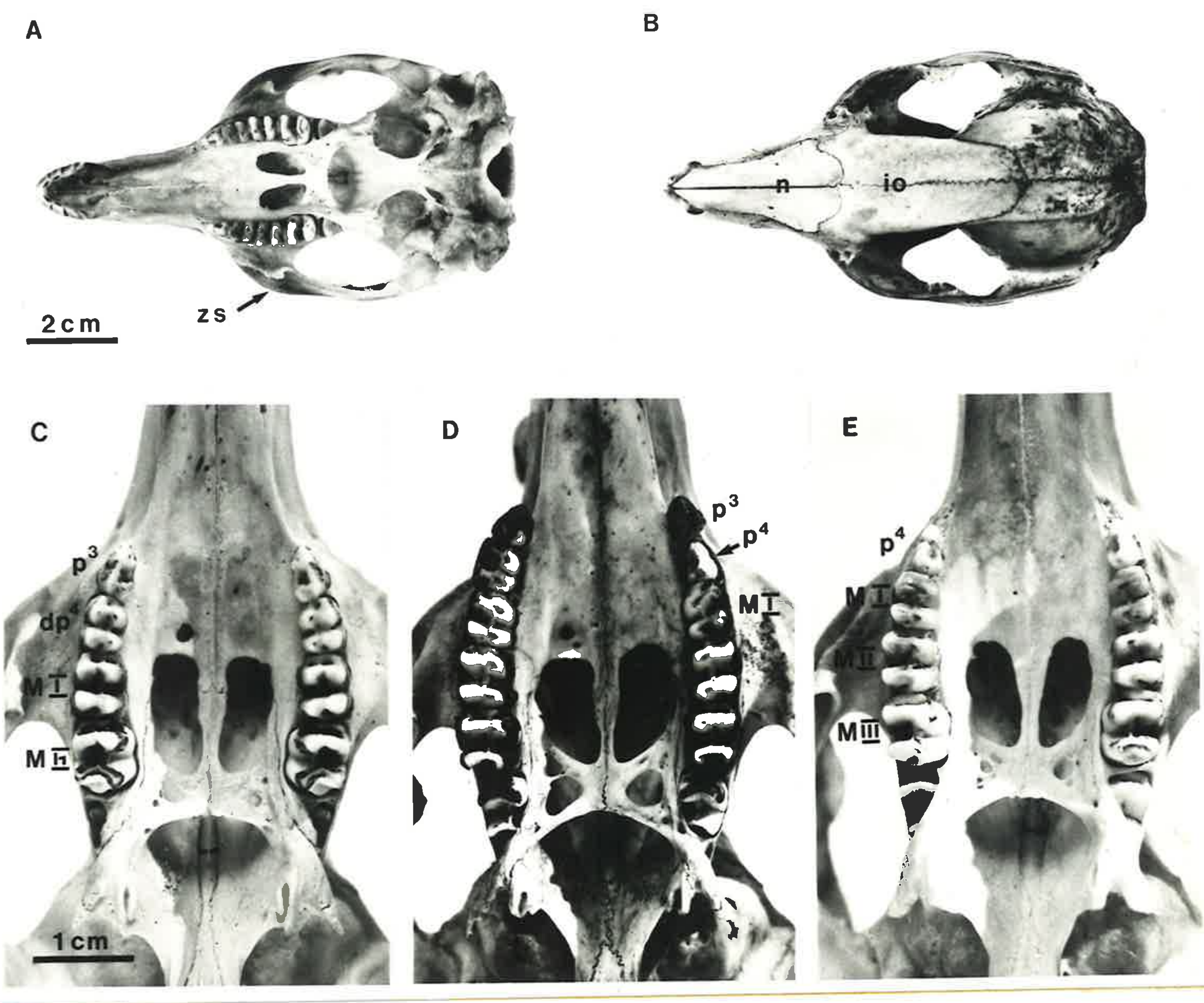

A
B
zs
2cm
n
io
C
D
E
p3
dp4
MI
MII
p3
p4
MI
p4
MI
MII
MIII
1cm

TABLE 3.2 SKULL MEASUREMENTS

FOR ANIMALS OF DENTITION p^3 dp^4 MI.0 - MIII.0

(ALL MEASUREMENTS IN MILLIMETRES)

Measurements	Females				Males				Students t-test (20df)
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	
Basal Length	85.50	5.55	79.0-93.0	9	91.00	6.61	81.7-98.7	13	2.111*
Nasal Length	34.32	3.23	30.6-40.0	9	37.70	3.18	32.4-41.3	13	2.429*
Nasal Width	16.31	1.72	13.7-18.1	9	17.70	1.72	15.6-20.3	13	N.S.
Inter-Orbital Width	16.66	1.05	15.1-17.8	9	17.83	.92	16.5-19.5	13	2.702*
Palate Length	53.88	3.61	49.8-58.8	9	57.85	4.70	51.4-63.4	13	2.238*
Diastema	19.26	.99	18.0-20.9	9	20.95	1.39	18.4-23.1	13	3.330**

* Significant at 5% level

** Significant at 1% level

N.S. Not significant

TABLE 3.3 SKULL MEASUREMENTS

FOR ANIMALS OF DENTITION p^4 MIII - IV

(ALL MEASUREMENTS IN MILLIMETRES)

Measurements	Females				Males				Students t-test (45df)
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	
Basal Length	93.27	2.39	89.8-96.2	12	99.69	4.00	91.9-106.3	35	6.646***
Nasal Length	39.19	1.72	36.7-41.6	12	42.55	2.62	36.5-47.5	35	5.050***
Nasal Width	18.33	1.44	15.9-20.2	12	19.91	1.67	17.2-22.9	35	3.144**
Inter-Orbital Width	16.33	.99	13.8-17.6	12	16.87	1.27	14.6-19.8	35	1.511 N.S.
Palate Length	60.42	1.59	58.2-62.7	12	64.49	2.78	59.0-70.5	35	6.196***
Diastema	22.13	2.65	19.1-29.3	12	25.11	1.89	20.8-28.0	35	3.595***

N.S. Not significant

* Significant at 5% level

** Significant at 1% level

*** Significant at 0.1% level

(Tables 3.4, 3.5 and 3.6). These teeth can also be distinguished on morphological features. With p^3 the main cutting ridge is in line with the outer cusps on the lophs of dp^4 and the molar row while the inner cusps of p^3 are in line with the inner cusps of dp^4 and the molars. In the permanent premolar (p^4) the central ridge is not in line with either the outer or inner cusps of the molars (Figure 3.1). Although the tooth dp^4 is very similar morphologically to MI it is significantly smaller in size (Tables 3.3 and 3.5). The anterior cingulum is more clearly separated in MI than dp^4. In dp^4 it is extended upwards towards the labial surface almost to the paracone.

There was little sexual dimorphism in tooth size apart from dp^4 and MII which were longer in juvenile males, and MIV which was longer in adult males (Tables 3.4 and 3.5).

3.3.3 Tooth Eruption Pattern

By the time the young have permanently left the pouch at 245 - 270 days (Murphy and Smith, 1970) two of the three pairs of upper incisors have fully erupted while the third has just broken through the gum. Both p^3 and dp^4 emerge before the third incisor and before the young has left the pouch while MI is fully erupted just after the young leaves the pouch. The permanent premolar (p^4) erupts at a mean age of 1049 days with a range of 901 to 1196 days (N = 9).

The sequence of eruption of the molar teeth is shown in Figure 3.2. The line of best fit is drawn through the mean ages at which each stage was first observed. Data for males and females is combined. This information was supplemented with examination of five captive females of

TABLE 3.4 TOOTH MEASUREMENTS

FOR ANIMALS OF DENTITION p^3 dp^4 M^{I-III}

	Measurements	Females Mean	S.D.	Range	N	Males Mean	S.D.	Range	N	Students t-test (20 df)
p^3	anterior width	2.66	.17	2.4-2.9	9	2.62	.09	2.5-2.8	13	.646 N.S.
	posterior width	3.23	.15	3.0-3.5		3.23	.15	3.0-3.5		0 N.S.
	length	4.63	.09	4.5-4.8		4.71	.31	4.1-5.1		.878 N.S.
dp^4	anterior width	4.02	.21	3.8-4.5	9	4.00	.16	3.7-4.2	13	.241 N.S.
	posterior width	4.08	.23	3.8-4.5		4.18	.20	3.8-4.5		1.057 N.S.
	length	4.70	.15	4.6-5.0		4.87	.19	4.5-5.1		2.342 *
M^I	anterior width	4.66	.18	4.5-5.1	9	4.78	.23	4.3-5.1	13	1.370 N.S.
	posterior width	4.69	.27	4.4-5.2		4.76	.21	4.3-5.0		.653 N.S.
	length	5.46	.16	5.1-5.6		5.60	.22	5.1-5.9		1.728 N.S.
M^{II}	anterior width	4.97	.25	4.7-5.5	9	5.10	.18	4.7-5.4	13	1.339 N.S.
	posterior width	4.82	.29	4.6-5.4		4.95	.16	4.8-5.3		1.222 N.S.
	length	6.17	.24	5.8-6.6		6.53	.19	6.3-6.8		3.758 **
M^{III}	anterior width	5.30	.24	5.0-5.6	4	5.36	.21	5.1-5.7	8	.425 N.S. (10 df)
	posterior width	5.15	.34	4.8-5.6		5.09	.24	4.7-5.4		.316 N.S.
	length	6.90	.28	6.5-7.1		7.15	.29	6.8-7.6		1.441 N.S.

N.S. Not significant

* Significant at 5% level

** Significant at 1% level

TABLE 3.5 TOOTH MEASUREMENTS

FOR ANIMALS OF DENTITION p^4 M^{III-IV}

Measurements		Females Mean	S.D.	Range	N	Males Mean	S.D.	Range	N	Students t-test (45 df)
p^4	anterior width	2.56	.18	2.3-3.0	12	2.53	.19	2.2-3.0	35	.491 N.S.
	posterior width	3.10	.15	2.9-3.5		3.10	.14	2.9-3.4		0 N.S.
	length	5.09	.25	4.8-5.7		5.07	.21	4.8-5.6		.249 N.S.
M^I	anterior width	4.96	.21	4.6-5.3	12	4.97	.22	4.6-5.7	35	.141 N.S.
	posterior width	5.04	.19	4.7-5.3		5.03	.24	4.6-6.0		.147 N.S.
	length	5.52	.21	5.2-5.8		5.44	.31	4.9-6.2		.999 N.S.
M^{II}	anterior width	5.44	.24	5.0-5.7	12	5.47	.27	5.0-6.0	35	.361 N.S.
	posterior width	5.21	.21	4.8-5.6		5.20	.24	4.8-5.9		.137 N.S.
	length	6.20	.40	5.5-6.9		6.22	.32	5.4-6.8		.157 N.S.
M^{III}	anterior width	5.64	.29	5.2-6.2	12	5.79	.27	5.2-6.4	35	1.574 N.S.
	posterior width	5.39	.33	5.0-6.0		5.40	.25	4.9-6.0		.096 N.S.
	length	6.99	.40	6.4-7.5		6.99	.34	5.8-7.5		0 N.S.
M^{IV}	anterior width	5.45	.33	5.0-6.1	11	5.42	.33	4.8-6.2	33	.261 N.S. (42 df)
	posterior width	4.75	.33	4.1-5.3		4.75	.33	4.1-5.2		0 N.S.
	length	6.91	.32	6.4-7.3		7.21	.31	6.5-7.8		2.713 **

N.S. Not significant

** Significant at 1% level

TABLE 3.6

STUDENTS t - TESTS ON TOOTH MEASUREMENTS

p^3 AND p^4

	Females	Males
anterior width	t_{19} = 1.300 N.S.	t_{46} = 2.211 *
posterior width	t_{19} = 1.967 N.S.	t_{46} = 2.714 **
length	t_{19} = -5.882 ***	t_{46} = -3.871 ***

dp^4 AND M^1

	Females	Males
anterior width	t_{16} = 6.941 ***	t_{24} = 10.039 ***
posterior width	t_{16} = 5.161 ***	t_{24} = 7.214 ***
length	t_{16} = 10.397 ***	t_{24} = 9.057 ***

N.S. Not significant

* Significant at 5% level

** Significant at 1% level

*** Significant at 0.1% level

unknown age which were examined at the same time. These animals had tooth eruption stages of MII.2 to MIII.2 when first examined and were used to extend the graph up to when the fourth molar was fully erupted. The eruption sequence for each of these animals was plotted on graph paper and then adjusted to the curve constructed from known age animals to give the best fit.

This method was also used to plot the eruption sequence of 10 females and 10 males that were caught several times in the field (Figure 3.3).

3.3.4 Molar Index

The plot of molar index against age for nineteen animals is shown in Figure 3.4.

The regression equation obtained is:

Log Age (days) = 2.0939 + .4067 Molar Index

(Correlation Coefficient, r = .9837)

3.4 DISCUSSION

When estimating ages of pouch young in the field using data from captive animals it is necessary to assume either that the growth rates are the same or to actually measure growth rates of field animals. Sharman, Frith and Calaby (1964) suggested that growth of red kangaroos in the pouch approximated an all-or-none phenomenon. Shield and Woolley (1961) considered that as the growth proportions were similar in captive and wild caught quokkas it was probable that their growth rates were similar. Sadleir (1963) also found this to be true for euros and concluded that nutrition was never poor enough to retard the growth of pouch young.

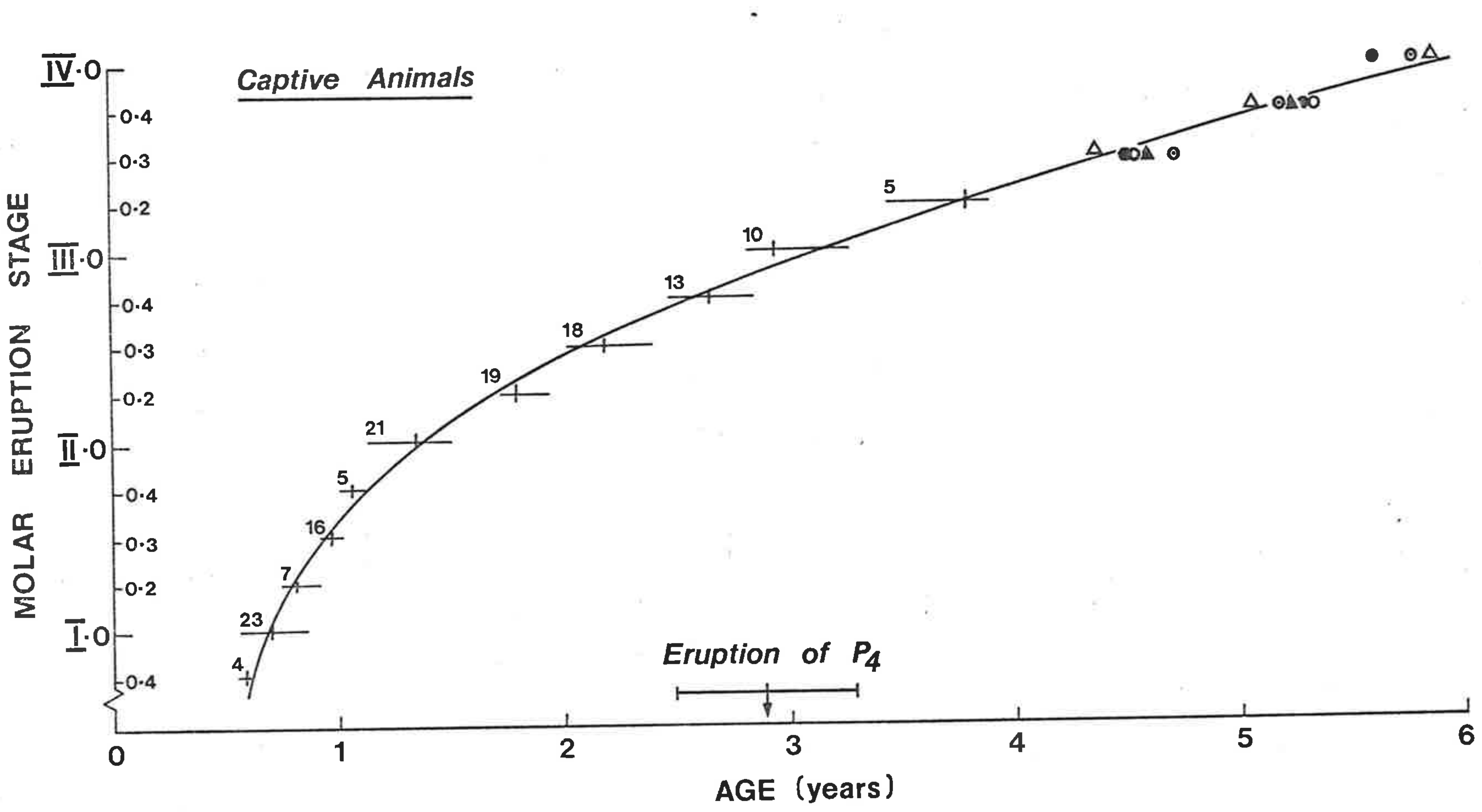


Figure 3.2 Molar eruption sequence of captive Kangaroo Island Wallabies. Vertical lines represent mean age and horizontal lines the range. Numbers above horizontal lines represent the sample size. Symbols are for 5 females that were of unknown age when first caught.

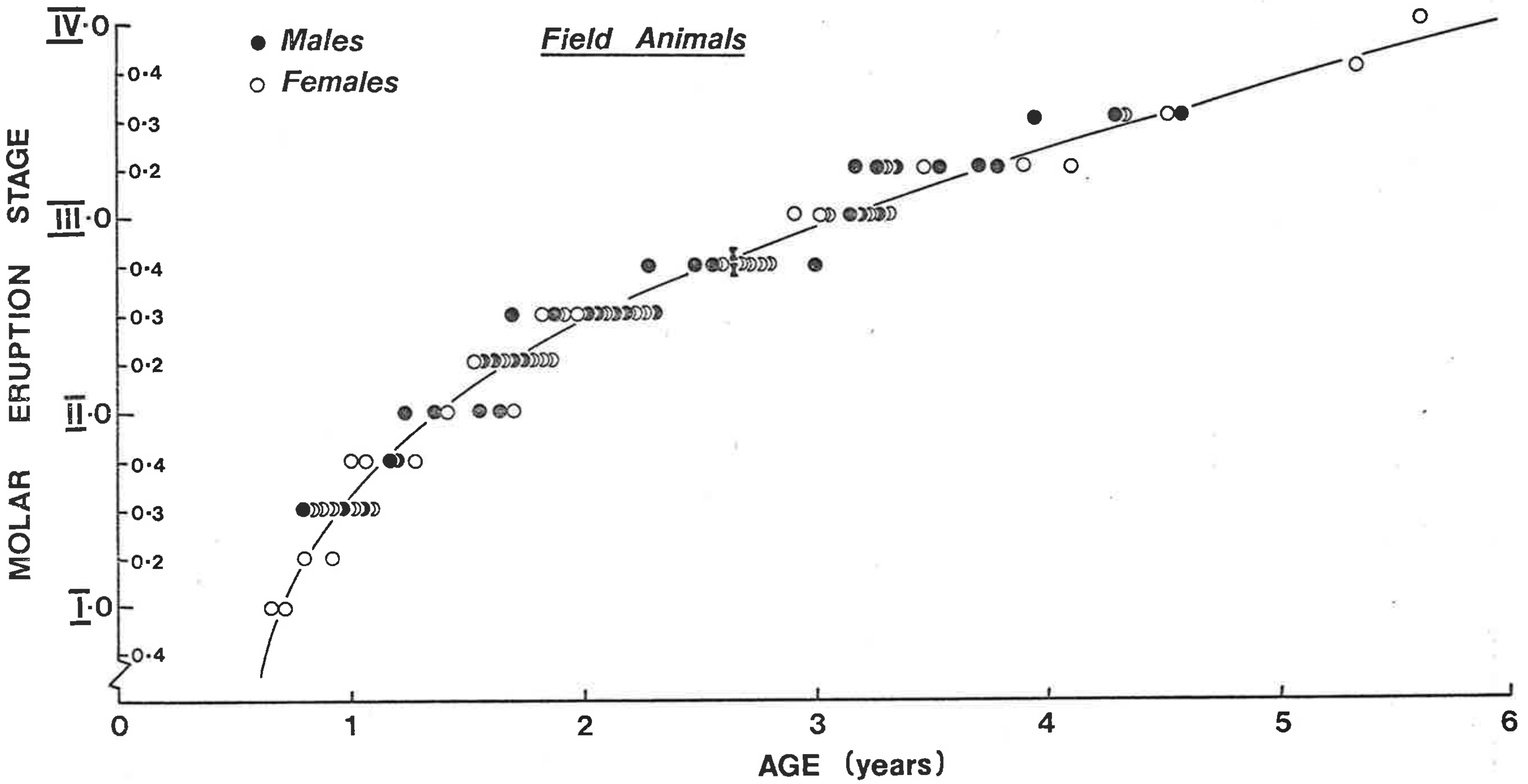


Figure 3.3 Molar eruption sequence of 10 females and 10 males re-captured at various intervals in the field. Curved line is the line of best-fit obtained from captive animals.

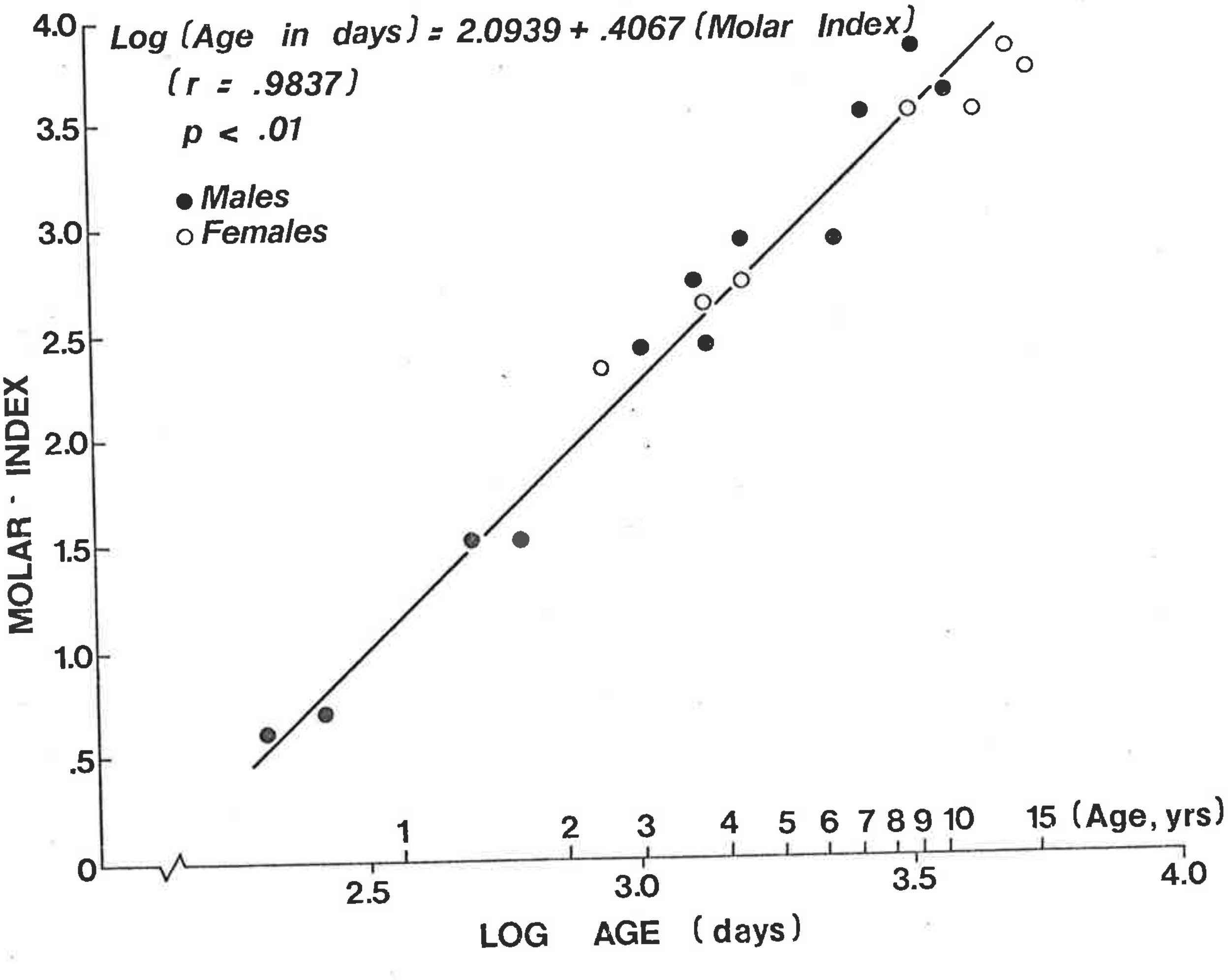


Figure 3.4 The molar index of 19 animals plotted against log. age in days.

However, Ealey(1967c) demonstrated that euro pouch young in the field can have a slower growth rate than captive animals under conditions of severe drought. The information gained from the present study on the Kangaroo Island Wallaby also indicates that in some years growth of pouch young may be retarded. This occurred in 1978 which began with a long, dry summer. However in normal years it seems that estimating the age of pouch young in the field is quite accurate.

For animals older than one year body measurements are no longer useful for aging purposes. By using the molar eruption sequence it is possible to establish the age of Kangaroo Island Wallabies in the field up to the eruption of the fourth molar which occurs between 5 and 6 years of age. An animal that is caught after the eruption of the fourth molar cannot be aged with this technique. Although there is variation in the age at which each eruption stage is first observed it is nevertheless possible to place animals within year-classes in the following ways. If a number of observations have been made on different occassions the "best fit" can be reliably determined. When only one observation is available the time of year when it was made can aid in placing the animal in the appropriate age-group. This is because the Kangaroo Island Wallaby has a strict seasonal breeding pattern so that age-classes are quite distinct (Andrewartha and Barker, 1969).

When applying tooth eruption data from captive animals to the field situation Sharman, Frith and Calaby (1964) observed what they considered was an excess of animals in the MI.1 and MII.1 stages. They assumed that these stages were of longer duration in field animals than the data on captive animals indicated. Variations in the timing of tooth eruption stages has also been observed in mule deer, *Odocoileus hemionus*, (Robinette, Jones, Rogers and Gashwiler, 1957) and Himalayan thar, *Hemitragus jemlahicus*, (Caughley, 1965). Despite this, Sharman, Frith and Calaby (1964), Ealey (1967c) and Shield (1968) concluded that the sequence of molar eruption provides a useful means of determining the ages of macropods in the field. This would also appear to be the case for the Kangaroo Island Wallaby.

Sharman, Frith and Calaby (1964) measured the forward progression of molars relative to the zygomatic process in red kangaroos but found there was some variablity in the position of the process in animals of the same age. Ealey (1967c) showed that in euros the movement of the molar row was directly related to the eruption of the molars but he did not relate molar progression directly to age beyond full tooth eruption. However he did relate molar progression to a dental wear pattern which was used to separate out age groups. Kirkpatrick (1964, 1965b) found that it was possible to measure the forward progression of the molars relative to the anterior border of the eye orbits, using either skulls or radiographs of living animals. Dudzinski, Newsome, Merchant and Bolton (1977) in a study on agile wallabies, *Macropus agilis* concluded that molar progression is more accurate than molar eruption for determining age because it is objective and has narrower confidence limits. However this method entails using skulls or obtaining radiographs of living animals. For a field study of a population of live animals, unless access to an X-ray apparatus is readily available, molar eruption remains the only method. Molar progression is useful in aging a series of skulls from animals that have died in the field or in constructing life-tables from animals obtained by shooting. Wilson (1975) used this method to construct life-tables for red kangaroos, grey kangaroos and wallaroos that were obtained by professional shooters. Molar progression in the Kangaroo Island Wallaby was linearly related to log age and could be used to age animals up to about 15 years. However, due to the small number of observations and the variation in ages of animals with the same molar index these results are provisional only.

The technique of using histological sections of incisors to count annual increments to dentine or cementum does not seem to have been investigated in macropods. It has been found useful in aging several species of ungulates, such as moose, *Alces alces*, (Sergeant and Pimlott, 1959), barren ground caribou, *Rangifer tarandus*, (McEwan, 1963), and deer of the genus *Odocoileus* (Low and Cowan, 1963; Gilbert, 1966; Lockard, 1972). Kingsmill (1962) found that sections of the incisors of brush-tailed possums (*Trichosurus vulpecula*) did not show regular annual rings although several age-classes could be recognized. Pekelharing (1970) showed that the age of possums could be determined by counting cementum layers in ground sections of molars. A single molar from a red-necked wallaby, *Macropus rufogrisea*, ground in the same way also showed layers in the cementum.

It was of interest to determine whether annual growth rings also occurred in the teeth of the Kangaroo

Island Wallaby. The first incisors and first molars of eight animals (5 M, 3 F) ranging in age from 1 - 14 years were examined using the sectioning technique of Lockard (1972) for incisors and the methods of Pekelharing (1970) for grinding, etching and staining molars.

For animals up to 4 years the number of layers could be correlated with the age of the animals using either method. In ground molars from older animals the layers were hard to distinguish while in the sections of incisors there were always fewer rings than the animal's age in years. This was because the outer rings were close together and could not be clearly resolved.

Thus it would seem that molar progression still remains the best method of aging macropods beyond the stage of full tooth eruption.

4.0 ASPECTS OF REPRODUCTION

4.1 INTRODUCTION

A knowledge of the reproductive characteristics of an animal plays an important part in understanding the population dynamics of that species.

A considerable amount of information is now available on the reproductive physiology of female macropod marsupials (reviewed by Tyndale-Biscoe, Hearn and Renfree, 1974). This includes the reproductive pattern of the female Kangaroo Island Wallaby which can be summarized as follows:

There is a well defined breeding season with most young being born in late January and early February (Andrewartha and Barker, 1969). There is a post-partum oestrus, and if conception occurs the embryo will develop only to the stage of a unilaminar blastocyst (Berger, 1966) and the corpus luteum also will become quiescent. If the pouch young is lost, or removed, between January and June the quiescent corpus luteum and blastocyst resume development and another young is born 26 - 27 days later (Renfree and Tyndale-Biscoe, 1973). Loss of the pouch young after June has no effect on the corpus luteum and blastocyst. Usually the first pouch young is reared successfully and remains in the pouch for 8 - 9 months (Murphy and Smith, 1970). During this time the mother is in lactational anoestrus (Berger and Sharman, 1969) which merges with the seasonal anoestrus from around June to December. The quiescent corpus luteum and blastocyst resume development a few days after the summer solstice in late December (Berger and Sharman, 1969; Renfree and Tyndale-Biscoe, 1973). Thus the cycle is completed by the birth of another pouch young about a month later. The slight decrease in daylength after the summer solstice is thought to be responsible for reactivating the blastocyst as Berger (1970) has shown that transferring wallabies to the northern hemisphere reversed their breeding cycle.

Investigations into the hormonal mechanisms controlling embryonic diapause in the Kangaroo Island Wallaby have shown that the pituitary is inhibiting the corpus luteum (Hearn, 1973, 1974). This inhibition is initiated and maintained by the suckling stimulus. Tyndale-Biscoe and Hawkins (1977) showed that prolactin appears to be the pituitary factor that is responsible for suppression of the corpus luteum during embryonic diapause.

Despite our knowledge of the female marsupial reproductive system there have been few studies on the male. The only male marsupials that have been studied in any detail are the dasyurid *Antechinus stuartii* (Woolley, 1966) and the brush-tailed possum (Gilmore, 1969). In the seasonally breeding brush-tailed possum Gilmore (1969) found that the testis and epididymis did not show any weight changes during the breeding season but the size of the prostate gland increased considerably.

For the macropods, field studies on sexual maturity in red kangaroos were made by Frith and Sharman (1964) and Newsome (1965c). Sadleir (1965) studied the euro and the red kangaroo in the arid Pilbara region of Western Australia but did not find any seasonal changes in testis weight, density of sperm and total number of sperm in the ejaculate. He assumed that males were fertile all the year round which correlated with the continuous breeding pattern of the females.

Hearn (1975) found no difference in testis, epididymis, prostate or Cowper's glands weights between the breeding and non-breeding season in male Kangaroo Island Wallabies in captivity. Although plasma gonadotrophin levels did not change during the year, after hypophysectomy they were undetectable and this was followed by shrinkage of the seminiferous tubules and a decline in weight of the accessory sex organs. Thus it seemed that the pituitary was necessary for maintenance of the testis but there was no seasonal cycle in the reproductive tract.

Because of the large seasonal changes observed in the accessory reproductive system of the brush-tailed possum by Gilmore (1969) the present study was designed to establish whether male Kangaroo Island Wallabies in their natural environment showed any seasonal reproductive cycle, and to determine the ages at which males and females reached sexual maturity.

4.2 MATERIALS AND METHODS

4.2.1 Collection of Samples

Animals were collected at 2-monthly intervals from May 1975 to April 1977. They were shot at night after they had emerged from scrub to feed on farmland.

Immediately after the animals had been shot blood samples were collected by cardiac puncture and kept on ice in heparinized centrifuge tubes until later, when they were centrifuged for collection of plasma. Plasma samples were stored frozen.

The right testis and epididymis, the prostate gland

and the three pairs of Cowper's glands were dissected out and fixed in formol-acetic-80% alcohol (1: 1: 18 v/v) and later stored in 80% alcohol.

Body weights were measured and the teeth examined for age determination.

Testis biopsies and measurements of the right testis diameter within the scrotal sac were performed on live animals caught in Flinders Chase National Park.

4.2.2 Histology

The testis and epididymis, prostate gland and paired Cowper's glands were weighed and small pieces dissected out for histological examination.

Tissue for histology was dehydrated via graded alcohols, cleared in benzene and embedded in paraffin wax. Sections were cut at 7 µm and routinely stained with Ehrlich's Haematoxylin and Eosin.

The Periodic acid-Schiffs reaction, following the method of Drury and Wallington (1967), was used to detect the presence of mucopolysaccharides in prostate and Cowper's gland tissue.

Measurements of testis tubule diameters were made with a calibrated micrometer eyepiece.

4.2.3 Testosterone Assay

Plasma testosterone was assayed by a radio-immunoassay procedure using polyethylene glycol 6000 for precipitation of the bound steroid. Samples of wallaby plasma (50 - 100 µl) were extracted with ether: ethyl acetate (1:1) and the amount of testosterone in the extract measured when compared to standards extracted from an equal quantity of hormone-free wallaby plasma. The antiserum was raised in sheep to testosterone-3-(o-carboxymethyl) oxine conjugated to bovine serum albumin. The dilution of the antiserum was 1:20,000. The antiserum was obtained from Dr. R.I. Cox Division of Animal Physiology, C.S.I.R.O. The antiserum cross-reactivity to other steroids is shown in Table 4.1.

TABLE 4.1

TESTOSTERONE ANTISERA SPECIFICITY

Steroid	% Cross-reactivity Sheep 6050 17.6.76
Testosterone (17*B*-hydroxy-4-androsten-3-one)	100
Epitestosterone (17*α*-hydroxy-4-androsten-3-one)	0.11
Etiocholanolone (5*B*-androstan-3*α*-ol-17-one)	0.10
Androsterone (5*α*-androstan-3*α*-ol-17-one)	0.02
Androstenedione (4-androsten-3,17-dione)	1.3
Dehydroepiandrosterone (5-androsten-3*B*-ol-17-one)	<0.01
5*α*-dihydrotestosterone (5*α*-androstan-17*B*-ol-3-one)	31
4-androsten-17*B*,19-diol-3-one	3.5
4-androsten-3*B*,17*B*-diol	30
Progesterone (4-pregnene-3,20-dione)	0.004
17*α*-hydroxyprogesterone (4-pregnene-17*α*-ol-3,20-dione)	<0.003
Pregnenolone (5-pregnen-3*B*-ol-20-one)	0.004
17*α*-hydroxypregnenolone (5-pregnen-3*B*,17*α*-diol-20-one)	<0.003
Cortisol (4-pregnene-11*B*,17*α*,21-triol-3,20-dione)	<0.003
Oestrone (1,3,5(10)oestratrien-3*B*-ol-17-one)	<0.003
Oestradiol-17*B*(1,3,5(10)oestratrien-3*B*,17*B*-diol)	0.10
Oestriol (1,3,5(10)oestratrien-3*B*,16*α*,17*B*-triol)	<0.003

4.2.4 N-Acetylglucosamine Assay from Prostate Tissue

The concentration of N-acetylglucosamine in prostate gland tissue and secretion was assayed by the following method.

Frozen glands were partially thawed and divided into two by a dorsi-ventral cut along the length of the urethra. Frozen fluid secretion was recovered from the urethral lumen when possible and extracted. A cross-sectional slice of the central prostatic segment was then taken, exluding the outer urethral muscle coat. Both secretion and tissue were weighed and then homogenized following the method of Rodger and White (1974) except that the tissue was homogenized in ice cold 2N Perchloric acid at an approximate dilution of 1 gm/30 ml. The deproteinized homogenates were left standing at iced water temperature for at least 30 minutes, centrifuged and the supernatant neutralized by the addition of solid potassium bicarbonate. The neutralized extracts were stored frozen and then assayed by the Modified Morgan-Elson method for N-acetylglucosamine (Reissig, Strominger and Leloir, 1955).

4.3 <u>RESULTS</u>

4.3.1 Sexual Maturity of Males

Male Kangaroo Island Wallabies reached sexual maturity at around 18 - 20 months of age when rapid growth of the testes occurred (Figure 4.1).

Testis weight increased with body weight and age (Figure 4.2) although after 3 years of age the testis weight remained fairly constant.

Spermatogenesis began at around 18 months of age ·

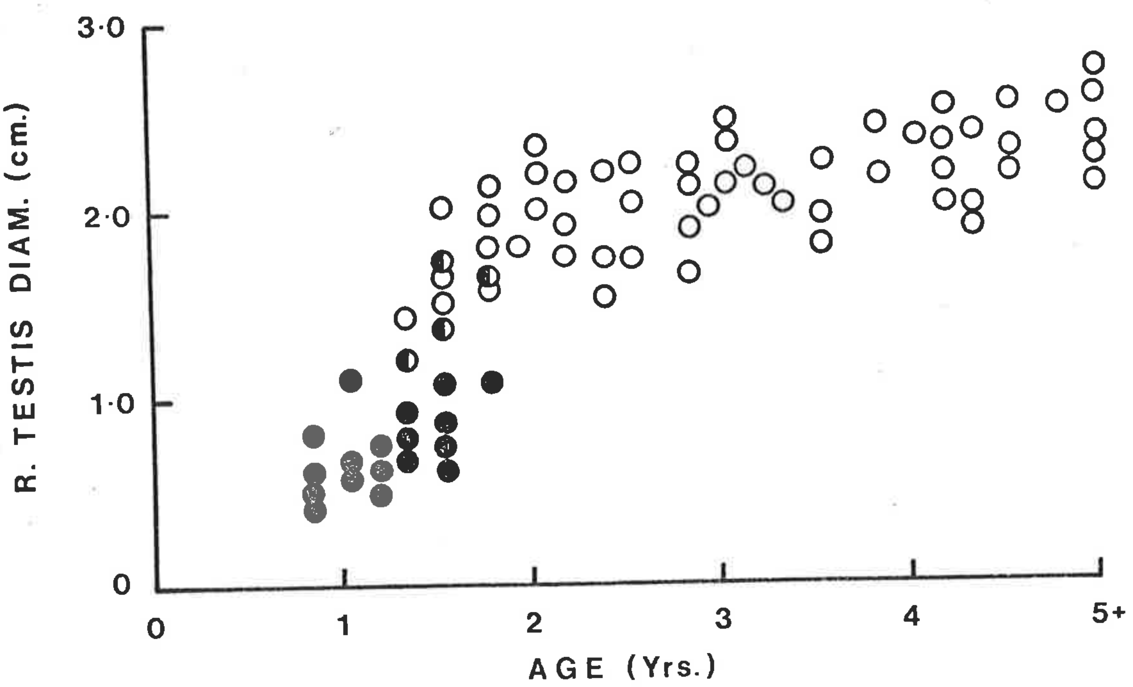


Figure 4.1 Measurements of right testis diameter within the scrotal sac of live animals.
Open circles represent open tubules with sperm present.
Half-open circles represent partly open tubules where spermatogenesis has begun.
Closed circles represent closed tubules with no sperm.

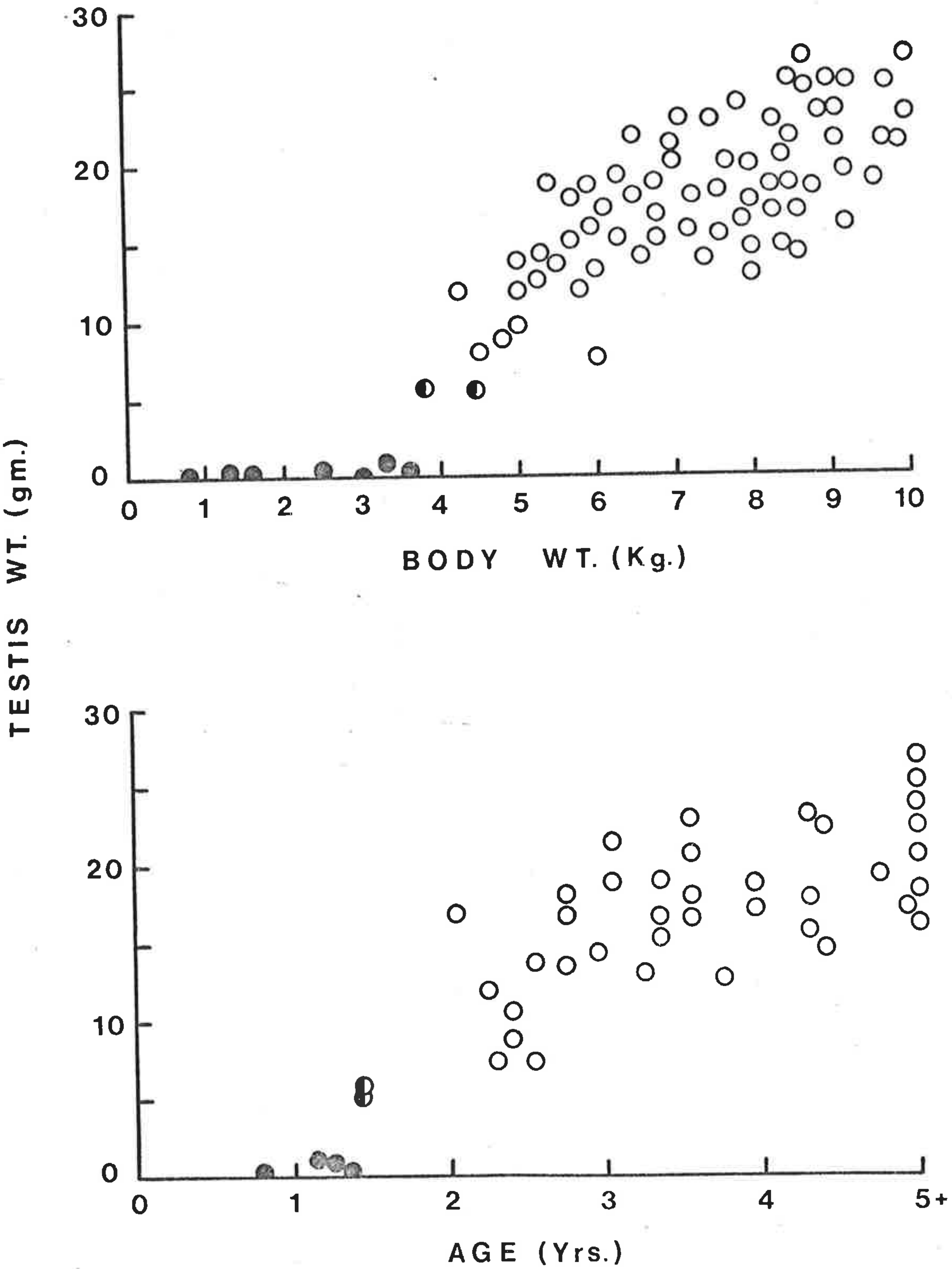


Figure 4.2 Relationship between testis weight and body weight (top figure), and age (bottom figure). Symbols as for Figure 4.1.

when the seminiferous tubules increased in diameter and developed a lumen (Figure 4.3). By 2 years of age the seminiferous tubules were fully open and contained spermatozoa. The diameter of the tubules showed virtually no further increase after 2 years of age.

4.3.2 Seasonal Changes

Analysis of Results

To test for significant seasonal changes in the reproductive organs and testosterone assay, each set of data was analysed by means of a one-way Analysis of Variance. The results of these tests are summarized in Table 4.2.

Testis and Epididymis

There were no seasonal changes in testis weight, testis tubule diameter or epididymis weight ($P > 0.05$) (Figure 4.4). Spermatogenesis occurred throughout the year and sperm were always present in the testis tubules and epididymis.

Accessory Reproductive Organs

The only accessory sex glands are the prostate and three pairs of Cowper's glands. The anatomy, histology and histochemistry of the accessory reproductive glands of several species of male marsupials has been described by Rodger and Hughes (1973).

(a) Prostate Gland

The prostate gland (Figure 4.5) of the Kangaroo Island Wallaby is carrot-shaped and located at the posterior end of the body cavity within the pelvic region. The gland consists of glandular tissue surrounded by the smooth muscle coat of the membranous urethra. The vasa deferentia enter at the anterior end of the gland just below where the bladder

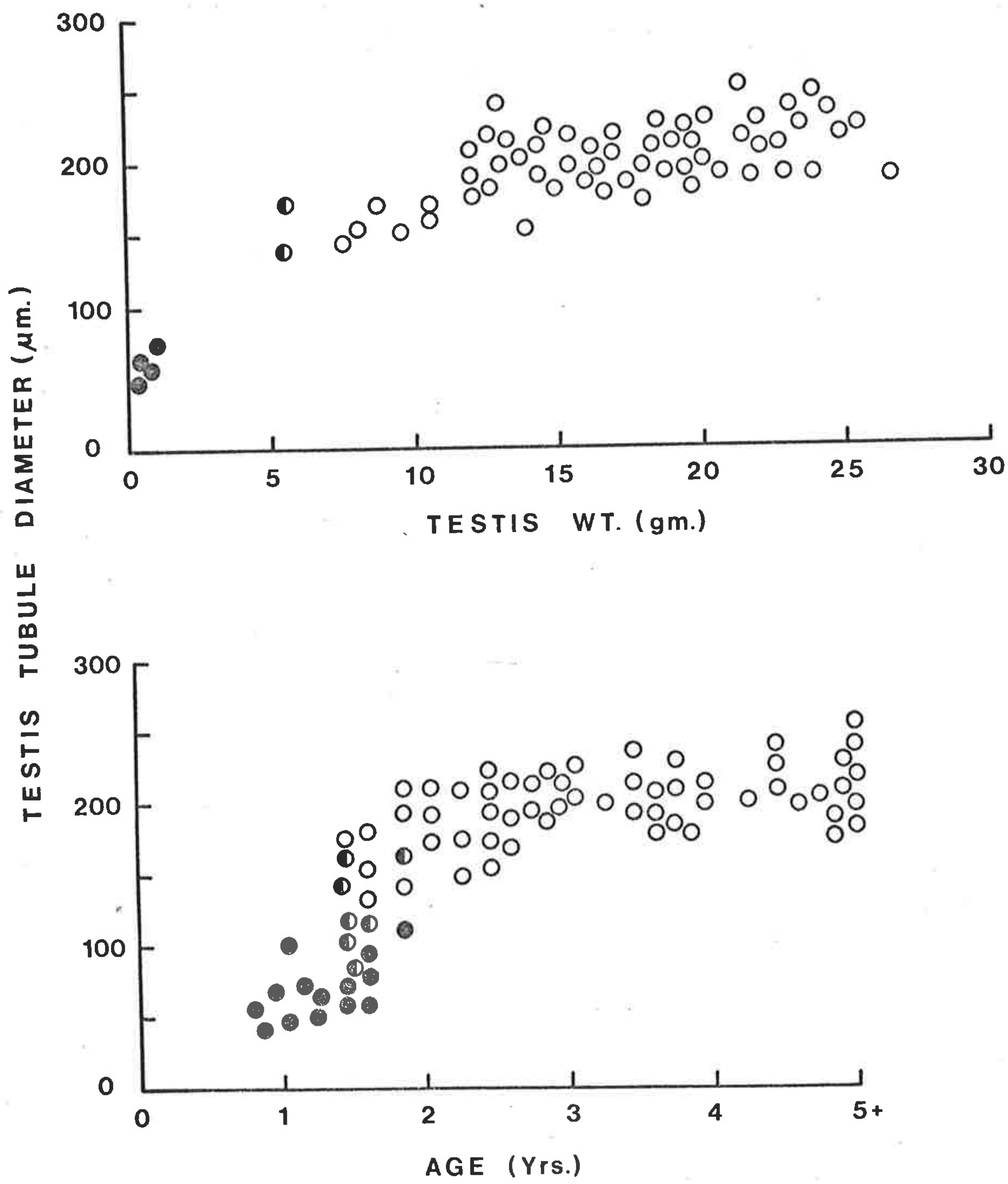


Figure 4.3 Relationship between testis tubule diameter and testis weight (top figure), and age (bottom figure).
Symbols as for Figure 4.1.

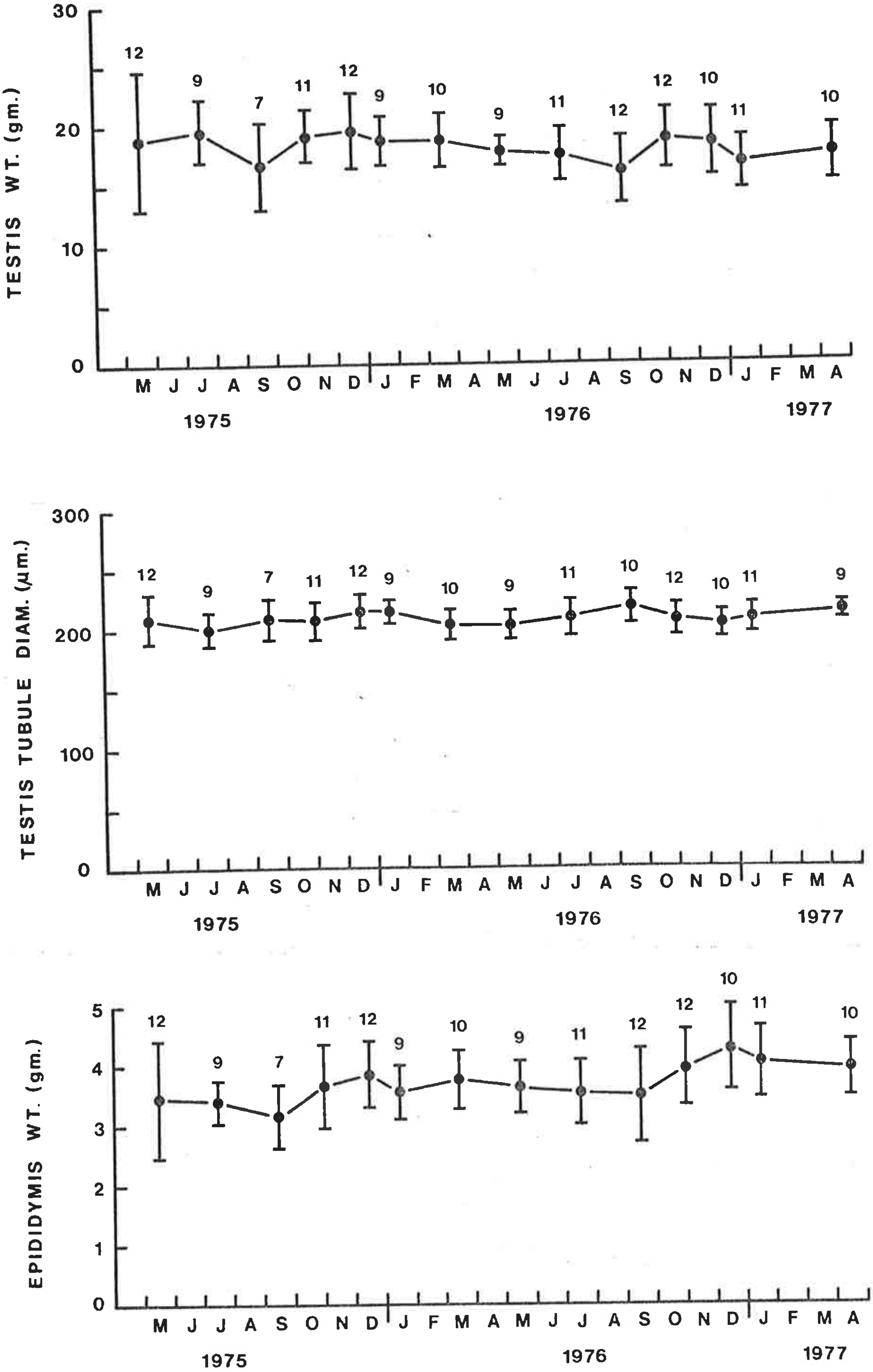


Figure 4.4 Mean values (dots) and standard deviations about the means (vertical lines) for testis weight, testis tubule diameter and epididymis weight of sexually mature wallabies.
Numbers above vertical lines represent the sample size.

Figure 4.5 Prostate glands taken from male Kangaroo Island Wallabies, in the breeding season (left) and the non-breeding season (right).

TABLE 4.2 ANALYSIS OF VARIANCE FOR SEASONAL CHANGES IN MALE REPRODUCTIVE ORGANS AND PLASMA TESTOSTERONE LEVELS

	*1975 - 1976	1976 - 1977
Testis Wt. (gm)	$F_{(7,72)}$ = 0.400 [+]N.S.	$F_{(6,68)}$ = 1.694 N.S.
Testis Tubule Diam. (μm)	$F_{(7,72)}$ = 1.238 N.S.	$F_{(6,66)}$ = 2.024 N.S.
Epididymis Wt. (gm)	$F_{(7,72)}$ = 1.273 N.S.	$F_{(6,68)}$ = 1.010 N.S.
Prostate Gland Wt. (gm)	$F_{(7,72)}$ = 28.797 $P<0.001$	$F_{(6,68)}$ = 16.528 $P<0.001$
Cowper's Glands Wt. (gm)	$F_{(5,44)}$ = 8.026 $P<0.001$	$F_{(6.60)}$ = 6.461 $P<0.001$
Testosterone Conc. (ng/ml)	$F_{(4,41)}$ = 17.555 $P<0.001$	$F_{(6,49)}$ = 6.366 $P<0.001$

* For Testis Weight, Testis Tubule Diameter, Epididymis Weight and Prostate Gland Weight the analysis of results for the two years was from May 1975 to May 1976, and May 1976 to April 1977.

For Cowper's Glands Weight analysis was from September 1975 to May 1976 and May 1976 to April 1977.

For Testosterone Concentration analysis was from October 1975 to May 1976 and May 1976 to April 1977.

\+ N.S. = Not significant at 5% level.

and the ureters join the urethra.

The gland can be divided into three segments, referred to as anterior, central and posterior segments. These segments can be discerned macroscopically and they differ in their histology and histochemistry. In each segment the glandular tissue consists of numerous simple branched tubules supported by connective tissue. The tubules radiate out from the central urethral lumen to which they are joined by short collecting ducts. The tubules are lined by a single layer of epithelial cells which vary in size and histochemistry between the different segments.

The size of the prostate gland showed a significant ($P < 0.001$) seasonal change, with two peaks (Figure 4.6). The first peak occurred at the end of October and the other was in the breeding season in late January.

To determine whether all three segments increased by the same proportion each segment was dissected out from prostate glands in the breeding and non-breeding seasons. The anterior segment, which is the smallest, doubled in size in the breeding season while both the central and posterior segments showed a five-fold increase in size (Table 4.3).

The size and appearance of the tubules in each segment also changed between the breeding and non-breeding season. In the non-breeding season the tubules appeared to be smaller in diameter and the height of the epithelium lining the tubules was reduced (Figure 4.7). However the PAS reaction showed that mucopolysaccharides were present throughout the year.

The major free sugar produced by the prostate gland

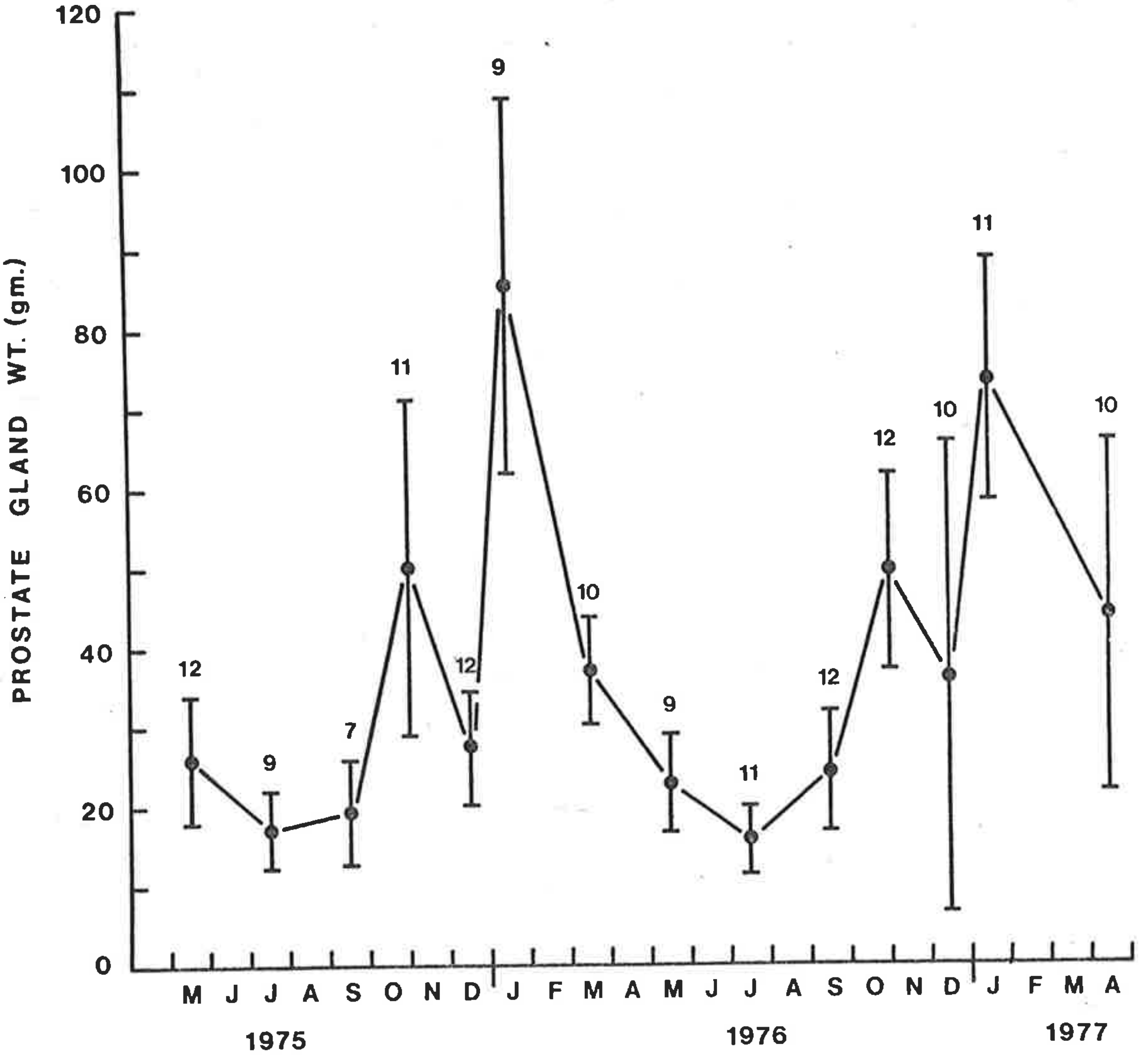


Figure 4.6 Seasonal changes in the size of the prostate gland of sexually mature wallabies. Symbols as for Figure 4.4.

TABLE 4.3

SEASONAL CHANGES IN THE WEIGHT

OF PROSTATE GLAND SEGMENTS (gm).

Gland Segment	Time of Year July 1976	 January 1977
	(N = 11)	(N = 11)
Anterior	1.35 ± 0.32 (0.78 - 1.99)	3.06 ± 0.91 (1.96 - 4.93)
Central	8.06 ± 2.46 (5.30 - 14.34)	41.11 ± 8.37 (27.04 - 53.01)
Posterior	6.04 ± 2.13 (4.02 - 11.72)	29.02 ± 8.38 (15.58 - 43.44)

Values are means ± standard deviation.

Ranges are presented in parentheses.

TABLE 4.4

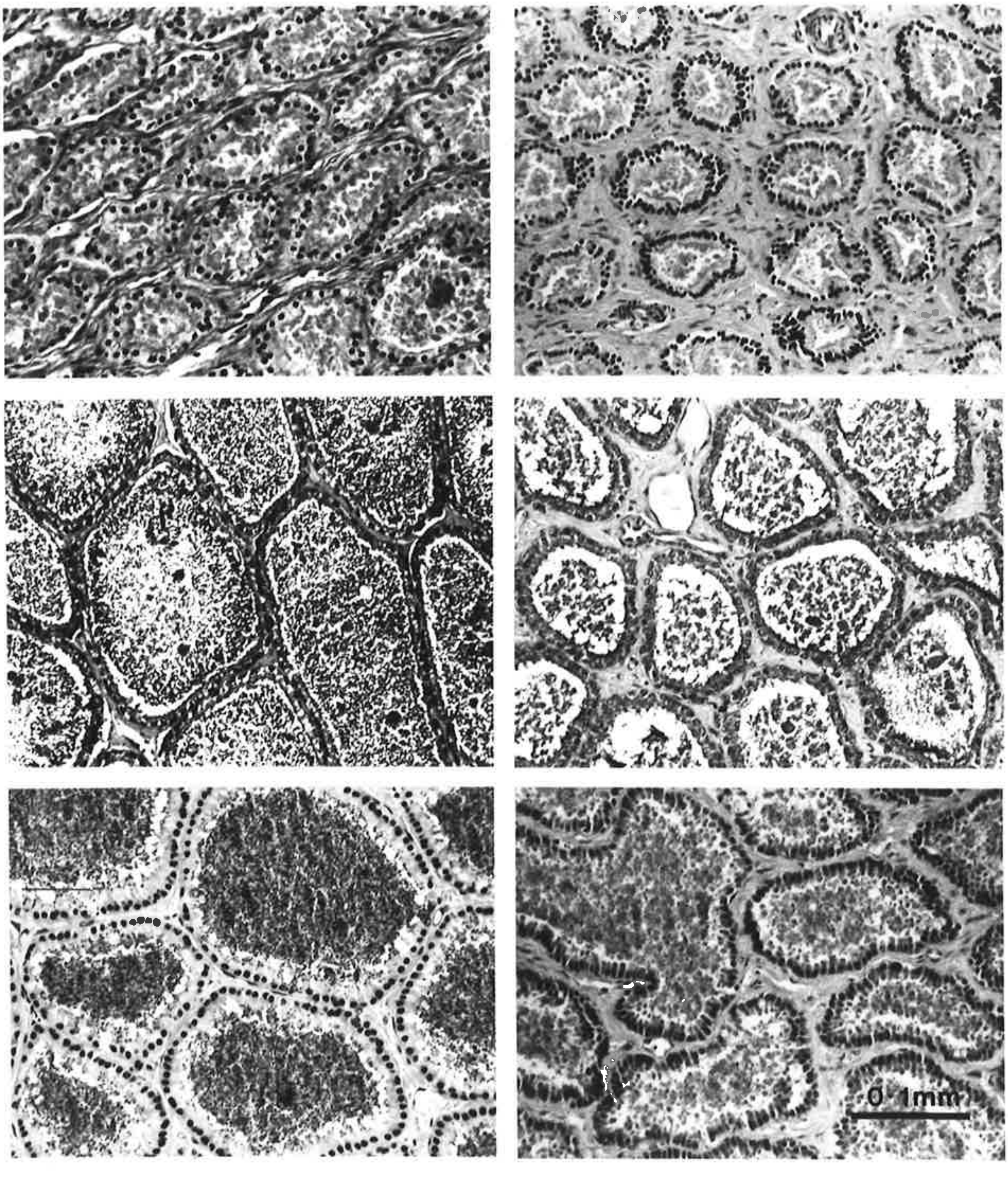
N-ACETYLGLUCOSAMINE CONCENTRATION IN PROSTATE

GLAND TISSUE AND SECRETION (mg/100gm)

Time of Year	Mean ± Standard Deviation	Range	N
January 1976	C.P. 601.4 ± 245.0	309 - 917	5
	S 506.5 ± 239.0	204 - 732	4
May 1976	C.P. 383.6 ± 99.4	253 - 522	5
	S 642.0 ± 200.8	327 - 840	5
September 1976	C.P. 545.4 ± 182.5	389 - 843	5
	S 444.0 ± 126.5	335 - 574	4

C.P. = A cross-sectional slice of central prostatic segment, excluding outer urethral muscle coat.
S = Fluid secretion recovered from the urethral lumen.
$F_{(2,12)}$ = 1.859, not significant at 5% level (Central Prostate Tissue).
$F_{(2,10)}$ = 1.227, not significant at 5% level (Fluid Secretion).

Figure 4.7 Changes in the histology of the three segments of the prostate gland between the breeding season (left) and the non-breeding season (right).
Top figures are the anterior segment, central figures are the central segment and the bottom figures the posterior segment.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of macropods is N-acetylglucosamine, occurring mainly in the central segment. The analysis of central prostate segment tissue and secretion for N-acetylglucosamine did not show any significant seasonal changes in concentration ($P>0.05$) (Table 4.4). However, because of the seasonal change in size, the total amount of secretion produced would increase during the breeding season.

(b) Cowper's Glands

The three pairs of Cowper's glands in the wallaby are located posterior to and on either side of the prostate gland. The glands are bulbous structures and are joined to the base of the urethra by ducts. The glands consist of numerous tubules, lined with columnar epithelium, and surrounded by a striated muscle coat.

The Cowper's glands were not separated but weighed as one structure. There was a significant seasonal change in weight ($P<.001$) (Figure 4.8) similar to that shown by the prostate gland. There was some difference between 1975 and 1976 however. In 1976, although the weight of the glands increased in October there was no decline in weight in December, as was shown in 1975.

Only the largest of the Cowper's glands was examined histologically. It showed similar changes to the prostate gland in that the tubules were larger in cross-section in the breeding season. Mucopolysaccharides were present throughout the year.

Testosterone Concentration

Despite large variation between animals the mean concentration of testosterone was elevated in the breeding

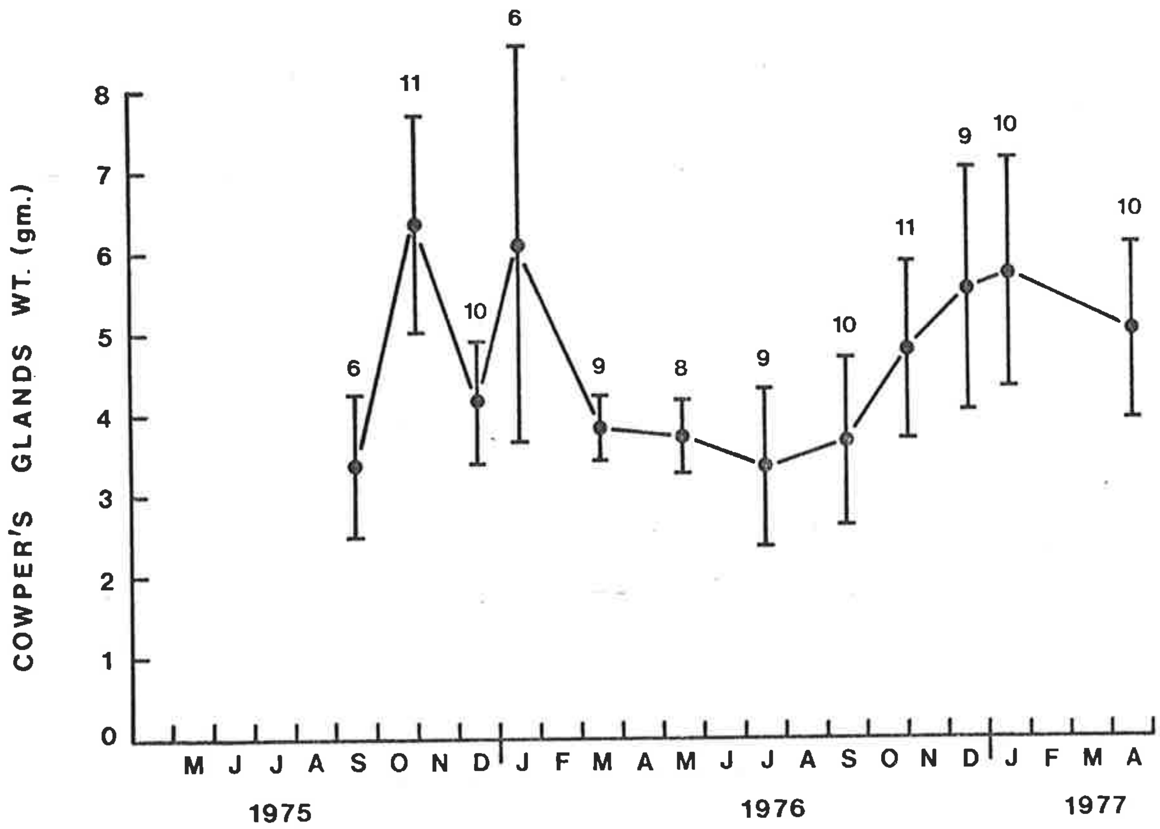


Figure 4.8 Seasonal changes in the weight of the Cowper's Glands of sexually mature wallabies. Symbols as for Figure 4.4.

season (Figure 4.9). However a double peak in concentration was not as evident for testosterone as was shown by prostate gland weight.

There was a significant correlation between prostate gland weight (in the breeding season) and testosterone concentration (Figure 4.10).

4.4 DISCUSSION

The results show that male Kangaroo Island Wallabies in the wild have a seasonal cycle in their accessory reproductive organs and in plasma testosterone concentration. The size of the testis and epididymis do not change seasonally and spermatozoa were produced in the testis throughout the year. Catt (1977) has shown that a similar increase in prostate gland size in the breeding season occurs in Bennett's Wallaby (*Macropus rufogrisea frutica*).

Testis function is controlled by a system involving the hypothalamic secretion of luteinizing hormone releasing hormone (LH-RH) and the anterior pituitary hormones, follicle stimulating hormone (FSH) and luteinizing hormone (LH). Although there was no seasonal change in testis weight, Hearn (1975) showed that in captive Kangaroo Island Wallabies normal testicular function was disrupted following hypophysectomy. This suggested that normally FSH is maintaining spermatogenesis throughout the year. Receptors for FSH have been demonstrated within the seminiferous epithelium of the rat (Means and Vaitukaitis, 1972) and it is likely that the Sertoli cell is the site of action of this hormone (Castro, Alonso and Mancini, 1972; Means and Huckins, 1974).

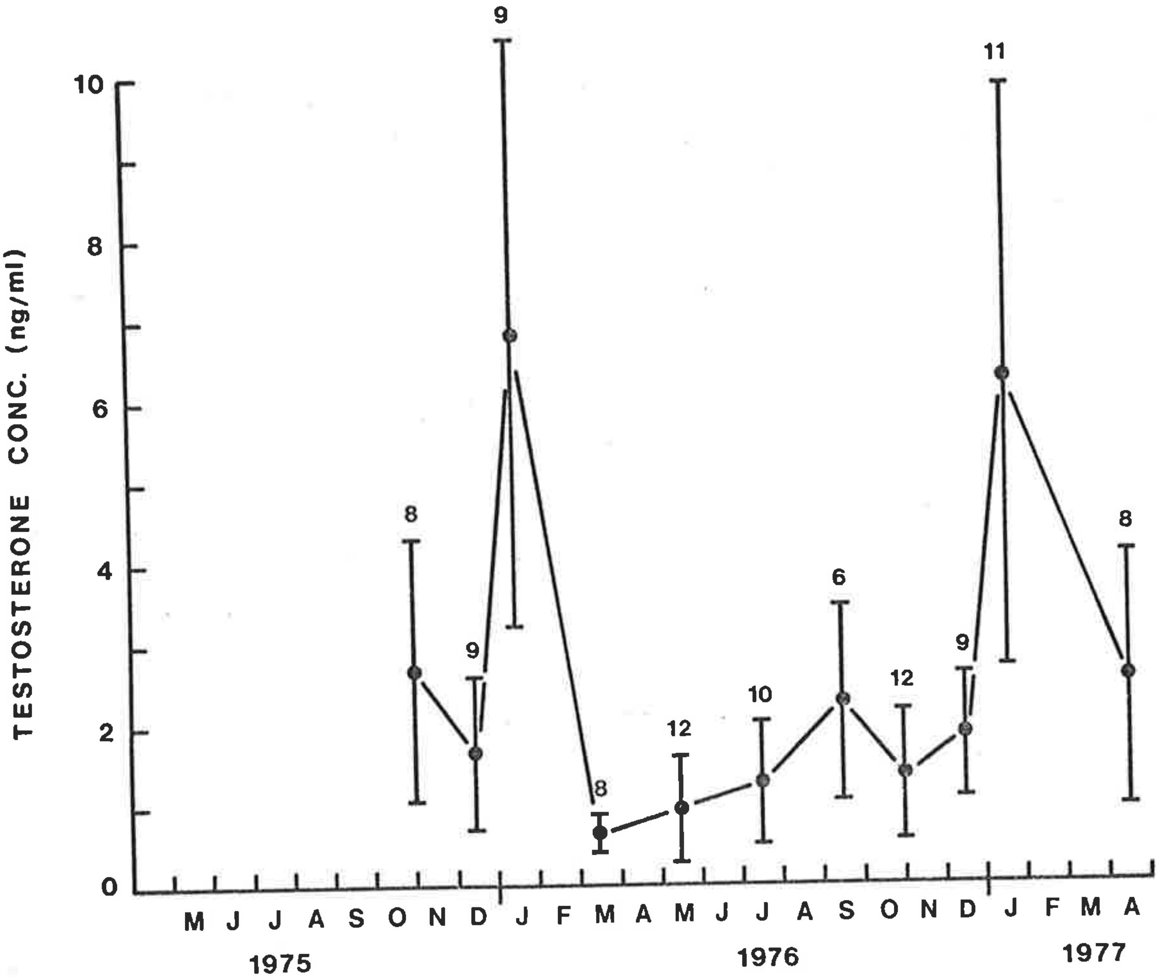


Figure 4.9 Seasonal changes in the concentration of testosterone in the peripheral plasma of sexually mature wallabies. Symbols as for Figure 4.4.

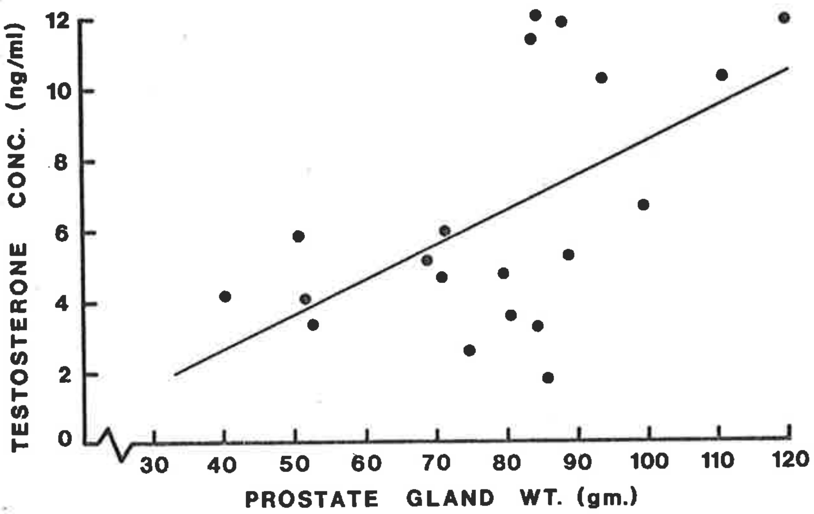


Figure 4.10 Relationship between weight of the prostate gland (in the breeding season) and testosterone concentration.

Testosterone Conc.(ng/ml)=0.098 Prostate Gland Wt(gm)-1.284

(r = .562, sig. at 1% level, N = 20)

The seasonal cycle in the accessory glands and testosterone concentration indicated that LH levels may also fluctuate seasonally. Receptors for LH exist on the interstitial cells of the rat testis (de Kretser, Catt and Paulsen, 1971) and can be stimulated by LH from a number of mammalian species resulting in testosterone secretion *in vitro* (Catt, Tsuruhara, Mendelson, Kietelslegers and Dufau, 1974). Lincoln (1978) showed that injection of LH-RH induced a rapid and substantial increase in the level of testosterone in five species of macropod marsupial, including the Kangaroo Island Wallaby. Thus release of LH during the breeding season would cause the interstitial cells of the testis to secrete testosterone which in turn would act on the accessory reproductive system. Recent work by Catling and Sutherland (in press) has confirmed that males in contact with sexually mature females in the breeding season showed a significant increase in plasma LH and testosterone, whereas males isolated from females did not show this increase. Levels of FSH did not change in either group in the breeding season.

Cook, McDonald and Gibson (1978) suggested that in the brush-tailed possum the complex of arteries and veins surrounding the urethra and radiating into the body of the prostate gland might be capable of transferring androgens carried from the epididymis to the urethra into the prostatic tissue. Anderson and Liao (1968) suggested that in rats the nuclear chromatin of prostate cells contains an androgen receptor which can selectively retain dihydrotestosterone.

Another of the interesting aspects of the seasonal changes in accessory reproductive organs was the double peak in activity, one at the end of October and the other in January during the normal breeding season. This indicated that some sexual activity was occurring around October - November before the main breeding season had begun. At this time of the year young animals are just leaving the pouch and thus it was possible that the young females could be entering oestrus. Tyndale-Biscoe and Hawkins (1977) have observed young females entering oestrus in October and reported that of a sample of nine juveniles collected on Kangaroo Island in December, seven had ovulated and had a quiescent corpus luteum and four had a blastocyst. This was confirmed by the present study when the reproductive systems of eight juvenile females were collected in early December 1977. All the females had a corpus luteum present in one ovary and from six animals a blastocyst was recovered from the uterus.

Hence it appears that young females that have just left the pouch in October - November enter oestrus immediately, mate, and the blastocyst resulting from this mating remains dormant until just after the summer solstice, when the blastocysts in older animals start to develop.

It is probable that it is the presence of oestrous females that stimulates sexual activity in the males and that this may be due to a pheromome. The lack of any changes in the reproductive system of male Kangaroo Island Wallabies observed by Hearn (1975) may have been due to keeping males separate from females.

In summary, the male Kangaroo Island Wallaby does have a seasonal reproductive cycle which appears to be influenced by the presence of oestrous females. Release of LH-RH from the hypothalamus, due to the action of a pheromone, would stimulate release of LH from the anterior pituitary. This in turn acts on the interstitial cells of the testis to secrete testosterone which causes the increase in size and activity of the accessory reproductive organs.

5.0 HOME-RANGE AND MOVEMENT PATTERNS

5.1 INTRODUCTION

Initial observations on the movements of wallabies onto the cleared area surrounding the Park Ranger's Head-quarters suggested that there were four main groups, or populations (Figure 5.1). Each of these groups utilized a different part of the cleared area as a feeding site. These divisions were particularly obvious when trying to capture wallabies at night. Individuals from the different groups could not be forced beyond a certain distance from their point of entry to the feeding area. For the population study the only capture records analysed were of the animals using the Main Study Area (Figure 5.2).

It was important to ensure that these animals did belong to a single population because any widespread dispersal, either temporarily or permanently, once they had re-entered the scrub would affect the estimates of population size. It was therefore necessary to determine the extent of both the daily and seasonal movements of individuals. This would show whether or not these wallabies occupied a distinct home-range, and if so, their size and the amount of overlap with other home-ranges.

Burt (1943) defined home-range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young,". The concept of home-range is thus distinguished from a territory which is regarded as a defended area or object (Howard, 1920). Areas of heavy and regular use within a home-range or territory may be called core-areas (Kaufmann, 1962).

Radio-tracking has become widely used in recent years

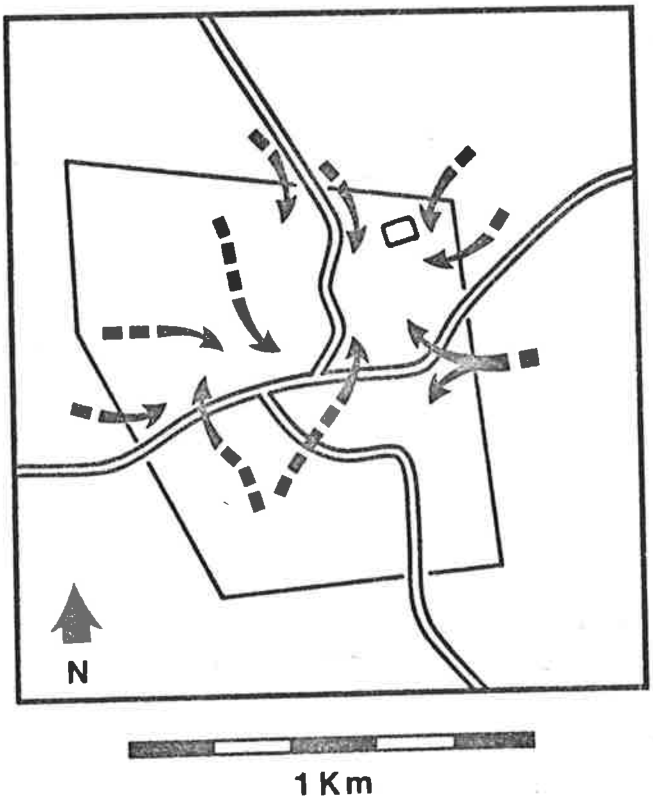


Figure 5.1 The main movement patterns of wallabies entering the cleared area from the surrounding scrub.

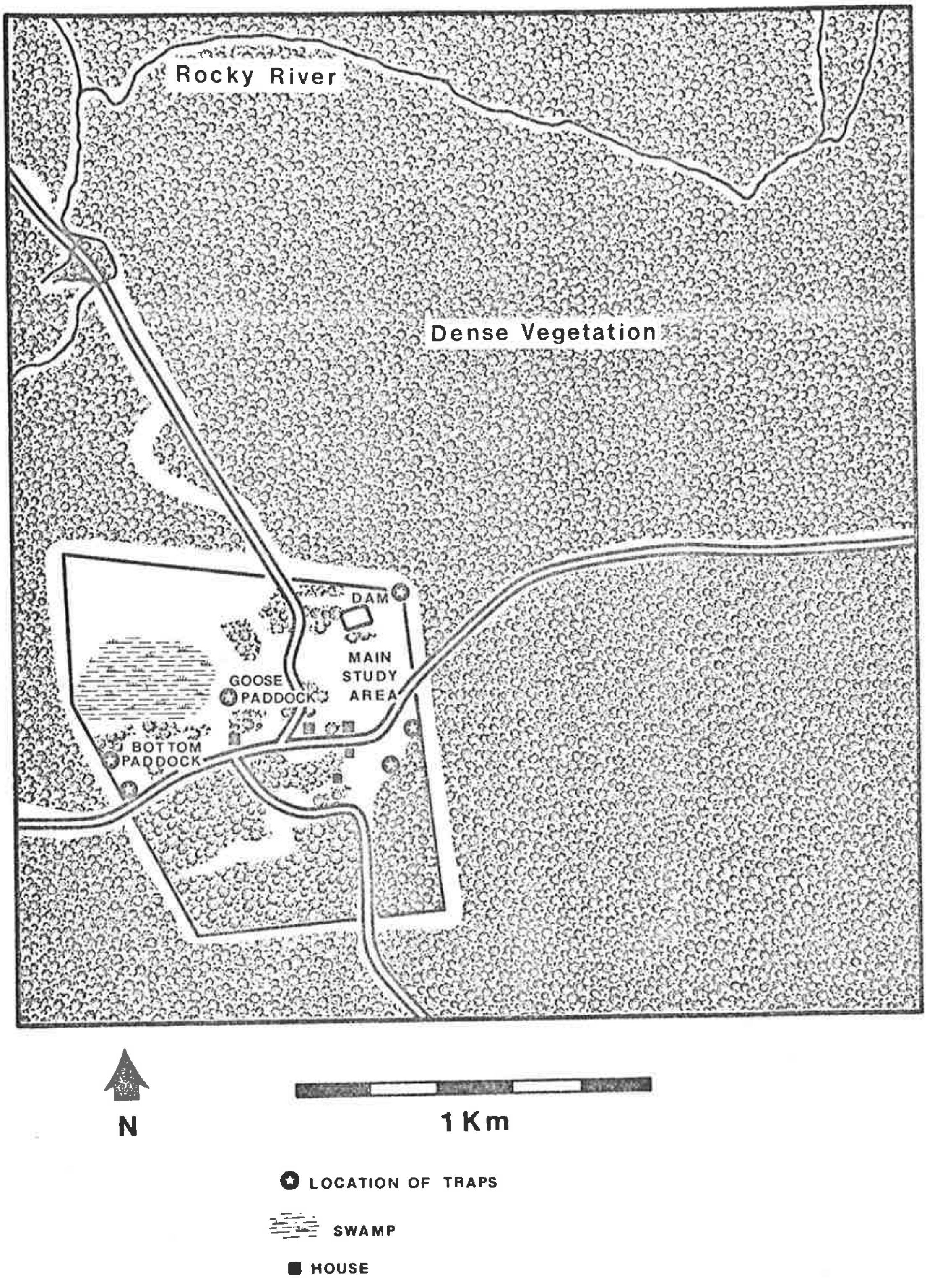


Figure 5.2 The Study Area in Flinders Chase National Park showing distribution of the vegetation and the location of trap-sites.

for studying the movements of animals. It is particularly useful for timid species or those inhabiting areas of dense vegetation. This was the case in the present study as the wariness of the wallabies within the thick scrub made visual observations particularly difficult. Hence to obtain the information on home-ranges and movement patterns radio-transmitters were used.

5.2 RESULTS

5.2.1 Activity and Movement Patterns

Sixteen individuals (8 M, 8 F) were radio-tracked for varying periods of time from December 1976 to July 1978. A summary of the time periods over which each wallaby carried a radio-transmitter, and the number of radio-locations made, are shown in Tables 5.1 and 5.2. A more complete history for each animal is presented in Appendix III.

Although radio-locations were only taken about every four hours over a period of three days some indication of the activity and movement patterns of the wallabies at different times of the year was obtained. The winter measurements were made from May to November while the summer measurements were from December to March, although in 1978 early April was included in the summer group because of the dry conditions. Maps showing the daily movement pattern of each wallaby during the periods of radio-tracking are shown in Appendix IV.

Winter Movements

In winter the movement patterns for the different individuals were similar. During the day there was little activity until the late afternoon when the wallabies began to

TABLE 5.1 TIME PERIODS OVER WHICH RADIO-TRANSMITTERS WERE CARRIED AND THE NUMBER OF MEASUREMENTS OF POSITION FOR MALE WALLABIES

Animal	Transmitter Type	Dates For Which Transmitter Was Carried	Number Days Transmitter Was Carried	Number Of Hours Over Which Observations Were Made	Number Of Measurements Of Position
	U.A.	7/12/76 - 9/12/76	3	58	25
1	C.S.I.R.O.	13/ 4/77 - 8/11/77	210	394	45
	A.V.M.	30/ 1/78 -		236	53
2	C.S.I.R.O.	7/ 4/77 - 5/11/77	213	254	18
	A.V.M.	12/12/77 - 12/ 7/78	213	271	69
3	C.S.I.R.O.	9/ 4/77 - 3/11/77	209	479	54
4	A.V.M.	12/12/77 -		299	73
5	A.V.M.	12/12/77 - Sept.'78	approx. 263+	144	38
6	A.V.M.	12/12/77 -		83	17
7	A.V.M.	25/ 1/78 -		144	38
8	A.V.M.	1/ 2/78 -		164	41

+ = Transmitter was recovered from dead animal September 1978.
U.A. = Transmitter made by Mr. N. Weste, Electrical Engineering Dept., University of Adelaide.
C.S.I.R.O. = Transmitters made by Mr. K. Newgrain, Division of Wildlife Research, C.S.I.R.O.
A.V.M. = Transmitters purchased from A.V.M. Instrument Company, Champaign, Illinois, U.S.A.

TABLE 5.2 TIME PERIODS OVER WHICH RADIO-TRANSMITTERS WERE CARRIED AND THE NUMBER OF MEASUREMENTS OF POSITION FOR FEMALE WALLABIES

Animal	Transmitter Type	Dates For Which Transmitter Was Carried	Number Days Transmitter Was Carried	Number Of Hours Over Which Observations Were Made	Number Of Measurements Of Position
1	C.S.I.R.O.	6/ 4/77 - 13/ 8/77	130	466	52
2	C.S.I.R.O.	7/ 4/77 - 2/11/77	210	446	39
	A.V.M.	25/ 1/78 - 11/ 7/78	168	144	38
3	C.S.I.R.O.	7/ 4/77 - 4/ 8/77	120	422	42
	A.V.M.	12/12/77 - 11/ 7/78	212	271	69
4	C.S.I.R.O.	7/ 4/77 - +		224	11
5	A.V.M.	12/12/77 -		227	56
6	A.V.M.	13/12/77 - 10/ 7/78	210	227	56
7	A.V.M.	1/ 2/78 -		163	41
8	A.V.M.	8/ 5/78 -		44	12

\+ Transmitter recovered from scrub, September, 1978.

move towards the edge of the scrub surrounding the Main Study Area. Just after dark they emerged from the scrub to feed. The time spent out on the feeding area varied a great deal between individuals although the early evening seemed to be the time of greatest activity.

To assess the activity pattern of wallabies feeding on the Main Study Area spot-light counts were made every hour over two consecutive nights for May and July. Although individual animals could not be followed the results do indicate the general pattern of feeding activity (Figure 5.3). No wallabies were seen out during the day but just after dark large numbers emerged from the scrub. The maximum number was observed from around 2000 hrs to 2400 hrs. From 0100 hrs to 0200 hrs the activity began to decline so that by dawn all the animals had returned to the scrub. Packer (1965) recorded the movement of quokkas through gates in a fence-line surrounding an area of food and water. There was a bimodal activity cycle with the greatest amount of movement just after sunset and just before dawn.

The effect of windy weather conditions on activity was observed on the second night of observation in July. Throughout the day there was a strong south-westerly wind which eventually stopped at around 2200 hrs. Few wallabies emerged from the scrub until after the wind had dropped. More wallabies were observed out feeding in the early morning than on any other night probably because the weather conditions had prevented them from feeding any earlier.

Although no quantitative data was obtained on the effect of other climatic conditions on activity it was

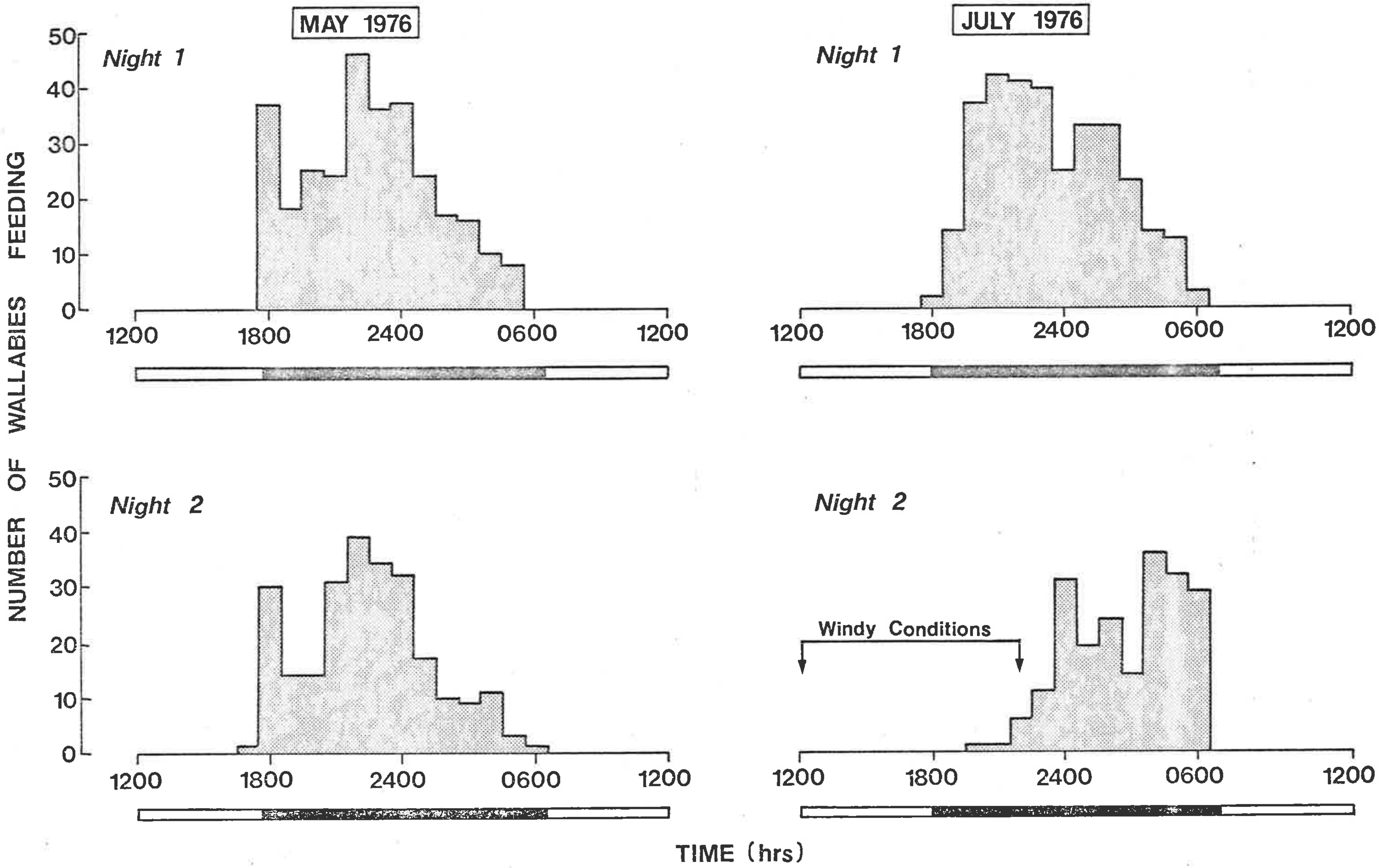


Figure 5.3 Pattern of feeding activity of wallabies on the Main Study Area.

observed that while light rain did not alter the pattern of feeding activity heavy rain did deter them. During wet, windy conditions wallabies were often observed sheltering under bushes along the edge of the cleared area.

Summer Movements

Activity on the feeding area was not recorded during summer but it was noticed that fewer wallabies were present, and this was confirmed by the movements of animals with transmitters. Many of these animals did not emerge from the scrub at all during the three days of radio-tracking observations. However, within the scrub there was more activity during the day than in winter and they moved over longer distances. An example of this was shown by Male 1 which was located several times in the vicinity of the Rocky River. This is approximately 1400 m from the centre of the animal's winter home-range.

Movements out of the Study Area

None of the animals that were radio-tracked were ever observed to move completely away from the Main Study Area or to permanently change the location of their home-range. However, one animal, Female 2, did show a shift in its main activity pattern in summer. This animal was from the 1973 cohort and was first captured on the Main Study Area in November 1975. In May 1977, when first radio-tracked, all locations were on the northern side of the main road leading into the study area. In the following summer the major part of its activity was on the southern side of the road. Another animal, Male 3, was first caught in the Goose Paddock in May 1976 when it was about 16 months of age. Two days later it was caught on the Main Study Area and was subsequently only caught there. It was first radio-tracked in April 1977 during its second year out of the pouch and it remained within a well defined home-range for the rest of the study. All other young animals which were radio-tracked in either their first or second year out of the pouch did not change the location of their home-range in any way.

5.2.2 Measurement of Home-range

All radio-locations for each animal were divided into summer and winter observations and plotted onto a base map of the study area. The results show that the wallabies in this population do have a well defined home-range which overlaps with the home-ranges of other wallabies of the same or opposite sex. Because wider movements took place during the summer the home-range area was larger at this time. Home-ranges for each individual for summer and winter are shown in Figures 5.4 to 5.9.

Home-range area was calculated using three methods. The simplest method was to measure the minimum area containing all the location points with an OTT Compensating Polar Planimeter. However this method is biased by the number of measurements and by individual judgement of the location of the boundary line. A similar method involved drawing the smallest convex polygon which contains all of the location points (Southwood, 1966; Jennrich and Turner, 1969). The third method was to calculate the area using the ellipsoid method of Jennrich and Turner (1969) who defined home-range as, "the area of the smallest region which accounts for 95% of an animal's utilization of its habitat.". The area of the home-ranges calculated by these methods are shown in Tables 5.3, 5.4 and 5.5.

The minimum area and convex polygon methods gave similar results but differed quite considerably from the ellipsoid method. The convex polygon method is known to have a sample size bias while the ellipsoid method has been recommended because of its high degree of statistical stability and lack of dependence on sample size (Jennrich and Turner, 1969). Furthermore, this method assumes that animals may be active outside the points of location, whereas the other two methods do not. Despite this I believe that the minimum area method does give a more accurate indication of the size of the home-range of wallabies as it does not assume that home-ranges are ellipsoid. Because the wallabies use runways or trails through the scrub to move to and from the feeding site much of the area calculated by the ellipsoid method would be unused. Hence I have used the results of the minimum area method for discussions of home-range size.

There was no significant difference in the mean size of the home-range between males and females in either summer or winter (Summer: $t_{10} = 0.380$, $P>0.05$; Winter: $t_9 = 1.143$, $P>0.05$). For both males and females the summer home-range was significantly larger than the winter home-range (Males: $t_{10} = 3.004$, $P<0.05$; Females: $t_9 = 3.113$, $P<0.05$).

It appears that the wallabies using the Main Study Area do belong to a single population and that within this they have overlapping home-ranges. The mean size of the summer home-range for all animals was 42.4 ± 17.6 ha while in winter it was 15.9 ± 8.1 ha. The total area over which observ-

TABLE 5.3 HOME-RANGE AREA FOR MALES (Hectares)*

Animal	Time Of Year	Number Of Observations	Area Of Home-range As Measured By: Minimum Area Method	Convex Polygon Method	Ellipsoid Method
1	Summer	61	79.3	91.5	120.6
	Winter	58	22.7	23.7	31.0
2	Summer	56	34.7	47.0	60.4
	Winter	30	11.3	15.0	30.2
3	Winter	54	33.5	37.0	56.6
4	Summer	44	31.4	29.7	39.5
	Winter	16	6.5	6.6	17.3
5	Summer	38	43.7	42.3	49.8
6	Summer	17	34.7	35.5	99.5
7	Summer	37	56.0	56.8	70.8
8	Summer	25	28.6	26.3	51.3
	Winter	16	21.4	19.5	50.6

* 1 Hectare = .01 Km^2 or 2.47 Acres

TABLE 5.4 HOME-RANGE AREA FOR FEMALES (Hectares)

Animal	Time Of Year	Number Of Observations	Area Of Home-range As Measured By: Minimum Area Method	Convex Polygon Method	Ellipsoid Method
1	Winter	51	17.6	19.7	26.2
2	Summer	38	56.4	54.7	91.0
	Winter	38	17.5	15.8	22.4
3	Summer	56	29.1	28.6	47.2
	Winter	49	16.6	25.3	41.6
4	Winter	10	4.9	3.5	12.8
5	Summer	52	40.3	44.2	96.4
6	Summer	55	59.4	69.0	93.6
7	Summer	25	14.8	16.3	32.3
	Winter	16	11.2	13.8	45.3
8	Winter	12	11.6	10.8	36.2

TABLE 5.5

MEAN HOME-RANGE AREA (Hectares) ± STANDARD DEVIATION

MALES

Method	Summer (N = 7)	Winter (N = 5)
Minimum Area	44.1 ± 18.1	19.1 ± 10.6
Convex Polygon	47.0 ± 22.2	20.4 ± 11.3
Ellipsoid	70.3 ± 29.5	37.1 ± 16.1

FEMALES

Method	Summer (N = 5)	Winter (N = 6)
Minimum Area	40.0 ± 18.7	13.2 ± 5.0
Convex Polygon	42.6 ± 20.8	14.8 ± 7.4
Ellipsoid	72.1 ± 30.1	30.8 ± 12.4

ations of the movements of wallabies were made was approximately 230 ha.

Holsworth (1967) reported that quokka populations also arranged themselves into mutually exclusive group territories within which the individuals had overlapping home-ranges of 4 - 24 acres (1.6 - 9.7 ha). Kitchener (1972) confirmed the existence of this type of social structure although both he and Nicholls (1971) found that there was more movement between groups than recorded by Holsworth (1967). Nicholls (1971) found that individual home-ranges were 2.5 - 31 acres (1 - 12.5 ha) in July to October and 5 - 42 acres (2 - 17 ha) in February to April. The changes in size, and sometimes location, of the areas occupied by quokkas and their movement patterns could be explained by the distribution of the vegetation which provided shelter and food.

Similarly, the increase in size of the home-range during summer for the Kangaroo Island Wallaby was probably due to changes in the abundance and/or quality of food on the study area.

Figure 5.4 Home-ranges for Male 1 and Male 2.
Each dot represents one radio-location.

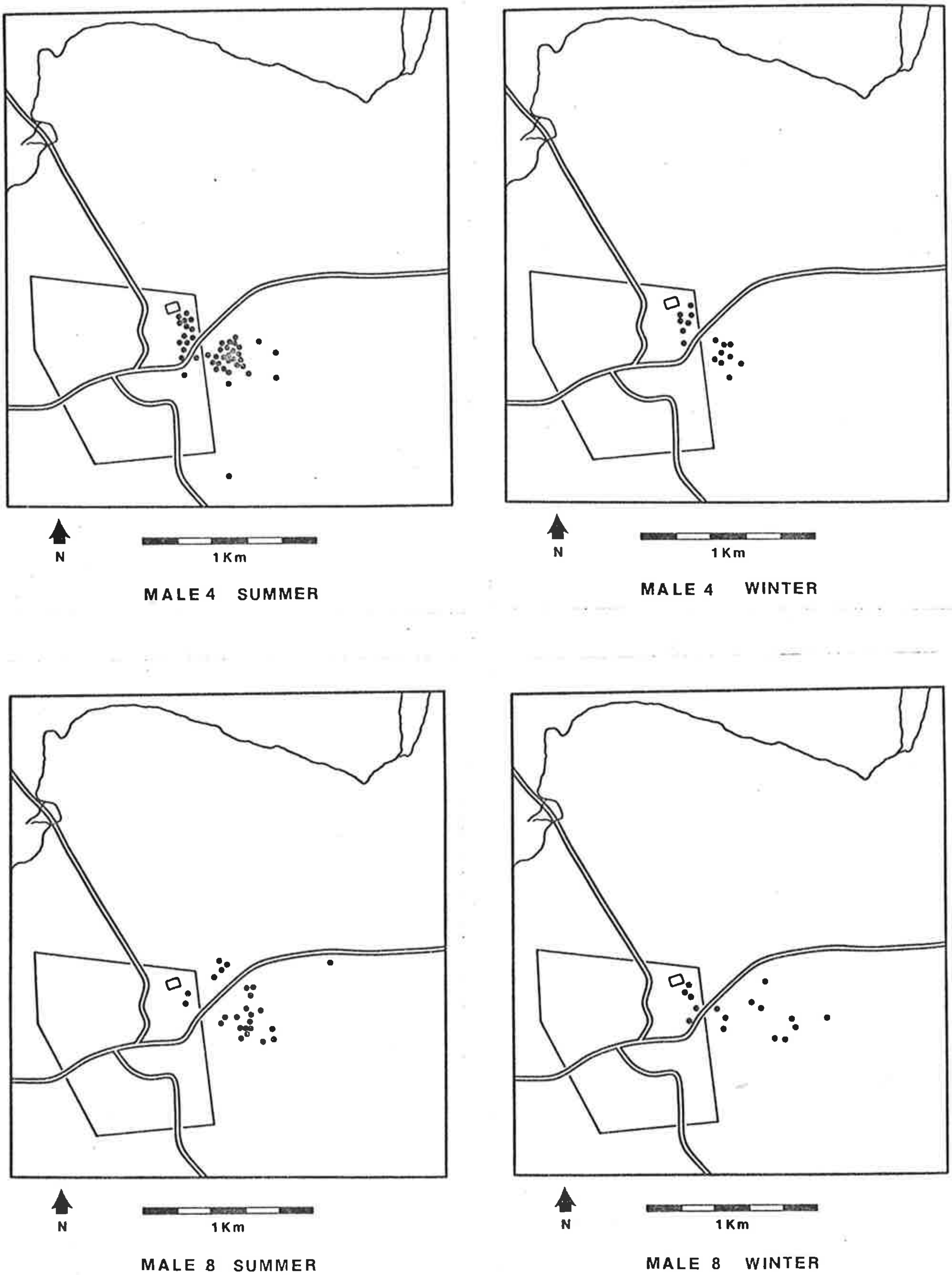


Figure 5.5 Home-ranges for Male 4 and Male 8.

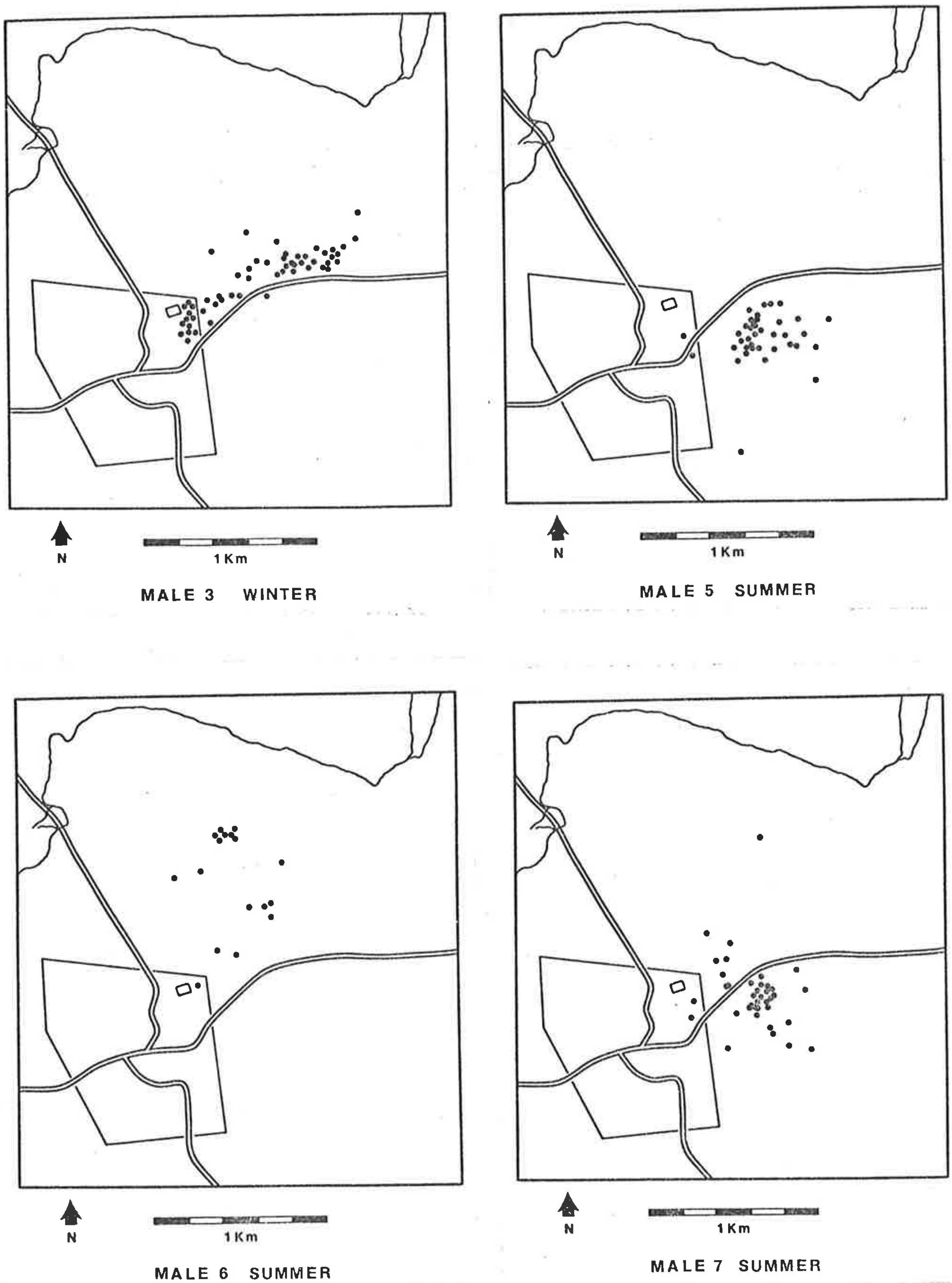


Figure 5.6 Home-ranges for Male 3, Male 5, Male 6 and Male 7.

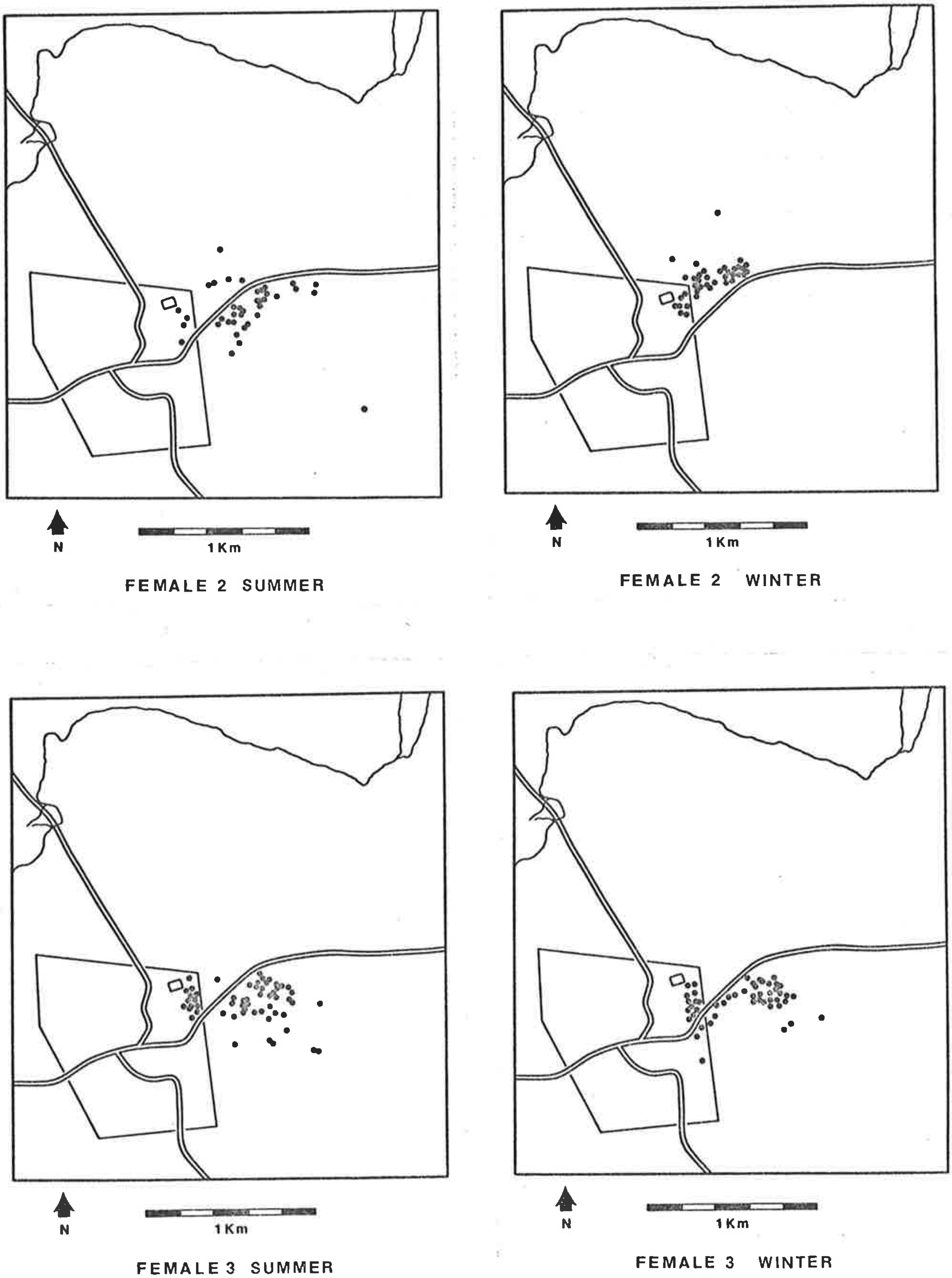


Figure 5.7 Home-ranges for Female 2 and Female 3.

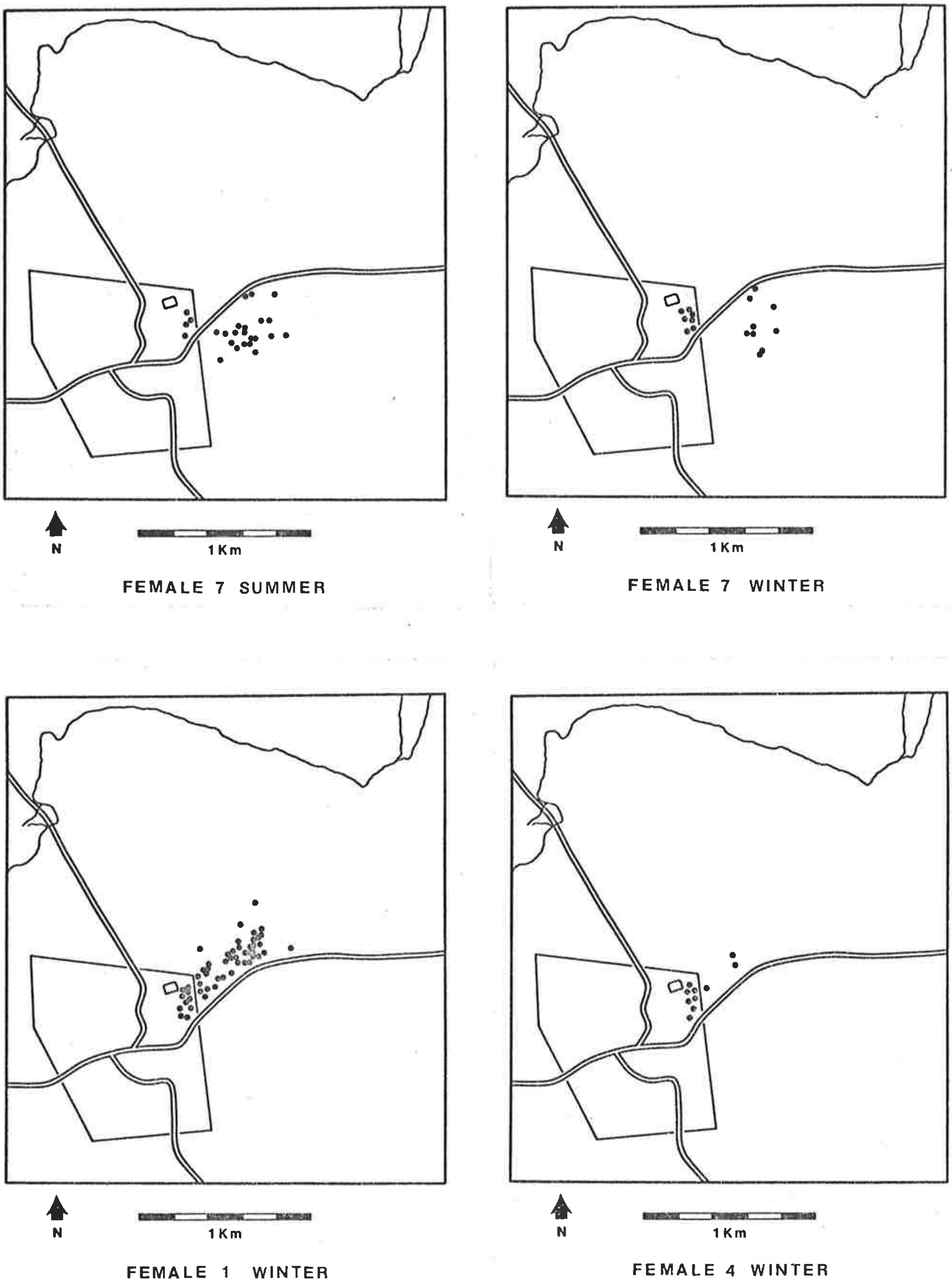


Figure 5.8 Home-ranges for Female 7, Female 1 and Female 4.

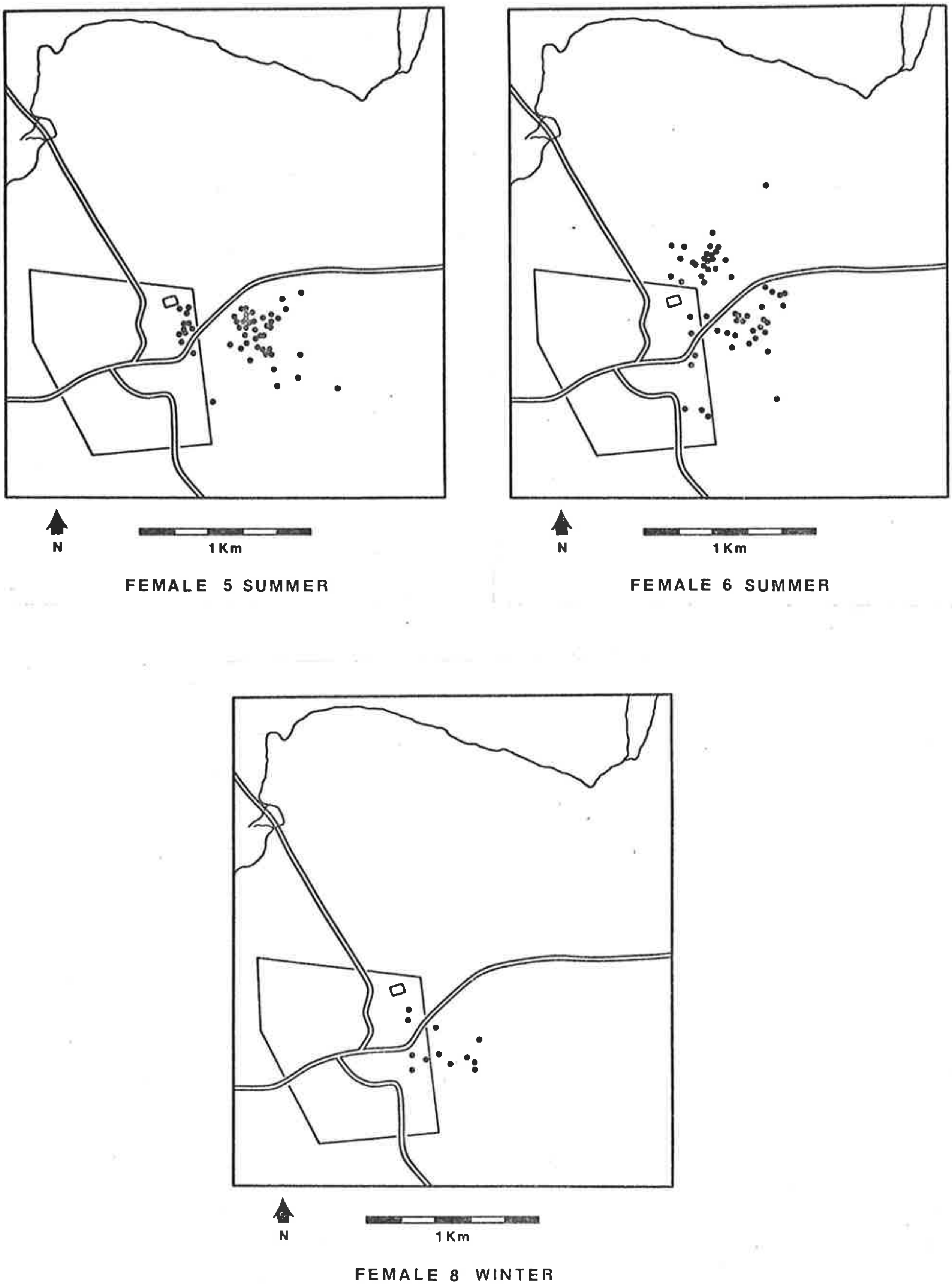


Figure 5.9 Home-ranges for Female 5, Female 6 and Female 8.

6.0 POPULATION DYNAMICS

6.1 INTRODUCTION

The size of a population can be measured as an absolute number, as a density measurement or by the use of indices which give some measure of abundance. The choice of method depends upon the species being studied, the type of habitat and the information the investigator wishes to obtain from the population.

Aerial surveys have been used quite extensively to estimate the population size or density of many species of animals, particularly in Africa (Lamprey, 1964; Talbot and Stewart, 1964; Goddard, 1967; Eltringham, 1973; Caughley, 1974). Such surveys, as well as being expensive to carry out, can only be used in relatively open country and for large, conspicuous animals. In Australia this method has been used to estimate numbers of red kangaroos which inhabit the lightly timbered areas of the inland (Frith, 1964; Newsome, 1965a; Bailey, 1971; Caughley, Sinclair and Scott-Kemmis, 1976). Because the Kangaroo Island Wallaby inhabits dense vegetation during the day aerial survey was impractical.

Ground surveys can be used to obtain density measurements by traversing the study area along transects, either on foot or by vehicle, and counting the number of animals seen. Eberhardt (1968) and Seber (1973) have reviewed the problems involved in making density measurements using this method and have suggested ways of designing the experiment and analysing the results. Ealey (1967a) used the transect method to estimate the density of euro populations in north-western Australia. By making counts at dawn and dusk he believed that reliable measurements were made. However, Kirkpatrick (1974) rejected this technique for monitoring kangaroo populations because of the lack of documentation on the precision and accuracy of the method of analysis. Although this method was a possibility for use on Kangaroo Island Wallabies the density of vegetation over the study area made observations extremely difficult. The other factor influencing my decision not to use this method was the limited amount of information that could be obtained. Although a measure of the density of the population was possible nothing would be known about the sex ratio, age structure or reproductive potential. Such information is essential in understanding the dynamics of a population. Nevertheless this method could be of use on farms where wallabies enter pasture at night to feed. Such counts could be used to indicate the level of control needed. Johnson (1977) found that the line transect spotlight count was the most efficient method for censusing Bennett's wallabies, pademelons (*Thylogale billardieri*) and brush-tailed possums in Tasmania, in areas where visibility was adequate.

For this study I decided that the best method for obtaining data on both population size and structure was the mark-recapture method. In this method a sample of animals from the population is captured, marked and released. An estimate of the size of the population can be made from the relative numbers of marked and unmarked animals in subsequent samples. Although this technique required a large amount of work in capturing wallabies I felt that the information that could be obtained on the biology of the animal made it worthwhile.

6.2 THE MARK-RECAPTURE METHOD

6.2.1 Assumptions underlying use of this method

Since the pioneering work of Lincoln (1930), Leslie, Chitty and Chitty (1953), Beverton and Holt (1957), Orians and Leslie (1958) and Ricker (1958) the methods of analysing mark-recapture data have been considerably improved (see Cormack, 1968; Seber, 1973). However, all of the mathematical models used for analysis are based on a number of assumptions. The main assumptions are that:

(1) the marked animals are not affected by being marked and the marks are not lost,

(2) upon release, the marked animals become completely mixed in the population before the next sample is taken,

(3) being captured once or more does not affect the chance of an animal being subsequently captured,

(4) the population is sampled randomly. This means that all individuals must be equally available for capture and that individuals of different age groups and sex are sampled in the proportion in which they occur in the population.

This last assumption that sampling is completely random is probably the most important but is difficult to verify (Jolly, 1965). For many animals differences in the probability of capture are associated with different age groups or sex. For this reason the data for these groups should be analysed separately.

6.2.2 Testing for Equal Catchability

The assumption of equal catchability of all animals in the population will be satisfied if there is random mixing of marked and unmarked animals, and all sampling is random. In a statistical appendix to a paper by Orians (1958), Leslie has suggested a test for equal catchability with respect to the marked population. This test uses the recapture history of a group of animals which are known to be alive by being in the i th sample and the $(i + s)$ th sample over a recapture period s. If the animals are equally catchable the frequencies of their recaptures will form a binomial distribution. The observed and expected variances of the distribution are then compared by means of a Chi-square test. Leslie suggested that the number of recapture periods should not be less than 3 and the number of animals that are known to be alive should be more than 20.

In the present study Leslie's test was first applied to the recapure data of a group of Kangaroo Island Wallabies marked by Dr. S. Barker, Zoology Department, University of Adelaide, over the period August 1966 to May 1969. As these animals were caught in the area in which my study was being conducted I thought that it would give a useful indication of whether the mark-recapture technique was feasible. Because of the minimum requirements for the number of animals known to be alive over the recapture period it was only possible to apply this test to females. From August 1966 to May 1967 92 females were marked with ear-tags and out of these a group of 24 were known still to be alive after July 1968. Table 6.1A shows the number of females recaptured in each trip from November-December 1967 to July 1968 and Table 6.1B shows the frequency of recaptures.

Because the assumption of equal catchability was

TABLE 6.1A

NUMBER OF FEMALES CAPTURED IN EACH TRIP

FROM NOVEMBER/DECEMBER 1967 TO JULY 1968

Month of Capture	Number of Recaptures
November/December 1967	5
February 1968	4
May 1968	7
July 1968	5

TABLE 6.1B

DATA FOR LESLIE'S TEST OF EQUAL CATCHABILITY

FOR FEMALES CAPTURED UP TO NOVEMBER/DECEMBER

1967 AND STILL ALIVE AFTER JULY 1968

Times Recaptured	Number of Animals
0	9
1	10
2	4
3	1
4	0

X^2_{23} = 24.619, $P>0.05$

Therefore, the null hypothesis of equal catchability is accepted.

accepted for these animals, a mark-recapture program was considered suitable for this population study.

A stochastic model for analysing mark-recapture data was derived independently by Jolly (1965) and Seber (1965). This model is less complicated and gives more valid results than the corresponding deterministic models (Cormack, 1968). For this reason it was decided to analyse the data obtained in this study using this method. As Jolly (1965) reviewed the development of the model and provided a detailed description of its use, his methods and notation are used here.

Before proceeding with the analysis of the recapture data the assumption of equal catchability was tested, again using the method outlined in Orians and Leslie (1958). The results for males and females were treated separately. Because the number of animals known to be alive over the entire study (July 1975 to November 1978) was small I divided it into two time periods. For females these were May 1976 to January-February 1977 (Tables 6.2A and 6.2B) and April 1977 to December 1977-January 1978 (Tables 6.3A and 6.3B). For males the first period was from July 1976 to January-February 1977 (Tables 6.4A and 6.4B) and the second was the same as for the females (Tables 6.5A and 6.5B).

For the recapture data obtained in the present study the assumption of equal catchability for both males and females could be accepted for 1976 but was rejected for 1977. According to Cormack (1966) and Eberhardt (1969) a failure of this test may be due to three causes:

(1) a behavioural property, inherent to the individual, when encountering a trap,

TABLE 6.2A

NUMBER OF FEMALES CAPTURED IN EACH TRIP FROM MAY 1976 TO JANUARY/FEBRUARY 1977

Month of Capture	Number of Recaptures
May 1976	10
July 1976	10
October/November 1976	17
December 1976	9
January/February 1977	9

TABLE 6.2B

DATA FOR LESLIE'S TEST OF EQUAL CATCHABILITY FOR FEMALES CAPTURED UP TO MAY 1976 AND STILL ALIVE AFTER JANUARY/FEBRUARY 1977

Times Recaptured	Number of Animals
0	10
1	13
2	11
3	4
4	2
5	0

$X^2_{39} = 51.002, P>0.05$

Therefore, the null hypothesis of equal catchability is accepted.

TABLE 6.3A

NUMBER OF FEMALES CAPTURED IN EACH TRIP

FROM APRIL 1977 TO DECEMBER 1977/JANUARY 1978

Month of Capture	Number of Recaptures
April 1977	18
June/July 1977	12
November 1977	17
December 1977/January 1978	11

TABLE 6.3B

DATA FOR LESLIE'S TEST OF EQUAL CATCHABILITY

FOR FEMALES CAPTURED UP TO APRIL 1977 AND

STILL ALIVE AFTER DECEMBER 1977/ JANUARY 1978

Times Recaptured	Number of Animals
0	8
1	6
2	8
3	8
4	3

$X^2_{32} = 58.924, P<0.01$

Therefore, the null hypothesis of equal catchability is rejected.

TABLE 6.4A

NUMBER OF MALES CAPTURED IN EACH TRIP FROM JULY 1976 TO JANUARY/FEBRUARY 1977

Month of Capture	Number of Recaptures
July 1976	8
October/November 1976	14
December 1976	13
January/February 1977	11

TABLE 6.4B

DATA FOR LESLIE'S TEST OF EQUAL CATCHABILITY FOR MALES CAPTURED UP TO JULY 1976 AND STILL ALIVE AFTER JANUARY/FEBRUARY 1977

Times Recaptured	Number of Animals
0	5
1	8
2	9
3	4
4	2

$X^2_{27} = 38.696$, $P>0.05$

Therefore, the null hypothesis of equal catchability is accepted.

TABLE 6.5A

NUMBER OF MALES CAPTURED IN EACH TRIP FROM APRIL 1977 TO DECEMBER 1977/JANUARY 1978

Month of Capture	Number of Recaptures
April 1977	14
June/July 1977	9
November 1977	10
December 1977/January 1978	5

TABLE 6.5B

DATA FOR LESLIE'S TEST OF EQUAL CATCHABILITY FOR MALES CAPTURED UP TO APRIL 1977 AND STILL ALIVE AFTER DECEMBER 1977/JANUARY 1978

Times Recaptured	Number of Animals
0	5
1	5
2	7
3	5
4	1

X^2_{22} = 34.985, $P<0.05$

Therefore, the null hypothesis of equal catchability is rejected.

(2) the previous capture history of an individual,

(3) lack of opportunity for the capure of an individual. For example, if some animals in the population do not always feed on the cleared area they will have a different probability of capture to those who forage nightly.

The first cause would be difficult to detect but it is unlikely to be important in this population due to the method of capture. If the second factor was operating it might be expected that the number of animals recaptured zero times would be high, due to avoidance of the traps through learning. However, this was not apparent during the times that the test for equal catchability failed. The third reason seems the most likely as the radio-tracking results (see Chapter 5.0) indicated that there were differences between the summer and winter feeding behaviour of individuals and also between individuals over summer. The very dry 1977-1978 summer may have been responsible for these changes in behaviour. This would lead to the unequal catchability over the period April 1977 to December 1977-January 1978.

Because of the possible bias introduced into the Jolly-Seber model by unequal catchability an independent estimate of population size was made using a different method. This was done by calculating the Minimum Number of Animals Known to be Alive. However, as the trapping data was available it was also decided to proceed with an analysis using the Jolly-Seber model. This would provide a useful basis for comparison with the Minimum Number of Animals Known to be Alive especially for the period when equal catchability could be assumed. I have chosen to present the results of the

Jolly-Seber model first as it facilitates explanation of the data.

6.2.3 The Jolly-Seber Stochastic Model for Mark-Recapture Analysis

The following is a brief summary of the formulae used in this model following the notation of Jolly (1965).

A number of samples of the population are taken on l occasions each animal being marked so that its recapture history is known. Thus at time i an estimate of the population size can be found from:

$$N_i = \frac{M_i}{a_i} \quad (i = 2,3, \ldots l-1)$$

where N_i = estimated number of animals in the population when the i th sample is captured.

M_i = estimated number of marked animals in the population at time i.

a_i = the proportion of marked animals in the i th sample,

= m_i/n_i, where m_i is the number of marked animals in the i th sample and n_i is the number caught in the i th sample.

The estimate M_i is calculated from $\frac{S_i \; Z_i}{R_i} + m_i \quad (i = 2,3, \ldots l-1)$

where S_i = number released from the i th sample after marking.

Z_i = the number marked before time i which are not caught in the i th sample but are caught subsequently.

R_i = the number of animals released from the i th sample that are caught subsequently.

Thus, the Population Estimate

$$N_i = n_i + \frac{S_i \; Z_i \; n_i}{R_i \; m_i} \quad (i = 2,3, \ldots l-1)$$

The probability that an animal alive at the time of release of the i th sample will survive to the time of capture of the $(i + 1)$th sample can be estimated from the capture histories of the marked portion of the population.

$$\text{Survival Rate } (\phi_i) = \frac{M_{i+1}}{M_i - m_i + S_i} \quad (i = 2,3, \ldots l-2)$$

In this estimation emigration and death are combined.

The number of new animals which join the population in the interval between the i and $(i + 1)$th samples and are still alive at time $(i + 1)$ is a combination of the birth rate (or animals leaving the pouch in the case of wallabies) and any immigration.

$$\text{Birth Rate } (B_i) = N_{i+1} - \phi_i(N_i - n_i + S_i) \quad (i = 2,3, \ldots l-2)$$

Variances of the population estimate (N_i), the survival rate (ϕ_i) and birth rate (B_i) can be calculated from the formulae given by Jolly (1965)

6.2.4 Results

Capture Data

Seventeen catching trips were made to the study area from May 1975 to November 1978. The total number of animals ear-tagged from the three capture sites was 479 (210 F, 269 M). The total number ear-tagged in each area are shown in Table 6.6. The number of animals caught during each trip for the present study, and the data for 1966 - 1969 are presented in Appendix V.

Only the recapture data obtained from animals caught on the Main Study Area were used for estimations of population size as these were believed to form a single population (see Chapter 5.0). To obtain a population estimate each animal

TABLE 6.6

TOTAL NUMBER OF WALLABIES EAR-TAGGED AT EACH CAPTURE SITE

Capture Site	Total Number Ear-tagged		
	Females	Males	Total
Main Study Area	171	202	373
Goose Paddock	28	62	90
Bottom Paddock	11	5	16

could only be 'effectively' caught once during a trip. The results for the number 'effectively' caught on each trip on the Main Study Area and the results of captures in 1966 - 1969 are shown in Tables 6.7 and 6.8.

Population Estimates from the Jolly-Seber Stochastic Model

The mark-recapture data for males and females were analysed separately but the different age groups were not, due to the small numbers involved in each group. The values of n_i, R_i and Z_i (see section 6.2.3) for 1975 - 1978 and 1966 - 1969 are shown in Appendix VI. The population estimates from these data are presented in Tables 6.9 to 6.12 together with estimates of survival (and/or emigration) and birth (and/or immigration) rates.

These population estimates show that for females in the period 1975 - 1978 there was an increase in population size around January of both 1976 and 1977 but not for 1978. The two peaks were followed by a rapid decline by March-April while over the rest of the year there was little fluctuation in size of the population. The males did not show peaks in population size at the same time as the females as the

TABLE 6.7 THE 'EFFECTIVE' NUMBER OF ANIMALS CAUGHT DURING EACH TRIP ON THE MAIN STUDY AREA

Date of Field Trip	Number Caught			Number Recaptured			% Recaptures		
	Females	Males	Total	Females	Males	Total	Females	Males	Total
July 1975	24	18	42						
October-November 1975	42	23	65	7	2	9	16.7	8.7	13.8
January 1976	19	17	36	5	2	7	26.3	11.8	19.4
March 1976	31	25	56	17	3	20	54.8	12.0	35.7
May 1976	25	27	52	17	12	29	68.0	44.4	55.8
July 1976	19	20	39	14	10	24	73.7	50.0	61.5
October-November 1976	43	38	81	31	22	53	72.1	57.9	65.4
December 1976	28	31	59	18	21	39	64.3	67.7	66.1
January-February 1977	30	25	55	19	20	39	63.3	80.0	70.9
April 1977	48	36	84	41	29	70	85.4	80.6	83.3
June-July 1977	32	30	62	28	19	47	87.5	63.3	75.8
November 1977	40	37	77	35	17	52	87.5	45.9	67.5
December 1977-January 1978	20	21	41	15	14	29	75.0	66.7	70.7
May 1978	27	24	51	25	15	40	92.6	62.5	78.4
July 1978	22	23	45	20	18	38	90.9	78.3	84.4
November 1978	22	25	47	9	14	23	40.9	56.0	48.9

TABLE 6.8 THE 'EFFECTIVE' NUMBER OF ANIMALS CAUGHT BY DR. S. BARKER, ZOOLOGY DEPARTMENT, UNIVERSITY OF ADELAIDE FROM AUGUST 1966 TO MAY 1969

Date of Field Trip	Number Caught			Number Recaptured			% Recaptures		
	Females	Males	Total	Females	Males	Total	Females	Males	Total
August 1966	38	21	59						
November-December 1966	38	17	55	4	2	6	10.5	11.8	10.9
May 1967	44	30	74	13	1	14	29.5	3.3	18.9
November-December 1967	38	32	70	13	3	16	34.2	9.4	22.9
February 1968	33	23	56	8	5	13	24.2	21.7	23.2
May 1968	44	39	83	21	17	38	47.7	43.6	45.8
July 1968	44	23	67	23	10	33	52.3	43.5	49.3
December 1968	40	26	6	18	3	21	45.0	11.5	31.8
March 1969	34	28	62	23	9	32	67.6	32.1	51.6
May 1967	44	19	63	26	8	34	59.1	42.1	54.0

Animals that were ear-tagged before August 1966 and were recaptured during the period August 1966 – May 1969 were recorded as having been newly caught, for the purposes of the population estimates. Thus, for this period a total of 450 animals were recorded as being ear-tagged.

TABLE 6.9 POPULATION ESTIMATES FOR FEMALES OVER THE PERIOD OCTOBER-NOVEMBER 1975 TO NOVEMBER 1978, DERIVED FROM THE JOLLY-SEBER STOCHASTIC MODEL

Date of Field Trip	Proportion Of Recaptures (a_i)	Number Of Marked Animals (M_i)	Population Size (N_i) ± Standard Deviation	Survival Rate (ϕ_i) ± Standard Deviation	Birth Rate (B_i) ± Standard Deviation
October-November 1975	0.167	21.7	130.0 ± 48.8	0.985 ± .158	78.6 ± 132.3
January 1976	0.263	53.9	204.7 ± 84.7	0.830 ± .127	-67.2 ± 79.6
March 1976	0.548	56.4	102.7 ± 20.0	1.175 ± .184	0.8 ± 30.7
May 1976	0.680	82.6	121.5 ± 26.0	0.697 ± .115	1.0 ± 17.9
July 1976	0.737	63.2	85.7 ± 15.1	1.011 ± .100	8.9 ± 13.7
October-November 1976	0.721	68.9	95.6 ± 13.8	0.914 ± .101	27.7 ± 18.9
December 1976	0.643	74.0	115.1 ± 20.5	1.166 ± .180	20.4 ± 28.7
January-February 1977	0.633	98.0	154.7 ± 31.8	0.729 ± .111	-19.8 ± 20.4
April 1977	0.854	79.4	93.0 ± 12.4	0.941 ± .130	5.4 ± 8.2
June-July 1977	0.875	81.3	93.0 ± 15.4	0.867 ± .149	4.0 ± 6.8
November 1977	0.875	74.0	84.6 ± 15.4	0.698 ± .140	14.3 ± 9.3
December 1977-January 1978	0.750	54.5	72.6 ± 16.3	1.057 ± .262	- 9.0 ± 10.4
May 1978	0.926	61.8	66.8 ± 17.4	1.003 ± .547	3.4 ± 5.3
July 1978	0.909	64.0	70.4 ± 39.2		
November 1978	0.409				

TABLE 6.10 POPULATION ESTIMATES FOR MALES OVER THE PERIOD OCTOBER-NOVEMBER 1975 TO NOVEMBER 1978, DERIVED FROM THE JOLLY-SEBER STOCHASTIC MODEL

Date of Field Trip	Proportion Of Recaptures (a_i)	Number Of Marked Animals (M_i)	Population Size (N_i) ± Standard Deviation	Survival Rate (ϕ_i) ± Standard Deviation	Birth Rate (B_i) ± Standard Deviation
October- November 1975	0.087	20.4	234.6 ± 205.8	0.269 ± .112	31.6 ± 107.2
January 1976	0.118	11.2	94.8 ± 65.9	1.071 ± .202	131.8 ± 157.4
March 1976	0.120	28.0	233.3 ± 133.3	0.955 ± .187	-115.4 ± 172.3
May 1976	0.444	47.8	107.4 ± 30.5	0.810 ± .165	13.8 ± 33.8
July 1976	0.500	50.0	100.0 ± 28.2	0.854 ± .146	3.1 ± 25.1
October-November 1976	0.579	51.2	88.5 ± 17.9	0.741 ± .091	8.0 ± 17.3
December 1976	0.677	49.9	73.6 ± 12.5	1.163 ± .172	1.1 ± 15.5
January-February 1977	0.800	68.4	85.5 ± 17.1	0.803 ± .147	4.5 ± 8.9
April 1977	0.806	59.0	73.2 ± 13.7	0.869 ± .175	26.4 ± 12.6
June-July 1977	0.633	56.5	89.2 ± 21.6	0.725 ± .150	41.8 ± 20.8
November 1977	0.459	49.0	106.5 ± 26.2	1.378 ± .444	- 4.3 ± 48.7
December 1977-January 1978	0.667	95.0	142.5 ± 50.6	0.504 ± .179	10.4 ± 19.2
May 1978	0.625	51.4	82.3 ± 22.7	5.335 ± 5.277	- 28.5 ± 76.7
July 1978	0.783	317.0	405.1 ± 400.3		
November 1978	0.560				

TABLE 6.11 POPULATION ESTIMATES FOR FEMALES OVER THE PERIOD NOVEMBER-DECEMBER 1966 TO MAY 1969, DERIVED FROM THE JOLLY-SEBER STOCHASTIC MODEL

Date Of Field Trip	Proportion Of Recaptures (a_i)	Number Of Marked Animals (M_i)	Population Size (N_i) ± Standard Deviation	Survival Rate (ϕ_i) ± Standard Deviation	Birth Rate (B_i) ± Standard Deviation
November-December 1966	0.105	61.0	579.5 ± 313.3	0.544 ± .133	-140.4 ± 243.2
May 1967	0.295	51.7	175.1 ± 49.8	0.938 ± .183	62.6 ± 89.3
November-December 1967	0.342	77.6	226.8 ± 64.8	0.948 ± .213	186.2 ± 142.2
February 1968	0.242	97.3	401.3 ± 145.0	1.179 ± .309	-171.1 ± 174.1
May 1968	0.477	144.2	302.1 ± 82.7	0.826 ± .252	14.6 ± 63.4
July 1968	0.523	138.1	264.1 ± 76.1	0.776 ± .264	69.3 ± 62.9
December 1968	0.450	123.5	274.3 ± 90.5	0.600 ± .221	- 35.6 ± 46.0
March 1969	0.676	87.2	128.9 ± 42.9		
May 1969	0.591				

TABLE 6.12 POPULATION ESTIMATES FOR MALES OVER THE PERIOD MAY 1967 TO MAY 1969, DERIVED FROM THE JOLLY-SEBER STOCHASTIC MODEL

Date of Field Trip	Proportion Of Recaptures (a_i)	Number Of Marked Animals (M_i)	Population Size (N_i) ± Standard Deviation	Survival Rate (ϕ_i) ± Standard Deviation	Birth Rate (B_i) ± Standard Deviation
May 1967	0.033	30.0	900.0 ± 961.4	0.586 ± .216	-164.3 ± 778.9
November-December 1967	0.094	34.0	362.7 ± 224.7	1.379 ± .560	-105.5 ± 398.5
February 1968	0.217	85.5	393.3 ± 217.1	0.572 ± .257	- 89.2 ± 127.1
May 1968	0.436	59.2	135.9 ± 52.8	0.714 ± .376	35.4 ± 45.1
July 1968	0.435	57.3	131.7 ± 72.2	1.314 ± .933	606.7 ± 553.0
December 1968	0.115	89.7	777.1 ± 633.9	0.328 ± .239	-140.1 ± 257.7
March 1969	0.321	37.0	115.1 ± 74.0		
May 1969	0.421				

Information from November-December 1966 was deleted from the analysis because no animals ear-tagged in this trip were subsequently recaptured.

highest estimates occurred in October-November 1975, March 1976, December 1977 - January 1978 and July 1978. The high population estimate for October-November 1975 was due to the low proportion of recaptures while for July 1978 it was due to the fact that only one of the animals released at this time was subsequently recaptured. This meant that the estimate of the number of marked animals in the population (M_i), and hence the estimate of population size, was large. Because young animals leave the pouch around October-November each year I expected an increase in the population size at this time. This would only be estimated if a large number of these young animals were caught at this time. However, the captures of this age-class tended to be spread over several trips so that no sudden increase in population estimates was observed in October-November. Over the time period that the assumption of equal catchability was valid the population estimates for females varied from 86 $\pm$ 15 in July 1976 to 155 $\pm$ 32 in January-February 1977. For males the lowest value was 74 $\pm$ 13 in December 1976 and the highest was 100 $\pm$ 28 in July 1976.

Over the 1966 - 1969 period the population estimates for both males and females tended to fluctuate from month to month. The high values appeared to be the result of a low proportion of recaptures at that time but whether this was due to new animals entering the population or marked animals avoiding being caught could not be determined. I suspect that despite the acceptance of equal catchability for females from November - December 1967 to July 1968 the population estimates are biased by changes in the behaviour of animals at different times of the year which affected their chance of being caught.

6.3 ESTIMATION OF THE MINIMUM NUMBER OF ANIMALS KNOWN TO BE ALIVE, AS A MEASURE OF POPULATION SIZE

6.3.1 The Assumptions and Calculations Necessary to Obtain Population Estimates by this Method

Krebs (1966) abandoned the mark-recapture method of estimating population size due to trap bias. He attempted to census a population of the California vole (*Microtus californicus*) by calculating the minimum number of animals alive at each capture period. This was obtained from (1) the actual number caught at time t, and (2) the number of previously marked individuals caught after time t, but not at that time.

A similar method was used in this study which utilized the data obtained for the mark-recapture method. However, a further two calculations were needed to obtain the population estimate. One of these calculations involved the number of animals not caught at time t but which belonged to a cohort that left the pouch before time t and were caught subsequently. The other calculation estimated the number of pouch young which enter the population at around October-November each year. To do this the number of females 1 - 2 years old and older than 2 years, that were known to be alive in October-November, were first calculated. By multiplying these numbers by the proportion of females carrying a pouch young during the appropriate year, the total number of young leaving the pouch could be estimated. The number of males and females was then calculated by using the mean sex ratio obtained for pouch young during the study.

To obtain a population estimate by this method an intensive trapping program was required and it was assumed that immigration and emigration were negligible. Howard (1960) defined dispersal as "the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate.". Animals may disperse for several reasons, such as to escape from harsh environmental conditions or high population densities (Howard, 1960; Lidicker, 1962; Joule and Cameron, 1975), movement of animals as they approach sexual maturity due to aggressive interactions with territorial residents (Blair, 1953; Healey, 1967), or movement into new or previously depopulated habitats (Joule and Cameron, 1975). Among macropods, dispersal does not occur in quokka populations (Dunnet, 1962; Holsworth, 1967; Kitchener, 1970) but Kaufmann (1974) concluded that for male sub-adult whip-tail wallabies some dispersal occurred as they approached sexual maturity.

For the Kangaroo Island Wallaby the information obtained from the recapture of animals and the limited amount of data from radio-tracking (Chapter 5.0) suggests that little dispersal occurs. Of all the animals recaptured only the following instances of an animal being caught in a different area from that in which it was first caught were recorded. A female was first captured on 28/10/75 in the Main Study Area after it had recently left its mother's pouch. It was next captured on 25/5/76 in the Goose Paddock but was not subsequently recaptured. A male that was first caught in the Goose Paddock (Male 3 from radio-tracking results) on 27/5/76 when 15-16 months old was recaptured two days later on the Main Study Area. All subsequent recaptures of this animal were made only on the Main Study Area. Another male that was first captured in the Goose Paddock on 27/7/76 when 17-18 months old was next caught on 9/4/77 on the Main Study Area. No tagged animals from the Main Study Area were caught in the Bottom Paddock nor were any from this area caught in either the Goose Paddock or Main Study Area. Four animals (3 F, 1 M) that were first tagged in the Goose Paddock were caught close by in the Bottom Paddock but three of these were later recaptured in the Goose Paddock again.

For this study I have assumed that dispersal is not a major factor influencing the number of animals on the Main Study Area and that the population size can be estimated by calculating the minimum number of animals known to be alive. This estimate is for the population which uses approximately one quarter of the cleared area as a feeding site (see Chapter 5.0) and is the same area where wallabies were caught in 1966-1969.

6.3.2 Results

The results obtained in estimating the population size as the Minimum Number of Animals Known to be Alive (M.N.A.) on the Main Study Area are shown separately for males and females for 1975-1978 in Figure 6.1 and for 1966-1969 in Figure 6.2. The proportion of the population belonging to each cohort is also shown in these figures.

There is an annual fluctuation in numbers with a peak occurring around October-November of each year when young animals leave the pouch. Over the following summer there was an initial sharp drop in population size followed by a slightly lower decline over the winter. Population size was similar in 1975 and 1976 but was lower towards the end of 1977 and early

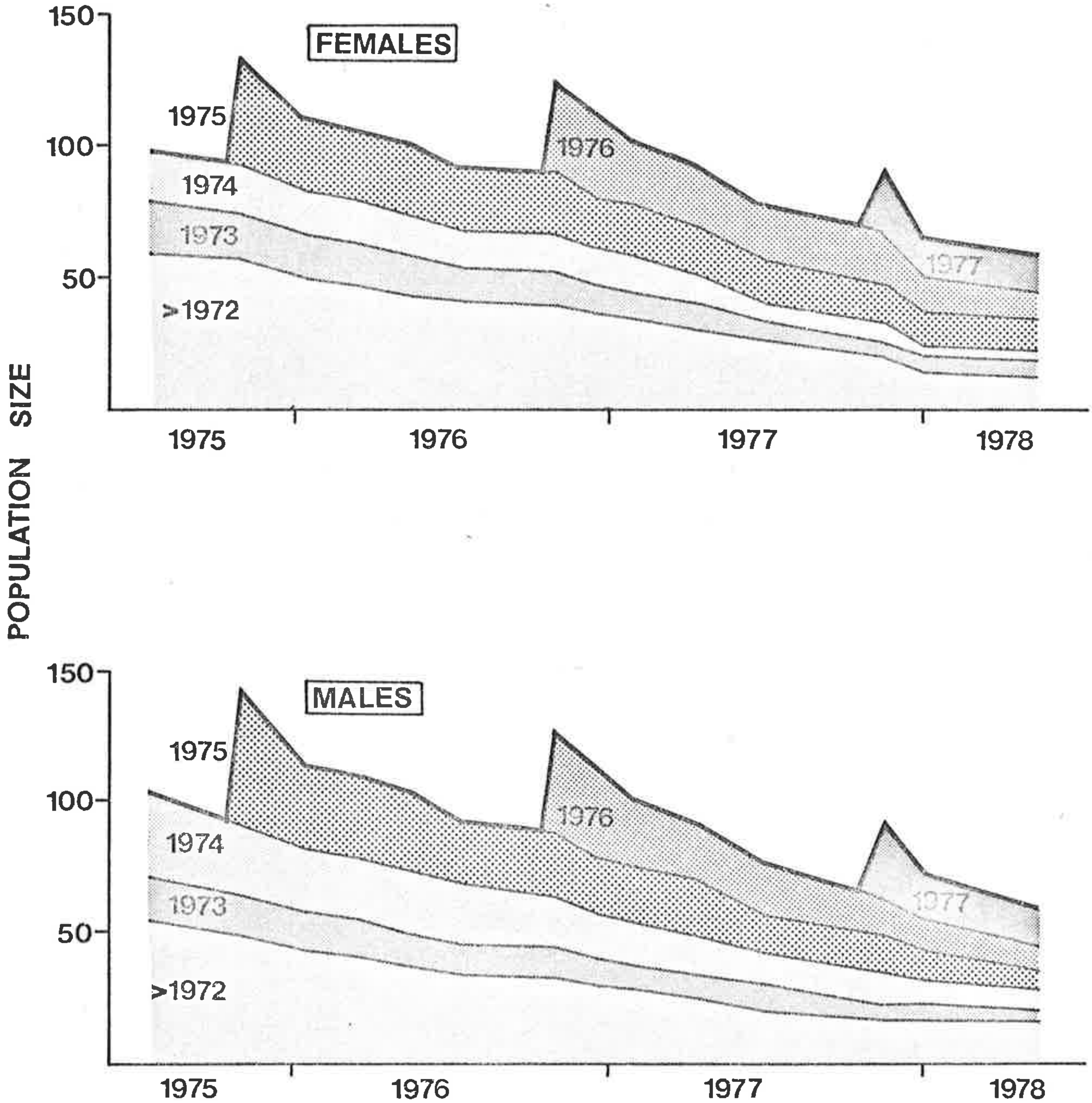


Figure 6.1 Population size for wallabies using the Main Study Area from 1975 - 1978.
Top thick line represents total population, shaded areas represent the number of animals from a particular cohort.

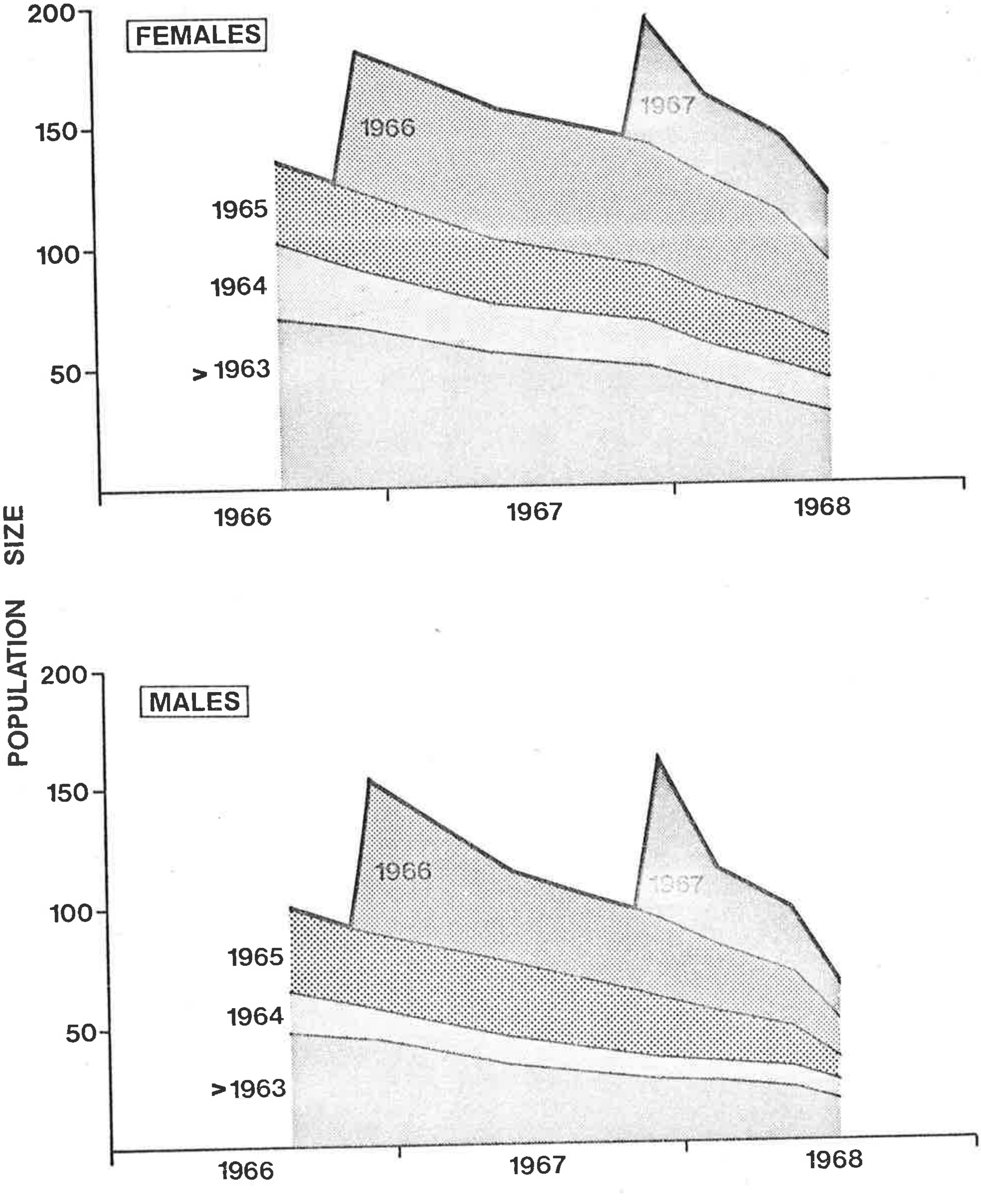


Figure 6.2 Population size of wallabies, obtained from the data collected by Dr. S. Barker, Zoology Department, University of Adelaide.
These animals were caught in the same area as for the present study.

1978. Confirmation of a population decline in 1978 was obtained from observations of many dead animals on the study area over the winter. Similar observations were made by Murphy (1970) over the 1968 winter and the population estimates at this time also show that a decline in population size occurred.

A comparison with the results obtained from the Jolly-Seber method for 1975-1978 is shown in Table 6.13. Many of the estimates obtained by the two methods are quite similar although there are some which do show a considerable difference. For females, the times when values for the M.N.A. were beyond one standard deviation of the Jolly-Seber estimate were January 1976, October-November 1976 and January-February 1977 while for males it was in October-November 1976 and December 1977 - January 1978. The differences in October-November 1976 would be due to the calculation of the number of pouch young entering the population by using the M.N.A. method. The other differences occured in summer when it is likely that changes in the feeding behaviour of animals affects the chance of an animal being captured and hence the population estimate made by the Jolly-Seber method.

6.4 REPRODUCTIVE CHARACTERISTICS OF THE POPULATION

6.4.1 Season of Births

In the Kangaroo Island Wallaby there is a distinct breeding season with most young being born in late January and early February (Andrewartha and Barker, 1969; Berger, 1970). This was confirmed in the present study as shown by the results for 1975-1977 (Figure 6.3). When the results from these years were combined (Figure 6.4) it shows that 14% of young were

TABLE 6.13 COMPARISON OF POPULATION ESTIMATES OBTAINED BY THE MINIMUM NUMBER KNOWN TO BE ALIVE (M.N.A.) AND THE JOLLY-SEBER METHOD

FEMALES

Date Of Field Trip	M.N.A. Estimate	Jolly-Seber Estimate ± S.D.	% Difference 100(M.N.A.-JS)/JS
October-November 1975	132	130.0 ± 48.8	+ 1.5
January 1976	110	204.7 ± 84.7	-46.3
March 1976	105	102.7 ± 20.0	+ 2.2
May 1976	100	121.5 ± 26.0	-17.7
July 1976	91	85.7 ± 15.1	+ 6.2
October-November 1976	123	95.6 ± 13.8	+28.7
January-February 1977	101	154.7 ± 31.8	-34.7
April 1977	90	93.0 ± 12.4	- 3.2
June-July 1977	77	93.0 ± 15.4	-17.2
November 1977	89	84.6 ± 15.4	+ 5.2
December 1977-January 1978	64	72.6 ± 16.3	-11.8
May 1978	57	66.8 ± 17.4	-14.7

Cont'd. on pg. 95

TABLE 6.13 CONT'D.

COMPARISON OF POPULATION ESTIMATES OBTAINED BY THE MINIMUM NUMBER KNOWN TO BE ALIVE (M.N.A.) AND THE JOLLY-SEBER METHOD

MALES

Date of Field Trip	M.N.A. Estimate	Jolly-Seber Estimate ± S.D.	% Difference 100(M.N.A.-JS)/JS
October-November 1975	141	234.6 ± 205.8	-39.9
January 1976	114	94.8 ± 65.9	+20.3
March 1976	110	233.3 ± 133.3	-52.9
May 1976	103	107.4 ± 30.5	- 4.1
July 1976	93	100.0 ± 28.2	- 7.0
October-November 1976	126	88.5 ± 17.9	+42.4
January-February 1977	100	85.5 ± 17.1	+17.0
April 1977	91	73.2 ± 13.7	+24.3
June-July 1977	76	89.2 ± 21.6	-14.8
November 1977	90	106.5 ± 26.2	-15.5
December 1977-January 1978	73	142.5 ± 50.6	-48.8
May 1978	59	82.3 ± 22.7	-28.3

born in the period January 15th - 21st, 21% from January 22nd - 28th, and 28% from January 29th - February 4th. The mean date of birth was estimated as February 6th with a standard deviation of 17.8 days. The data for 1978 was not included because it was possible that errors may have occurred in estimating the age of pouch young from body measurements (see Chapter 3.0). For the purposes of this study I have taken the breeding season to be from the beginning of January to the end of March.

6.4.2 Fecundity and Pouch-young Mortality

The fecundity of an animal can be defined as the number of offspring produced over an interval of time. For this study fecundity was measured as the proportion of females of reproductive age in any one year having either a young in the pouch, or, a lactating teat if examined in October-November.

It was shown earlier that female Kangaroo Island Wallabies become sexually mature at 9 months of age, just after leaving the pouch (Chapter 4.0). However, they do not give birth until the January - March breeding season. To assess fecundity the animals were divided into Juveniles (1 - 2 years) and Adults (older than 2 years). Except for a trip in late March 1976 only animals caught after the end of the breeding season were scored for the presence or absence of pouch young.

The results for these animals for the years 1975 - 1978 and 1966 - 1969 are shown in Tables 6.14 and 6.15. There was a high fecundity for adults in all years while the fecundity of juveniles fluctuated from year to year. All

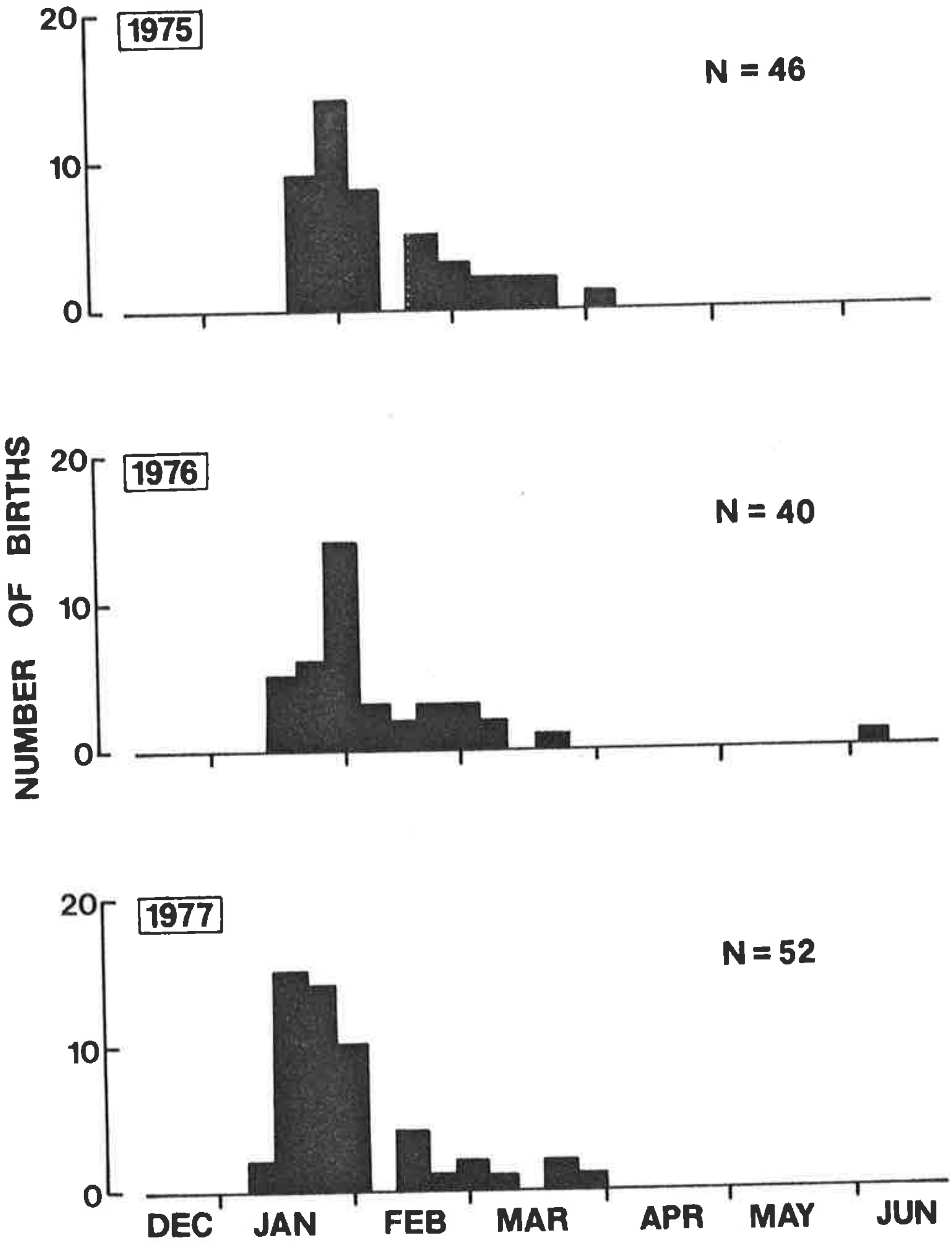


Figure 6.3 Dates of birth of pouch young (in one week periods starting January 1st) for the years 1975, 1976 and 1977.

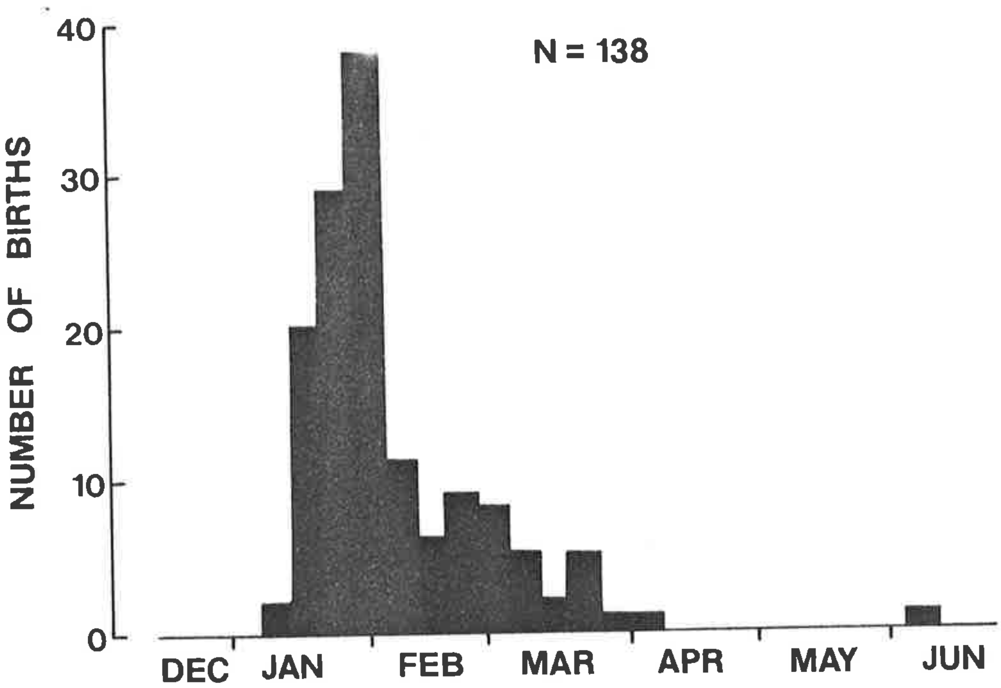


Figure 6.4 Dates of birth of all pouch young examined over the period 1975 - 1977.

TABLE 6.14

PROPORTION OF FEMALES CARRYING A POUCH YOUNG

IN EACH YEAR FROM 1975-1978 (MAIN STUDY AREA)

JUVENILES (1 - 2 YEARS OLD)

Year	Number Examined	Number With A Pouch Young Or Lactating Teat	Proportion Of Females Carrying A Pouch Young
1975	10	10	1.00
1976	19	14	.74
1977	15	6	.40
1978	8	0	0

ADULTS (OLDER THAN 2 YEARS)

Year	Number Examined	Number With A Pouch Young Or Lactating Teat	Proportion Of Females Carrying A Pouch Young
1975	40	38	.95
1976	60	51	.85
1977	53	49	.93
1978	51	43	.84

TABLE 6.15

PROPORTION OF FEMALES CARRYING A POUCH YOUNG IN EACH YEAR, FROM 1966-1969

JUVENILES (1 - 2 YEARS OLD)

Year	Number Examined	Number With A Pouch Young Or Lactating Teat	Proportion Of Females Carrying A Pouch Young
1966	12	11	.92
1967	13	10	.77
1968	22	16	.73
1969	10	9	.90

ADULTS (OLDER THAN 2 YEARS)

Year	Number Examined	Number With A Pouch Young Or Lactating Teat	Proportion Of Females Carrying A Pouch Young
1966	45	43	.96
1967	44	41	.93
1968	87	76	.87
1969	56	52	.93

the juveniles examined in 1975 had pouch young while for 1976, 74% had pouch young and in 1977 it had fallen to 40%. In 1978 none of the juveniles examined had a pouch young. However, the number of animals examined in each year was small. For the 1966 - 1969 period the fecundity of juveniles was high in 1966 and in 1969 but was lower for 1967 and 1968 (77% and 73% respectively).

This method of assessing fecundity does not take into account any pouch young mortality that may occur during the year. To estimate the amount of this mortality the number of animals with a pouch young that were caught in each trip were recorded. The percentage of adult females with pouch young that were captured in each trip are shown in Figure 6.5. If there was no loss of pouch young during the year it would be expected that the proportion with young early in the year would be the same as later in the year. Tables 6.16 and 6.17 show the number with pouch young that were caught in each trip and the expected number for the subsequent trip, if no pouch young mortality occurred.

Pouch young mortality among adult females was negligible in 1975, 1976 and 1977 but was apparently high in 1978. From July to November 1978 the proportion of females with a pouch young fell from 95% to 46%. None of the juveniles sampled in 1978 had a pouch young while for other years the number examined was too small to determine whether young were being lost from the pouch or whether fecundity was lower for this group. In the 1966 - 1969 period pouch mortality was only apparent in 1968 when the number of adults carrying a pouch young fell from 97% in May to 76% in

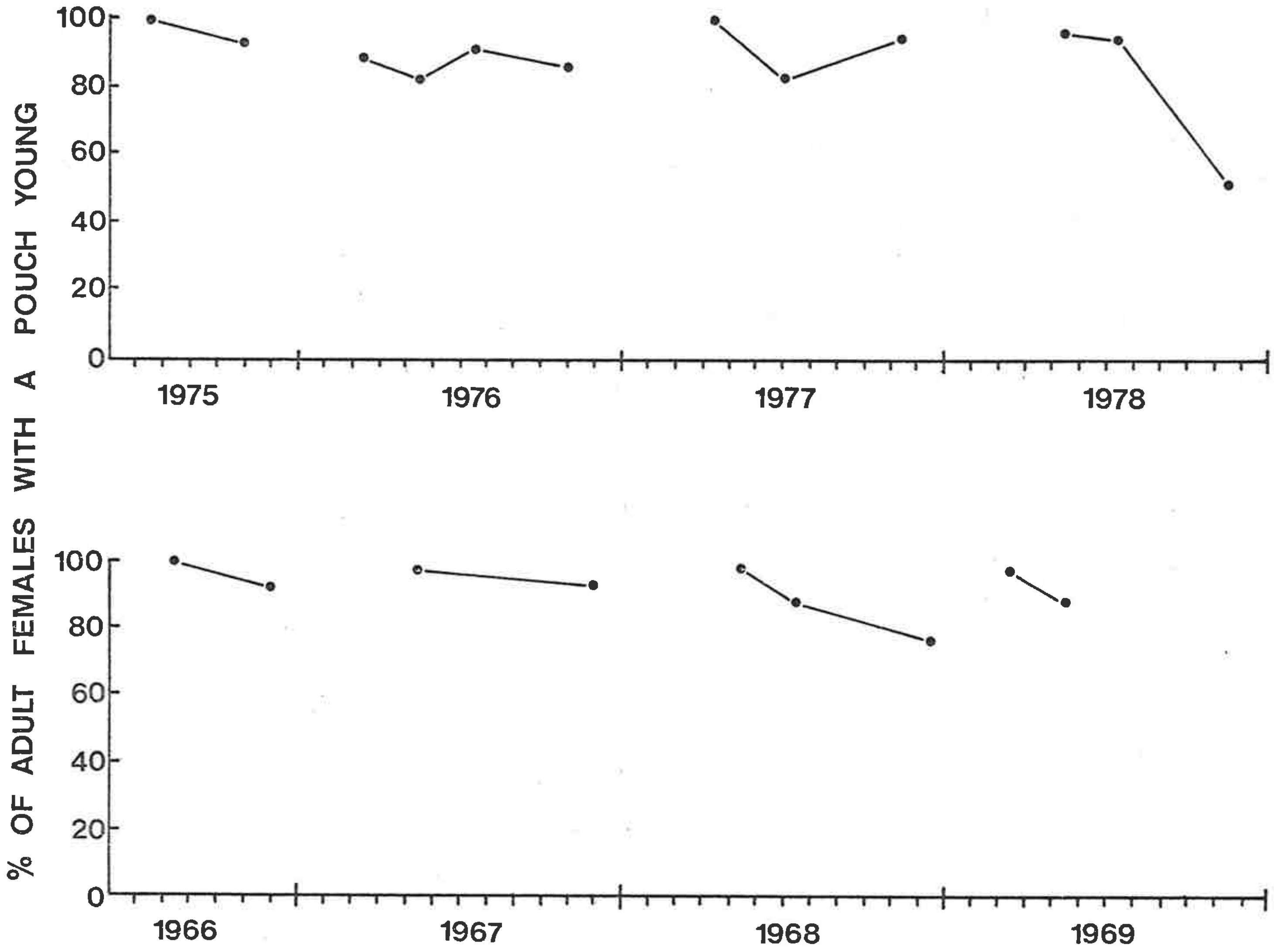


Figure 6.5 Percentage of Adult Females with a Pouch Young or Lactating.

TABLE 6.16 ESTIMATES OF POUCH-YOUNG MORTALITY IN THE KANGAROO ISLAND WALLABY FOR 1975 - 1978

Trip Date	Number Of Females Capable Of Reproducing	Number Of Pouch Young	Trip Date	Number Of Females Capable Of Reproducing	Number Of Pouch Young	Expected * Number Of Pouch Young If No Mortality
July 1975	21(3)	21(3)	Oct-Nov 1975	25(7)	23(7)	25
March 1976	24(7)	21(5)	May 1976	18(7)	15(5)	16
May 176	18(7)	15(5)	July 1976	12(7)	11(3)	10
July 1976	12(7)	11(3)	Oct-Nov 1976	28(9)	24(5)	26
April 1977	41(7)	41(4)	June-July 1977	22(10)	18(3)	22
June-July 1977	22(10)	18(3)	Nov 1977	21(12)	20(5)	17
May 1978	24(3)	23(0)	July 1978	19(3)	18(0)	18
July 1978	19(3)	18(0)	Nov 1978	11(2)	5(0)	10

Numbers in parentheses refer to the number of Juveniles in the sample.

*Because of the small number of Juveniles in each sample the Expected Number of Pouch Young was only calculated for adults.

TABLE 6.17 ESTIMATES OF POUCH-YOUNG MORTALITY IN THE KANGAROO ISLAND WALLABY FOR 1966 - 1969

Trip Date	Number Of Females Capable Of Reproducing	Number Of Pouch Young	Trip Date	Number Of Females Capable Of Reproducing	Number Of Pouch Young	Expected Number Of Pouch Young If No Mortality
August 1966	29(9)	29(8)	Nov-Dec 1966	25(3)	23(3)	25
May 1967	34(10)	33(9)	Nov-Dec 1967	25(8)	23(5)	24
May 1968	36(8)	35(6)	July 1968	34(10)	30(9)	33
July 1968	34(10)	30(9)	Dec 1968	25(7)	19(4)	22
March 1969	30(4)	29(4)	May 1969	32(12)	28(10)	31

December.

6.4.3 Sex Ratios

A survey of the sex ratio of pouch young of marsupials by Caughley and Kean (1964) showed that in only one species, a macropod, was there a significant difference in the numbers of males and females (Table 6.18). The results for the Kangaroo Island Wallaby from both the present study and from the period 1966 - 1969 showed that although there were slightly more males than females this was not significantly different from a 1 : 1 ratio (Table 6.19).

Newsome (1977) found that in red kangaroos in central Australia the sex ratio at birth was not different from 1 : 1 and this continued to be so up to 3 years of age. After that age females started to outnumber the males for each age group examined. From about 3 years of age the males become sexually mature and the difference in size between the sexes is more apparent. Newsome concluded that there was probably selective predation by man on the larger males which resulted in the biased sex ratio. Any differences in natural mortality between the sexes would have been masked by the human predation. In the present study the wallaby population was protected from human interference so that any changes in the sex ratio of the different age groups would reflect differences in their survival.

The total number of animals in each age class that were caught in each year for the period 1975 - 1978 are shown in Table 6.20. There was no significant difference in the number of males and females in each age group up to five years. However, for animals older than five years there were

TABLE 6.18 A SURVEY OF THE SEX RATIO OF POUCH YOUNG FOR SEVERAL SPECIES OF MARSUPIALS, FROM CAUGHLEY AND KEAN (1964) AND THE PRESENT STUDY

Species	Number Of Females	Number Of Males	P_f*	X_1^2	
Didelphidae					
Didelphis virginiana	606	632	.49	.546	N.S.
Phalangeridae					
Trichosurus vulpecula	425	483	.47	3.705	N.S.
Peramelidae					
Perameles nasuta	55	57	.49	.036	N.S.
Macropodidae					
Setonix brachyurus	322	279	.54	3.077	N.S.
Macropus robustus	315	281	.53	1.940	N.S.
M. rufus	208	202	.51	.088	N.S.
M. canguru	178	242	.42	9.752	$.001<P<.05$
M. eugenii	196	233	.46	3.191	N.S.
(This study and unpublished results of Dr. S. Barker)					

* P_f is the proportion of females

TABLE 6.19

SEX RATIO OF POUCH YOUNG IN THE KANGAROO ISLAND WALLABY FOR THE PERIODS 1966-1969 AND 1975-1978

Year	Number Of Females	Number Of Males	P_f	X_1^2	
1966	18	18	.50	0	N.S.
1967	18	23	.44	.610	N.S.
1968	39	50	.44	1.360	N.S.
1969	31	34	.48	.139	N.S.
Total	106	125	.46	1.563	N.S.
1975	23	30	.43	.925	N.S.
1976	29	30	.49	.016	N.S.
1977	22	28	.44	.720	N.S.
1978	16	20	.44	.444	N.S.
Total	90	108	.45	1.636	N.S.

significantly more females, suggesting that females are surviving better than males in the older age groups.

TABLE 6.20

TOTAL NUMBER OF MALES AND FEMALES OF EACH AGE-CLASS THAT WERE CAUGHT IN EACH YEAR FOR THE 1975-1978 PERIOD. DATA FOR EACH YEAR WAS ADDED TOGETHER

Age Class (Years)	Pouch Young	1-2	2-3	3-4	4-5	Older Than 5
Males	108	75	47	38	29	69
Females	90	61	50	44	28	96
Sex Ratio(P_f)	.45	.45	.52	.54	.49	.58
X_1^2	1.636	1.441	0.093	0.439	0.018	4.418
	N.S.	N.S.	N.S.	N.S.	N.S.	$.025<P<.05$

6.4.4 Presence of More Than One Young in the Pouch

Two females out of the 262 caught with pouch young were carrying two young. The ages of one pair differed by 31 days, which is only slightly longer than the length of gestation (Calaby and Poole, 1971). It is probable that after the first young was born, and the normal post-partum fertilization occurred, the mechanism initiating embryonic diapause failed. Hence normal embryonic development took place rather than being delayed at the blastocyst stage. The second pair of young were true twins as they were the same age.

6.5 SURVIVAL RATES AND LIFE TABLES

6.5.1 Estimation of Survival Rates.

Survival curves for the various cohorts of both males and females over the period 1975 - 1978 are shown in Figures 6.6 and 6.7. These curves were constructed from the data used to estimate the Minimum Number of Animals Known to be Alive. This assumes that if an animal disappears from the population it has died rather than emigrated. This assumption is supported by the lack of evidence for any significant dispersal of animals.

By dividing the population into 3 age-classes it was possible to see which age group had the highest mortality. The age-classes used were, Juveniles (from 0 - 1 years after emerging from the pouch), Young Adults (1 - 3 years after leaving the pouch) and Old Adults (more than 3 years since leaving the pouch).

Survival was different between age groups, between years for a particular age group, and in some seasons between the sexes. Juveniles just out of the pouch suffered a high mortality over their first summer. Tables 6.21 and 6.22 present the survival data for males and females over their first year after leaving the pouch. From the time they leave the pouch in October - November to the end of the summer period in March - April there was a 35% mortality of males and females of the 1975 cohort, while for the 1976 cohort over the same period mortality was 35% for females and 44% for males. The number of juveniles surviving one year after leaving the pouch was, for the 1975 cohort, 58% for females and 50% for males. For the 1976 cohort survival was 56% for

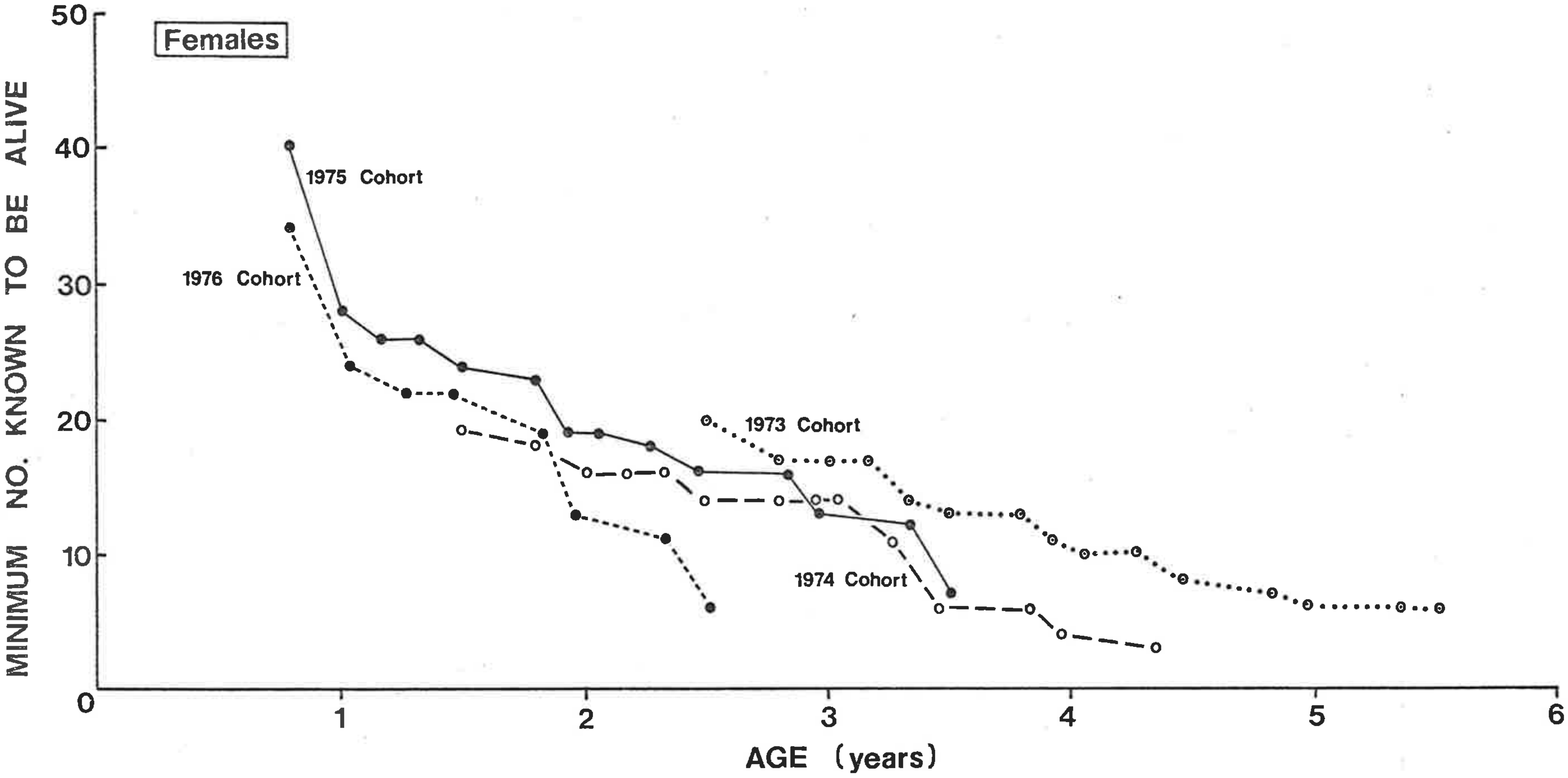


Figure 6.6 Survival curves for females over the 1975 - 1978 period. Each curve follows the survival of a particular cohort.

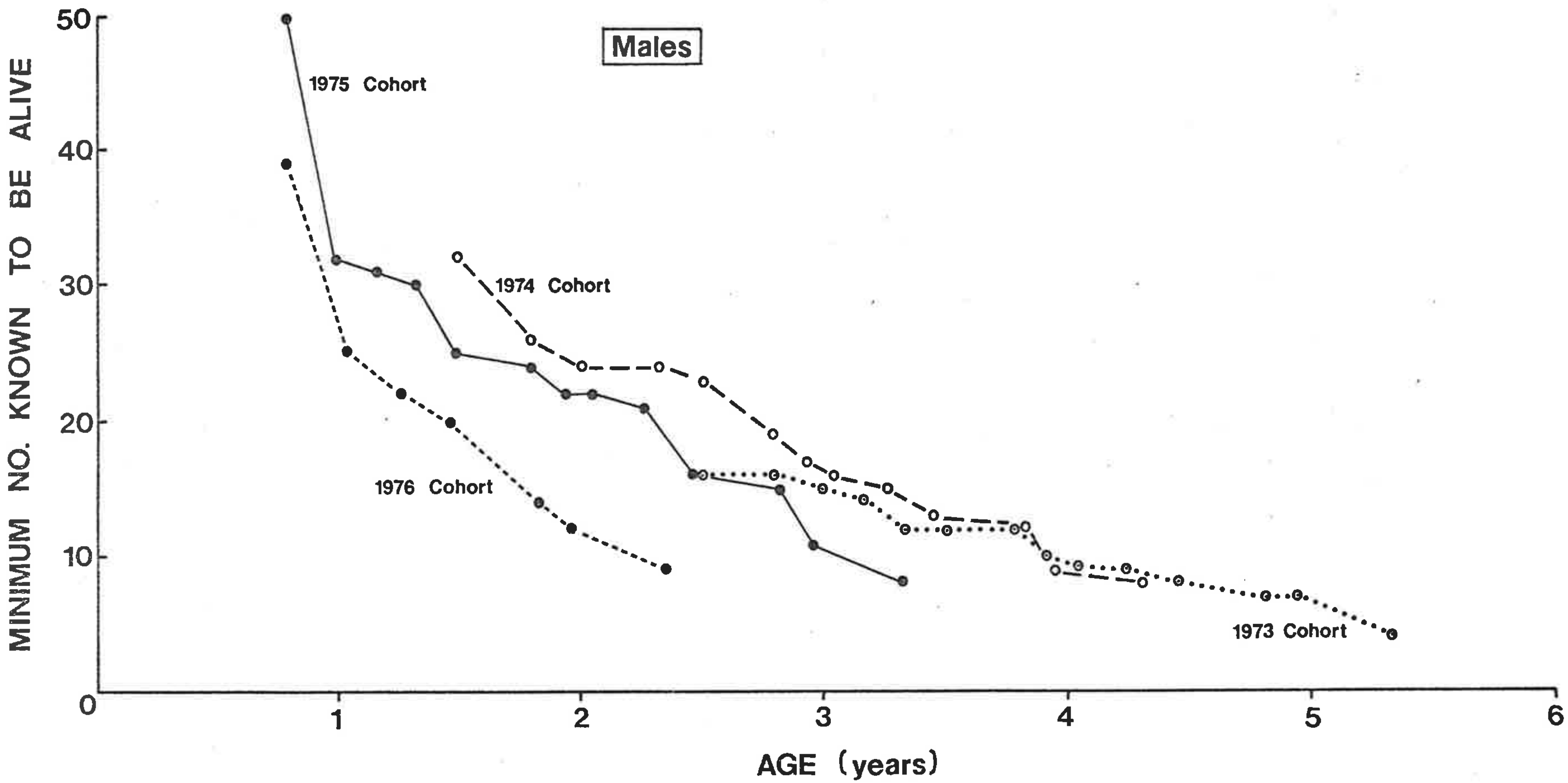


Figure 6.7 Survival curves for males over the 1975 to 1978 period. Each curve follows the survival of a particular cohort.

TABLE 6.21

SURVIVAL OF JUVENILE MALES

	1975	1976	1977
Maximum potential Number of young leaving the pouch in Oct-Nov each year.	50	48	36
Actual number of young leaving the pouch in Oct-Nov.	48	39	28
Number of juveniles alive in the following January.	32	25	19
Number of juveniles alive in March-April.	31	22	15*
Number of juveniles alive in June - July.	25	20	-
Number of juveniles alive one year after leaving the pouch	24	14	-

*Denotes number alive in May.

TABLE 6.22

SURVIVAL OF JUVENILE FEMALES

	1975	1976	1977
Maximum potential Number of young leaving the pouch in Oct-Nov each year.	42	41	30
Actual number of young leaving the pouch in Oct-Nov.	40	34	23
Number of juveniles alive in the following January.	28	24	15
Number of juveniles alive in March-April.	26	22	13*
Number of juveniles alive in June-July.	24	22	-
Number of juveniles alive one year after leaving the pouch.	23	19	-

*Denotes number alive in May.

females and 36% for males.

The annual survival rate for all adults (Young adults plus Old adults) was calculated from the number present in October - November of one year to the number still alive in October - November of the following year (Table 6.23). For males it was 69% for 1975 - 1976 and 55% for 1976 - 1977. For females it was 72% for 1975 - 1976 and 53% for 1976 - 1977.

The percentage mortality for each age-class over summer and winter for 1975 - 1978 is shown in Table 6.24. The young adult animals had the lowest summer mortality rate. In both sexes mortality was higher during the 1977 summer than in 1976. For the old adults the mortality rate was higher than the young adults but not as high as in juveniles. There was little difference between the sexes but once again mortality was higher in 1977 than 1976. In the winter period the juvenile females had the lowest mortality, which was 12% in 1976 and 14% in 1977. Juvenile males and old males had the highest mortality in the 1976 winter (23% and 22% respectively) while in 1977 both they, and the old females, had a 36% mortality. The winter mortality of the young adults was higher than over the summer and was 18% for both males and females in 1976, and 25% and 24% for males and females in 1977.

In 1978 a large number of dead wallabies were found on the study area and many animals were seen to be in poor condition (see Chapter 7.0). The highest mortality occurred from late summer to the end of winter as judged by the number of dead animals found. Estimates of mortality are only available from November 1977 up to May 1978 and so are not

TABLE 6.23

SURVIVAL OF ADULTS (YOUNG ADULTS AND OLD ADULTS)

MALES

	1975	1976	1977
Number of Adults present in Oct-Nov.	91	87	62
Number of Adults alive in the following January.	82	75	54
Number of Adults alive in March-April.	79	69	44*
Number of Adults alive in June-July.	68	56	-
Number of Adults alive after one year.	63	48	-

FEMALES

	1975	1976	1977
Number of Adults present in Oct-Nov.	92	89	66
Number of Adults alive in the following January.	82	77	49
Number of Adults alive in March-April.	79	68	44*
Number of Adults alive in June-July.	67	55	-
Number of Adults alive after one year.	66	47	-

*Denotes number alive in May.

TABLE 6.24 PERCENTAGE MORTALITY FOR THREE AGE-CLASSES OVER SUMMER AND WINTER, FROM 1975-1978

Time Period	% Mortality					
	Juveniles		Young Adults		Old Animals	
	Males	Females	Males	Females	Males	Females
Oct/Nov 1975-Mar 1976	35.4	35.0	9.5	5.7	16.3	19.3
Mar 1976-Oct/Nov 1976	22.6	11.5	18.4	18.2	22.0	15.2
Oct/Nov 1976-April 1977	43.6	35.3	16.3	21.6	25.0	25.0
April 1977-Nov 1977	36.4	13.6	25.0	24.1	36.4	35.9
Nov 1977-May 1978	46.4	43.5	41.4	34.3	39.5	32.3

strictly comparable to the estimates from the previous years. However they do suggest that a large decline in the population occurred over 1978. From November 1977 to May 1978 the total population size decreased by 35%, compared with a decrease of 25% for the 1975 - 1976 period. Juvenile mortality for the 1977 - 1978 period was 43% for females and 46% for males. Although these rates are higher than in previous years, particularly for females, it was the adult animals that showed a greater increase in mortality.

6.5.2 Life-Tables

A life-table is a convenient form for summarizing the age-specific mortality pattern of a population.

Life-tables may be constructed in two ways. The survival of a cohort of animals is followed until all have died (an age-specific life-table) or the fate of an imaginary cohort is found by determining the age structure of a sample of individuals from the population at some point in time (a time-specific life-table). For the first type of life-table the population may be stationary or fluctuating but for the second the sample is assumed to have come from a population with a stationary age-distribution and zero intrinsic rate of increase.

For the Kangaroo Island Wallaby an age-specific life-table was constructed by obtaining data from an 'average' survival curve. This curve summarizes the number of animals still alive in each of the cohorts (Figures 6.6 and 6.7) by drawing a line of best fit through all the points. The first age interval was 3 months as survival was estimated from the time the young left the pouch (at 8 - 9 months) to one year of age. All subsequent points were at yearly intervals. The survival curve was extended beyond 5 years by incorporating the number of older animals that were still alive and caught during the study. This curve, although it averages out the variations that occur in recruitment and mortality from year to year, does present a useful summary of the mortality pattern of the population for comparison with other species. The figures obtained in the present study were transformed into the percentage of animals surviving in each age group (Figure 6.8).

From the frequency distribution of the numbers surviving in each age-class a composite life-table was constructed for both males and females from a cohort of 1000 young animals leaving the pouch (Tables 6.25 and 6.26). Age-specific mortality is also presented in graphical form in Figure 6.9. Although juvenile mortality was initially high for both males and females in their first few months after leaving the pouch, it did not show the subsequent rapid decline as reported by Caughley (1966) for several species of mammals. Nevertheless the general shape of the curves is similar. For males the mortality rate stayed relatively constant at about 30% for each age class up to 9 - 10 years, before it sharply increased, so that all had died by 12 years of age. The mortality rate of the females declined slowly after the first year reaching a minimum of 11 - 12% in the 7 - 9 year age-class before increasing again. No females survived beyond the 14 - 15 year age-class. Thus, females have a similar mortality rate to males in their first year after leaving the pouch but their survival in later years is

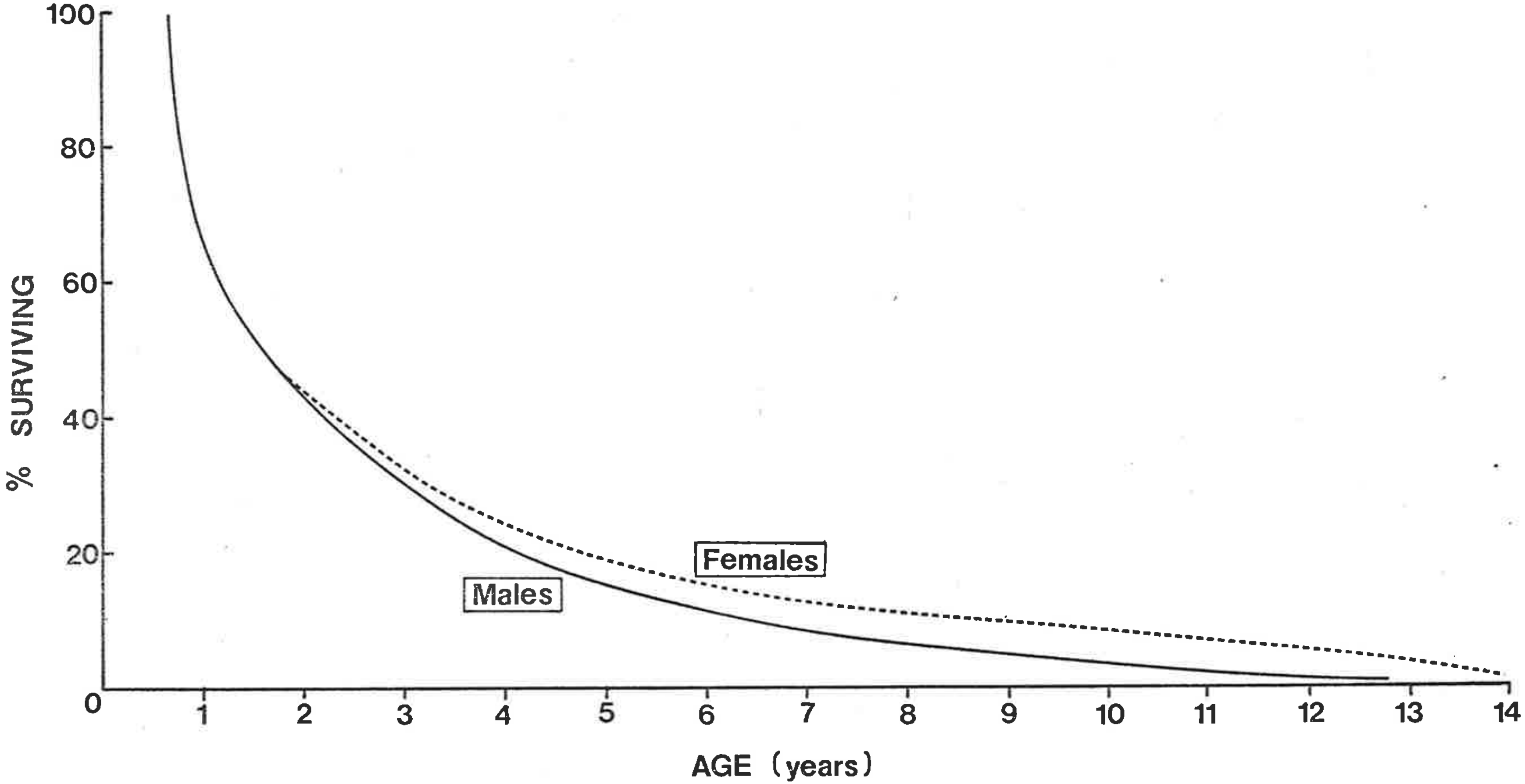


Figure 6.8 Percentage survival of male and female wallabies after leaving the pouch at 8 - 9 months of age.

TABLE 6.25

LIFE TABLE FOR FEMALE KANGAROO ISLAND WALLABIES

Age Class (yrs)	kl_x	kd_x	kq_x	e_x
* 0	1000	350	.350	3.03
1	650	212	.326	3.40
2	438	113	.258	3.80
3	325	75	.231	3.94
4	250	70	.280	3.98
5	180	30	.167	4.33
6	150	30	.200	4.09
7	120	15	.125	3.99
8	105	12	.114	3.43
9	93	13	.140	2.88
10	80	17	.213	2.26
11	63	13	.206	1.74
12	50	22	.440	1.06
13	28	28	1.000	0.50

*Age Class 0 - 1 represents the number of young leaving the pouch at 8 - 9 months of age (October - November).

The other age classes are at one year intervals from birth (January - February).

kl_x = survival, at begining of each age class, out of an initial cohort of 1000 animals leaving the pouch.

kd_x = number dying in age interval.

kq_x = age-specific mortality.

e_x = expectation of life.

TABLE 6.26

LIFE TABLE FOR MALE KANGAROO ISLAND WALLABIES

Age Class (yrs)	kl_x	kd_x	kq_x	e_x
0	1000	354	.354	2.56
1	646	208	.322	2.68
2	438	125	.285	2.72
3	313	105	.335	2.61
4	208	62	.298	2.67
5	146	42	.288	2.60
6	104	31	.298	2.44
7	73	21	.288	2.27
8	52	16	.308	1.98
9	36	11	.306	1.64
10	25	9	.360	1.14
11	16	16	1.000	0.50

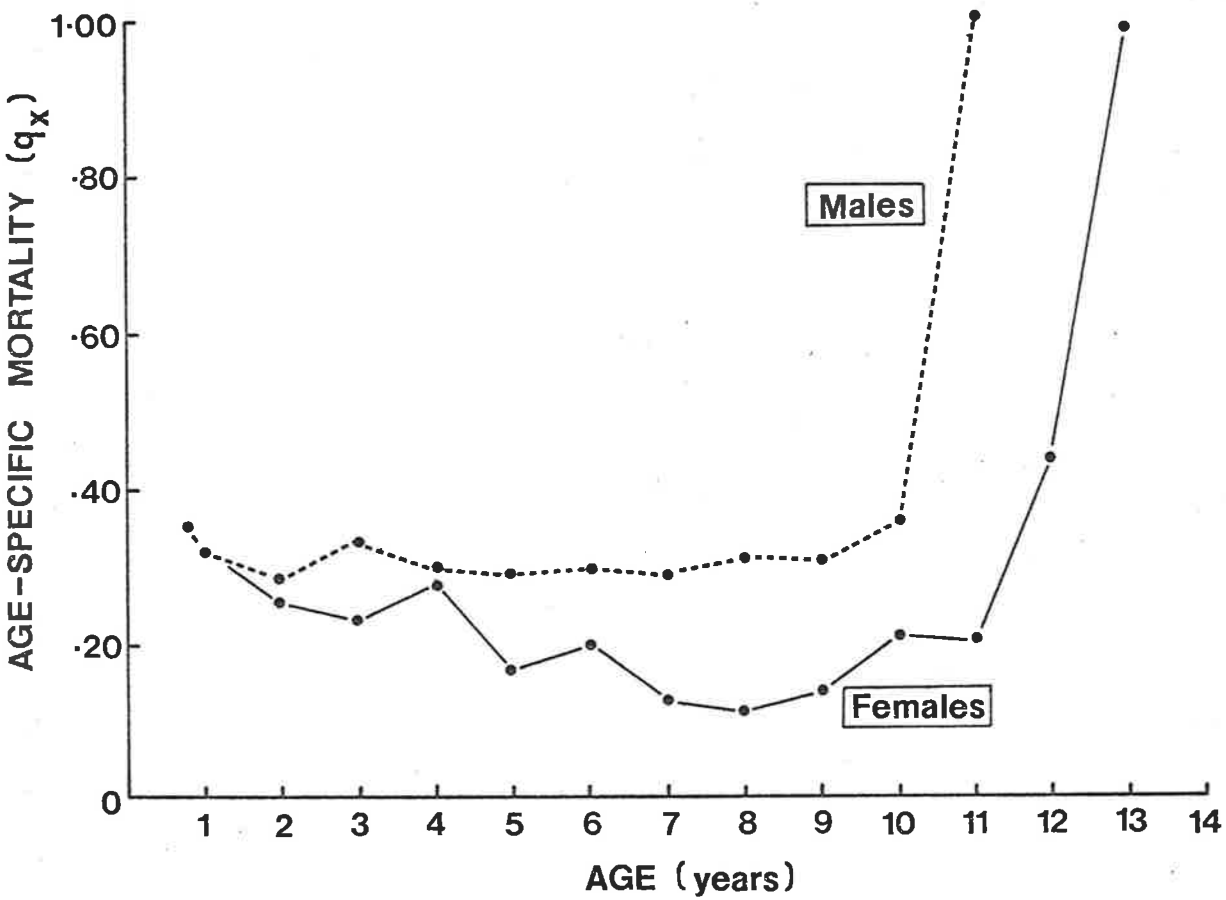


Figure 6.9 Age-specific mortality for male and female wallabies

higher.

6.5.3 Ages of Death Estimated from Skulls Collected on the Study Area and Longevity Records.

All skulls that were collected during each year from 1976 to 1978 were aged either by the stage of tooth eruption or by the molar index method (see Chapter 3.0). The results are shown in Table 6.27. Few skulls were collected in 1976 and 1977 but the number collected in 1978 shows that the highest mortality was in the 3 - 4 year olds and older. It is possible that the number in the youngest age group was under-represented due either to the skulls disappearing quickly because of their fragile nature or to animals dying in the scrub where they could not be found easily. Most of the adult skulls collected were from animals found either on or near the clearing. Not all of the skulls would have come from the Main Study Area population. However it does indicate that a high mortality was widespread at this time, and shows the age groups most affected.

Of the skulls that were collected in 1978 12 animals were older than 9 years, 2 of which were in the 14 - 15 year age group. A number of animals (17 F, 7 M) that had been ear-tagged by Dr. S. Barker between 1965 and 1972 were recaptured during the present study. The dates when first and last caught and their estimated age when last caught are shown in Tables 6.28 and 6.29. It is apparent that females are living longer than males as only 2 of the males caught were older than 9 years compared with 11 females. Many of the older females were still carrying pouch young, the oldest to do so being 13 - 14 years.

TABLE 6.27

AGES OF SKULLS COLLECTED

Age-Class (Years)	Number of Skulls Collected 1976	1977	1978
1 - 2	1	2	9
2 - 3	1	0	3
3 - 4	0	1	22
4 - 5	1	2	12
5 - 6	7	1	9
6 - 7	0		5
7 - 8	0		4
8 - 9	1		11
9 - 10	1		4
10 - 11	1		2
11 - 12	0		2
12 - 13	0		1
13 - 14	0		1
14 - 15	1		2
Total	14	6	87

TABLE 6.28 FEMALES TAGGED BEFORE 1975 AND STILL ALIVE DURING PRESENT STUDY

Number	Date When First Caught	Date When Last Caught	Age When Last Caught	Presence Of Pouch Young
F 88664	26/11/66	26/10/75	10 - 11	+
F 88684	6/12/66	7/11/75	10 - 11	+
F 88725	21/11/67	20/ 7/75	12 - 13	+
F 88927	15/ 5/68	26/10/75	10 - 11	+
F 88930	18/ 5/68	26/10/75	8 - 9	+
F 89051	26/ 7/68	30/10/75	9 - 10	+
F 89111	28/ 5/69	26/10/75	7 - 8	+
F 88541	22/ 8/66	23/ 5/76	11 - 12	-
F 88926	13/ 5/68	21/ 1/76	12	-
F 89115	8/ 3/72	17/ 3/76	5 - 6	+
F 88522	28/ 5/65	6/ 4/77	13 - 14	+
F 88536	19/ 8/66	27/ 6/77	12 - 13	-
F 88710	23/ 5/67	3/ 7/77	11 - 12	+
F 89067	9/12/68	3/ 7/77	9 - 10	+
F 89124	10/ 3/72	7/ 1/77	6	+
F 89130	14/ 3/72	8/ 4/77	7 - 8	+
F 89132	8/ 7/72	10/ 7/78	7 - 8	+

TABLE 6.29 MALES TAGGED BEFORE 1975 AND STILL ALIVE DURING PRESENT STUDY

Number	Date When First Caught	Date When Last Caught	Age When Last Caught
M 89006	8/ 3/69	31/10/75	7 - 8
M 89032	8/ 3/72	17/ 7/75	4 - 5
M 89040	10/ 3/72	19/ 7/75	8+
M 89043	13/ 3/72	28/10/75	8+
M 89047	13/ 3/72	29/ 5/76	9+
M 89034	9/ 3/72	16/ 4/77	6 - 7
M 88797	13/ 5/68	25/ 1/78	11

7.0 SOME ASPECTS OF THE PHYSIOLOGY OF THE KANGAROO ISLAND WALLABY UNDER FIELD CONDITIONS

7.1 INTRODUCTION

The availability of food, water and shelter are important factors influencing the distribution and population size of many animals.

The nitrogen status of macropods can be indicated by the ratio of urea nitrogen to total nitrogen excreted in the urine (Lintern and Barker, 1969; Kinnear and Main, 1975). An animal on a low nitrogen diet retains urea in the kidney (Lintern and Barker, 1969) thus lowering the amount of urea excreted in the urine. The urea retained by the kidney is recycled back to the fore-stomach via parotid saliva and across the stomach wall from the blood supply (Brown and Main, 1967). Recycled urea is converted into living microbial protein in the stomach and subsequently utilized as the main protein source of the host. By examining the ratio of urea nitrogen to total nitrogen in the urine, Barker (1971) concluded that the diet of Kangaroo Island Wallabies in the field was not nitrogen deficient at any time.

Measurements of total body water and water turnover can provide useful indications of the energy and water reserves of an animal in the field (Macfarlane and Howard, 1972). When an animal has more fat there is less water per unit weight while in lean animals or those suffering from starvation or disease an excess of body water is present. There is a dry summer period on Kangaroo Island when the pasture dries off and many of the rivers cease flowing (Bauer, 1959) although in Flinders Chase National Park artificial sources of water would still be available to the wallabies. Barker (1971) found that in field animals there was a reduction in excretion of water in urine and faeces in summer which was similar to the pattern of water excretion in laboratory animals on a restricted water intake (Barker, Lintern and Murphy, 1970). Hence a more detailed knowledge of the pattern of water usage of these animals could provide a better understanding of their physiology and behaviour in relation to survival over the summer months. This kind of investigation has never been done in a field population of the Kangaroo Island Wallaby.

In this study water turnover, urine and faecal water loss, urine and plasma concentrations and measurement of body fluid compartments were used to investigate the water metabolism of a population of free-living Kangaroo Island Wallabies. At the same time measurements of body weight, haematocrit and plasma protein concentration provided an indication of the physical condition of the animals.

7.2 RESULTS

7.2.1 Water Turnover

In Kangaroo Island Wallabies in the field there were no significant changes in total body water (Figure 7.1) at any time of the year ($F_{(10,252)} = 0.67$, $P>.05$).

The tritiated water turnover values of free-living wallabies in Flinders Chase are shown in Table 7.1 and Figure 7.2. As no difference was found in any month between males and females ($P>.05$) the data was pooled. Despite the small number of animals recaptured during the summer months the results do show that water turnover was reduced. The mean water turnover (ml/kg/day) for the summer of 1976 (January

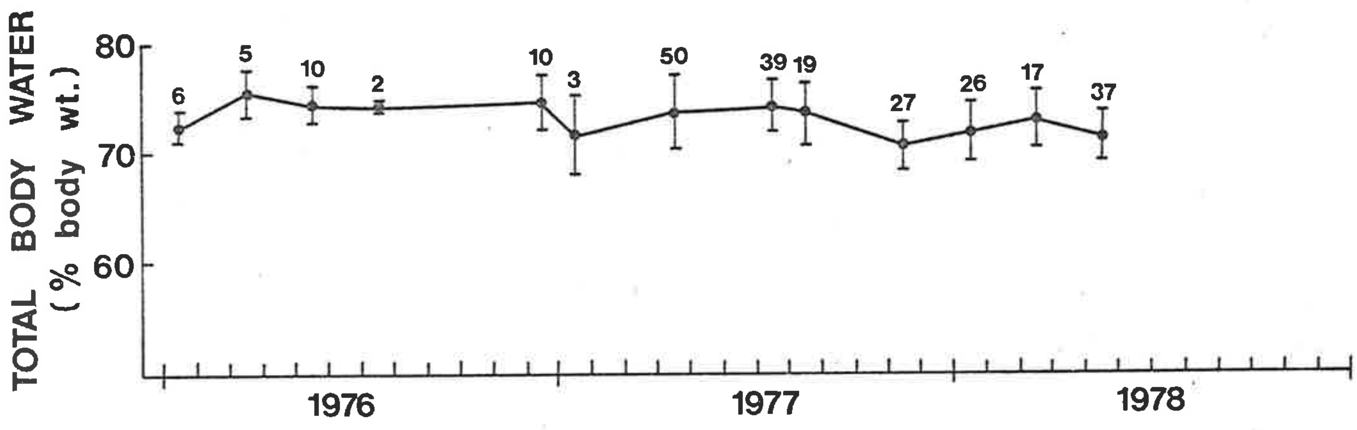


Figure 7.1 Measurements of Total Body Water of Kangaroo Island Wallabies at different times of the year.
Dots represent mean values and vertical lines the standard deviations.
Numbers above vertical lines represent the sample size.

TABLE 7.1 WATER TURNOVER OF KANGAROO ISLAND WALLABIES IN FLINDERS CHASE NATIONAL PARK

Date	% Total Body Water/day	ml/day	ml/kg/day	ml/kg$^{.82}$/day	N
January 1976	7.51 ± 2.04	245 ± 70	54.5 ± 15.4	70.8 ± 16.9	6
March 1976	6.63 ± 2.46	284 ± 109	50.0 ± 17.8	68.2 ± 24.5	5
May 1976	18.33 ± 2.62	584 ± 189	137.0 ± 20.3	176.8 ± 25.8	10
July 1976	10.71 ± 5.40	501 ± 281	98.0 ± 66.5	132.0 ± 86.3	2
December 1976	9.25 ± 2.58	327 ± 155	69.5 ± 20.1	90.4 ± 26.1	10
January 1977	12.18 ± 7.58	453 ± 217	88.7 ± 57.1	118.3 ± 72.1	3
April 1977	10.73 ± 2.42	366 ± 138	79.5 ± 18.1	104.3 ± 24.7	20
July 1977	24.22 ± 5.06	912 ± 343	182.5 ± 38.5	242.8 ± 56.3	10
August 1977	23.35 ± 4.19	808 ± 208	171.6 ± 31.7	225.0 ± 36.9	12
November 1977	10.48 ± 2.46	412 ± 100	74.5 ± 17.3	100.9 ± 23.2	10
January 1978	5.50 ± .52	212 ± 107	40.3 ± 3.5	54.0 ± 7.8	3
March 1978	8.43 ± .55	269 ± 194	62.5 ± 6.4	79.0 ± 4.2	2
May 1978	15.07 ± 8.44	430 ± 252	109.3 ± 59.4	138.4 ± 75.3	8

Values are means ± standard deviations

Analysis of Variance

$F_{(9,86)}$	27.54 ***	14.29 ***	28.51 ***	29.00 ***

*** = Significant at 0.1% level.

Values for July 1976 and January 1977 were omitted from analysis of variance due to small sample sizes.
Values for January 1978 and March 1978 were pooled to give a larger sample size for for the summer period of 1978.

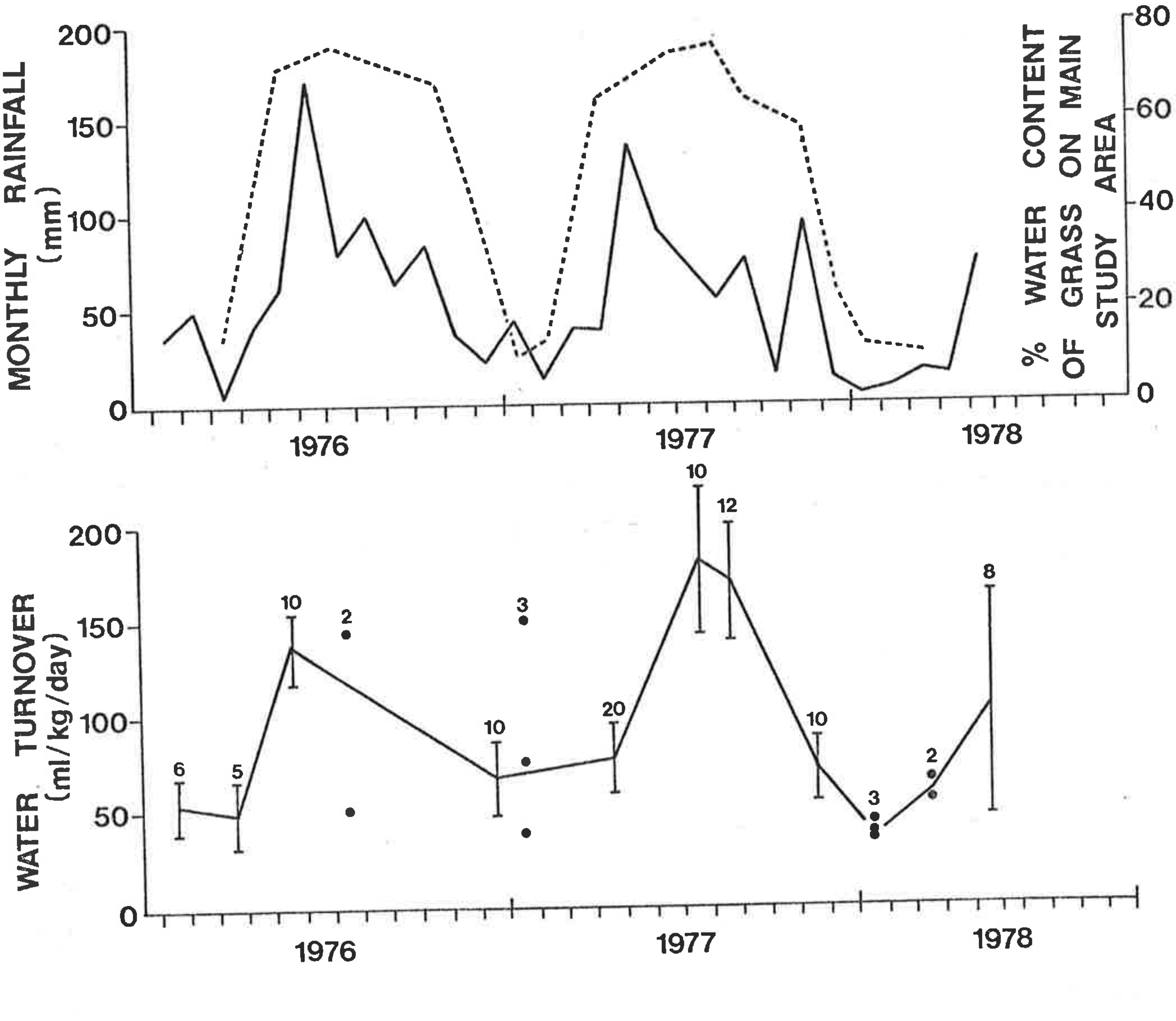


Figure 7.2 Seasonal changes in water turnover (bottom figure) of Kangaroo Island Wallabies in Flinders Chase National Park.
Top figure shows the seasonal distribution of rainfall over the study period (solid line) and the water content of grass on the Main Study Area (dotted line).

and March) was 52.5 ± 15.8, for 1977 (December 1976 and January 1977) it was 73.9 ± 30.3, and for the 1978 summer (January and March) was 49.2 ± 12.8. The higher water turnover obtained for the 1977 summer period was due to one animal with a turnover of 151 ml/kg/day.

During the winter months higher values for water turnover were obtained, except for July 1976 when only two animals were recaptured. The values obtained were 145 and 51 ml/kg/day. In the other winter months the mean turnovers ranged from 109.3 ± 59.4 ml/kg/day in May 1978 to 182.5 ± 38.5 in July 1977.

The lowest mean water turnover was 40.3 ± 3.5 ml/kg/day in January 1978. This is comparable to that found in free-ranging red kangaroos and euros during summer in north-western New South Wales, 39.5 ± 1.41 and 39.4 ± 2.29 ml/kg/day respectively (Dawson, Denny, Russell and Ellis, 1975). However, these authors pointed out that environmental conditions at this time were more mild than in the preceding summer. Kaethner and Good (1975) found that in captive Kangaroo Island Wallabies water turnover was highest in December (104.2 ml/kg/day), coinciding with the onset of hot weather. However these animals had water available at all times (M. Kaethner, pers. comm.) and were thus turning over more water due to increased use for thermoregulation. The field situation appears to be different as wallabies are conserving water during the summer. The intake of water with their feed is much higher in winter than in summer so that although wallabies in summer may imbibe more free water their total water intake is less. A comparison of water turnovers of other species of macropods under various conditions is shown in Table 7.2.

7.2.2 Urine and Faecal Water Loss

Results are presented separately for males and females in Tables 7.3 - 7.6.

There was a significant reduction in urinary water loss during the summer months while osmotic and electrolyte concentrations increased for both males and females. The maximum urine osmolality (1650 m-osmoles/kg) was obtained from a female caught in January 1977. The mean values obtained are similar to those found in quokkas on Rottnest Island (Bentley, 1955) but are lower than for red kangaroos and euros (Dawson and Denny, 1969). Electrolyte concentrations were considerably lower than for red kangaroos and euros.

The water content of the faeces declined during the summer months. However, more water was actually lost via the faeces during the summer. This is because the more indigestible diet over summer causes the excretion of a greater amount of faecal matter.

7.2.3 Plasma Osmotic and Electrolyte Concentration

There were significant changes in the osmotic concentration of the plasma of males but not females from April 1977 to November 1978 (Table 7.7).

For males the data showed a trend of increasing osmotic concentration over summer to early winter followed by a decrease later in the year. Although there was no significant seasonal difference in the values for females there was a similar trend in that the maximum value occurred in January 1978.

There were no significant changes in the sodium or

TABLE 7.2 TRITIATED WATER TURNOVER OF SOME MACROPODS UNDER VARIOUS ENVIRONMENTAL CONDITIONS

Species	Conditions	Water Turnover (ml/kg/day)	Reference
Petrogale inornata (Rock Wallaby)	Free - living	80.7	Kennedy and Heinsohn (1974)
	Captive, water *ad lib.*	112	
	no water	80.8	
Macropus agilis (Agile Wallaby)	Captive, no water	60	
Megaleia rufa (Red Kangaroo)	Free - living	39.5	Dawson, Denny, Russell and Ellis (1975)
Macropus robustus (Euro)	Free - living	39.4	
Macropus eugenii (Kangaroo Island Wallaby)	Captive, Water *ad lib.*	66.5 (Min) 104.2 (Max)	Kaethner and Good (1975)
Macropus eugenii	Free - living	40.3 (Min) 182.5 (Max)	This Study

TABLE 7.3 URINE EXCRETION IN MALES

Trip	Jan 1977	April 1977	Jun/Jul'77	Nov 1977	Jan 1978	March 1978	May 1978	Fs
ml/12 hrs	34.8 ± 29.8	114.7 ± 61.6	125.6 ± 79.7	120.4 ± 51.8	23.2 ± 12.1	70.9 ± 54.0	88.8 ± 51.8	7.14***
ml/kg$^{.82}$/12 hrs	9.0 ± 8.2	28.1 ± 13.7	32.8 ± 16.6	26.2 ± 8.7	6.7 ± 4.5	19.6 ± 13.6	23.1 ± 10.2	9.28***
Osmolality (milli-osmoles/kg)	1298 ± 251 (1625)	592 ± 205 (890)	604 ± 184 (990)	689 ± 205 (1180)	1073 ± 237 (1340)	695 ± 263 (1150)	507 ± 106 (685)	22.17***
Na^+ (mEqv/l)	115.7 ± 91.7 (278.3)	53.2 ± 27.0 (95.7)	62.8 ± 24.9 (108.7)	91.4 ± 53.6 (195.7)	106.5 ± 52.4 (173.9)	71.7 ± 47.4 (150.0)	39.0 ± 30.6 (130.4)	4.38***
K^+	151.0 ± 89.7 (297.4)	49.9 ± 17.8 (80.8)	60.7 ± 32.4 (141.0)	77.7 ± 41.8 (153.8)	143.8 ± 51.2 (220.5)	60.6 ± 44.8 (128.2)	38.0 ± 19.5 (85.9)	12.61***
Sample Size	10	18	16	15	12	7	13	

Values are means ± standard deviations
Values in parentheses are maximum values for urine osmolality
Fs = Variance Ratio
n.s. = not significant
* = significant at 5% level
** = significant at 1% level
*** = significant at .1% level

TABLE 7.4 URINE EXCRETION IN FEMALES

Trip	Jan 1977	April 1977	Jun/Jul'77	Nov 1977	Jan 1978	March 1978	May 1978	Fs
ml/12 hrs	48.9±31.7	121.5±60.5	161.6±55.5	113.0±43.8	42.4±38.7	79.2±43.8	97.0±24.7	10.55***
ml/kg$^{.82}$/12 hrs	12.8± 8.4	32.8±13.7	44.8±11.2	30.1±12.8	12.2±10.9	22.9±12.9	29.5± 8.0	12.01***
Osmolality (milliosmoles/kg)	1039± 340 (1650)	582± 206 (1150)	524± 115 (765)	655± 182 (1145)	996± 395 (1600)	654± 235 (1060)	399± 50 (440)	9.87***
Na^+ (mEqv/l)	107.6±54.5 (173.9)	63.7±21.0 (89.1)	54.3±15.9 (71.7)	88.2±38.3 (213.0)	102.8±62.2 (187.0)	70.2±59.4 (195.7)	46.0±31.7 (91.3)	3.22**
K^+	85.1±19.8 (123.1)	48.6±15.4 (94.9)	38.0±11.9 (65.4)	82.6±51.2 (230.8)	139.0±102.4 (307.7)	61.4±42.6 (154.4)	31.3±13.9 (52.6)	6.58***
Sample Size	12	$^{+}$16	11	14	14	11	7	

$^{+}$Sample size for urine volume measurements was 13.

TABLE 7.5 FAECAL EXCRETION IN MALES

Trip	April 1977	June/July 1977	Nov. 1977	Jan. 1978	March 1978	May 1978	Fs
Faecal Moisture							
gm/12 hrs	23.5 ± 14.0	21.7 ± 16.5	18.2 ± 12.5	21.3 ± 12.4	32.9 ± 24.7	40.1 ± 18.9	3.53*
$gm/kg^{.82}/12$ hrs	5.7 ± 3.3	5.9 ± 3.9	3.9 ± 2.3	5.5 ± 2.2	8.4 ± 4.0	10.3 ± 3.0	6.75***
%	52 ± 6	58 ± 6	57 ± 9	51 ± 5	49 ± 5	53 ± 5	3.53*
Dry Faeces							
gm/12 hrs	20.1 ± 9.9	14.4 ± 8.4	11.9 ± 5.8	19.8 ± 9.2	30.6 ± 17.4	34.6 ± 15.1	8.74***
$gm/kg^{.75}/12hrs$	5.6 ± 2.7	4.4 ± 2.3	3.0 ± 1.4	5.8 ± 1.9	9.1 ± 2.9	9.9 ± 2.4	17.05***
Sample Size	18	16	15	13	5	13	

Fs = Variance Ratio
n.s. = Not Significant
* = Significant at 5% level
** = Significant at 1% level
*** = Significant at .1% level
Values are means ± standard deviations.

TABLE 7.6 FAECAL EXCRETION IN FEMALES

Trip	April 1977	June/July 1977	Nov. 1977	Jan. 1978	March 1978	May 1978	Fs
Faecal Moisture							
gm/12 hrs	27.5±15.0	13.9±14.3	15.5± 8.0	17.7± 7.9	24.9±11.9	31.2±13.2	3.28*
gm/kg$^{.82}$/12 hrs	7.6± 3.5	3.9± 3.7	4.1± 2.2	5.8± 2.8	7.2± 4.1	9.4± 3.2	3.65**
%	56± 6	58± 7	60± 11	48± 5	47± 6	47± 6	8.21***
Dry Faeces							
gm/12 hrs	20.2± 8.1	8.5± 6.0	10.0± 5.2	18.8± 6.6	27.0±11.4	34.0± 9.6	12.52***
gm/kg$^{.75}$/12 hrs	6.2± 2.1	2.7± 1.8	2.9± 1.4	6.8± 2.8	8.6± 3.8	11.3± 1.6	14.50***
Sample Size	16	10	10	14	11	6	

TABLE 7.7 PLASMA OSMOTIC AND ELECTROLYTE CONCENTRATIONS

Values are means ± standard deviations.

MALES

Date Of Collection	Sample Size	Osmolality (m-osmoles/kg)	Sodium Conc. (m-Eqv/l)	Potassium Conc. (m-Eqv/l)
April 1977	6	283 ± 9.3	139.1 ± 8.7	3.0 ± .6
November 1977	5	288 ± 7.6	133.5 ± 8.5	3.3 ± .7
January 1978	10	304 ± 11.0	138.9 ± 6.6	3.8 ± 1.0
March 1978	4	312 ± 21.8	133.8 ± 2.6	3.3 ± .6
May 1978	7	310 ± 13.5	132.4 ± 3.2	3.2 ± .7
November 1978	5	287 ± 7.6	134.7 ± 6.0	3.0 ± .3
$F_{(5,31)}$		6.33 ***	1.41 N.S.	1.23 N.S.

FEMALES

Date Of Collection	Sample Size	Osmolality (m-osmoles/kg)	Sodium Conc. (m-Eqv/l)	Potassium Conc. (m-Eqv/l)
April 1977	7	289 ± 23.9	133.2 ± 6.0	2.7 ± .4
November 1977	6	292 ± 7.5	131.1 ± 5.4	2.8 ± .3
January 1978	13	304 ± 12.7	134.6 ± 6.5	3.3 ± .5
March 1978	8	290 ± 9.3	138.6 ± 9.9	3.0 ± .5
May 1978	7	294 ± 21.4	132.2 ± 4.8	2.9 ± .5
November 1978	4	291 ± 6.3	130.0 ± 6.2	3.2 ± .7
$F_{(5,39)}$		1.48 N.S.	1.35 N.S.	1.79 N.S.

potassium ion concentrations for males or females at any time of the year.

It is possible that the changes observed in the osmolality of the plasma of males reflects changes in urea concentrations. Barker (1971) found that in field animals plasma urea levels fluctuated during the year although they did not seem to be correlated with any environmental conditions. However, wallabies on a restricted water intake excreted less urea than control animals and maintained higher plasma urea concentrations (Barker, Lintern and Murphy, 1970).

7.2.4 Body Fluid Compartments

Measurement of body fluid compartments was achieved at the end of summer (March 1978) and in winter (May 1978). An attempt to repeat these observations in November 1978 resulted in only 4 animals being measured due to technical problems. The results for March and May are presented in Table 7.8 while those for November are shown separately (Table 7.9). There were no significant changes in total body water, plasma volume, blood volume, interstitial fluid volume, and intra-cellular fluid volume between March and May.

Blood volume was calculated from plasma volume/plasmatocrit, where plasmatocrit = 1.0 - .91 haematocrit. The value .91 is the ratio of the mean circulatory haematocrit to the true haematocrit obtained by Shield (1971) in quokkas and was the only value available for macropods.

Interstitial fluid volume = extra-cellular volume - plasma volume

Intra-cellular fluid volume = total body water - extra-cellular volume

= cell and gut water

TABLE 7.8 BODY FLUID COMPARTMENTS IN SUMMER AND WINTER

	March		May		t-test
	ml.	ml./kg	ml.	ml./kg	
Body Weight (kg)	4.82 ± 1.11		5.05 ± .93		N.S.
Total Body Water	3496 ± 774	732.4 ± 23.7	3581 ± 667	709.6 ± 15.0	N.S.
Plasma Volume	223.9 ± 52.3	46.6 ± 4.2	248.9 ± 49.0	49.3 ± 2.4	N.S.
Blood Volume	359.3 ± 94.8	74.5 ± 7.5	380.3 ± 71.8	75.5 ± 3.7	N.S.
Interstitial Fluid Volume	728.2 ± 178.5	151.4 ± 23.0	832.1 ± 185.1	167.7 ± 36.2	N.S.
Intracellular Fluid Volume	2544 ± 597	529.4 ± 38.7	2500 ± 600	492.6 ± 33.1	N.S.
Extracellular Fluid Volume	952.1 ± 215.1	199.5 ± 22.6	1081.0 ± 200.7	217.0 ± 36.3	N.S.

Sample Size = 7 in each group.

Values are means ± standard deviations.

N.S. = not significant at 5% level.

TABLE 7.9 BODY FLUID COMPARTMENTS OF FOUR ANIMALS CAUGHT IN NOVEMBER 1978

	Male 89753		Male 89791		Female 89217		Female 89683	
	ml	ml/kg	ml	ml/kg	ml	ml/kg	ml	ml/kg
Body Weight (kg)	5.3		5.7		5.9		4.3	
Total Body Water	3805	718.0	3985	699.1	4089	693.1	3070	714.0
Plasma Volume	261.0	49.2	272.7	47.8	274.1	46.5	237.3	55.2
Blood Volume	463.6	87.5	461.4	80.9	482.6	81.8	384.0	89.3
Interstitial Fluid Volume	706.1	133.2	652.4	114.5			729.8	169.7
Intracellular Fluid Volume	2838	535.5	3060	536.8			2103	489.1
Extracellular Fluid Volume	967.1	182.5	925.1	162.3			967.1	224.9

The lack of any difference in body fluid compartments between summer and winter would also suggest that the wallabies are not suffering from water stress.

It is known that extra-cellular fluid volume rises in animals without adequate food (Macfarlane, Morris, Howard and Budtz-Olsen, 1959; Morris, Howard and Macfarlane, 1962) while a reduction in the concentration of circulatory haemoglobin, number of red blood cells and total serum proteins is characteristic of starving animals, and gives rise to aneamia (Bethard, Wissler, Thompson, Schroeder and Robson, 1958; Shield, 1959; Ealey and Main, 1967; Casperson, 1968; Nasser and Platt, 1968). Although absolute plasma volume and blood volume were not significantly different in March and May there could be a change in blood volume in November. However, the number of animals measured is too small to test this statistically. Shield (1971) found a 16% reduction in blood volume of quokkas between October and May on Rottnest Island. He suggested that semi-starvation during late summer and autumn was responsible although the situation is probably much more complex than this (Barker, 1974).

7.2.5 Haematocrit and Plasma Protein Concentration

Both males and females showed a significant seasonal decline in haematocrit (Figure 7.3). Low haematocrits were observed in late summer to early winter when animals appeared to be in poor condition. The lowest haematocrits were observed in 1978 after a particularly dry summer.

From October - November 1976 to November 1977 there was no significant change in the plasma protein concentration of male wallabies, but for females there was a significant drop in January 1977. Over the period November 1977 to November 1978 there was a significant reduction in the plasma protein concentration over the late summer to early winter for both males and females (Figure 7.4).

7.2.6 Body Weight

The animals used for analysis of seasonal changes in body weight were all adult animals with the third molar fully erupted (3 years of age or older).

Male wallabies were heavier than females at all times of the year and showed a pronounced annual cycle in body weight. Maximum body weights occurred in spring to early summer (October - December) and then declined over the summer and autumn to reach their lowest values in mid-winter (June - July) (Figure 7.5). A similar cycle was shown in the deposition of fat around the kidneys (Appendix VII) and suggests that fat is being laid down in late winter and spring.

Female wallabies did not show the same seasonal variation in body weights although maximum weights did occur in spring and minimum weights in autumn to early winter. It is possible that the mating activities of the males over the summer period may use up more energy reserves than in females resulting in the decline in condition. However from November 1977 to the winter of 1978 there was a considerable loss in weight for both males and females. The mean weight loss for males was 21% and for females was 16% (Table 7.10).

Growth rates of young wallabies, once they have left the pouch, showed that over the late summer and winter there was little growth with animals just maintaining weight while in spring there was a rapid rise in weight. This indicates

TABLE 7.10 SEASONAL CHANGES IN BODY WEIGHT OF MALE AND FEMALE KANGAROO ISLAND WALLABIES

MALES

Time Interval	% Weight Loss
October-November 1975 to July 1976	16.8
December 1976 to June-July 1977	18.1
November 1977 to July 1978	21.3

FEMALES

Time Interval	% Weight Loss
October-November 1975 to July 1976	7.6
October-November 1976 to April 1977	6.1
November 1977 to May 1978	16.2

ANALYSIS OF VARIANCE OF SEASONAL CHANGES IN BODY WEIGHT

Males:	July 1975 to December 1976	$F_{(7,82)} = 3.50$ *
	December 1976 to November 1977	$F_{(4,75)} = 7.96$ ***
	November 1977 to November 1978	$F_{(5,72)} = 9.26$ ***
Females:	July 1975 to October-November 1976	$F_{(6,114)} = 1.82$ N.S.
	October-November 1976 to November 1977	$F_{(5,111)} = 1.97$ N.S.
	November 1977 to November 1978	$F_{(5,81)} = 4.89$ ***

that the requirements for growth of young animals are not being met over the summer to early winter period (Figure 7.6).

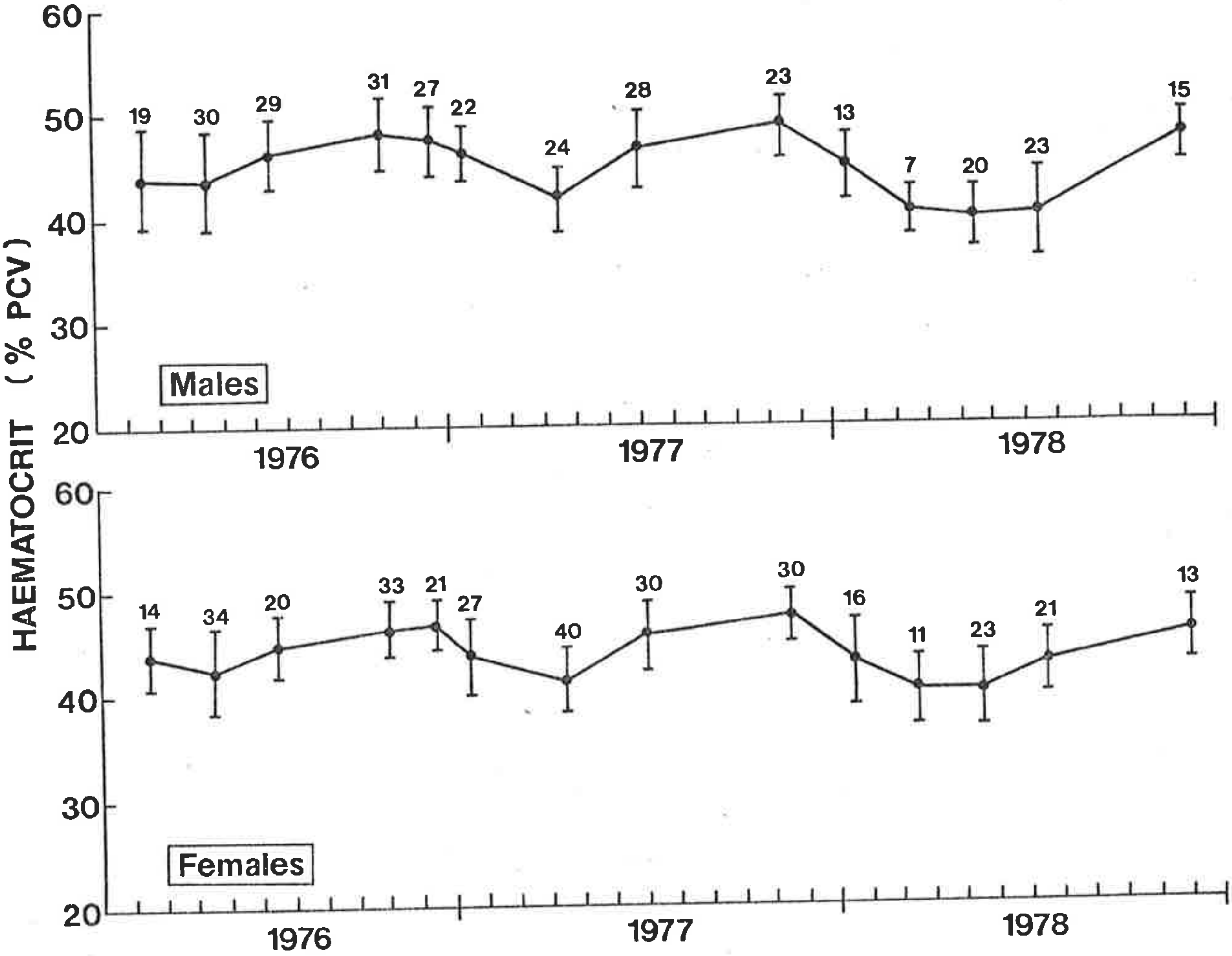


Figure 7.3 Seasonal changes in the haematocrit of male and female wallabies in Flinders Chase National Park.
Symbols as for Figure 7.1.

Analysis of Variance

Males	March 1976 to April 1977	$F_{(6,175)} = 8.95$ ***
	June-July 1977 to November 1978	$F_{(6,122)} = 24.24$ ***
Females	March 1976 to April 1977	$F_{(6,182)} = 11.55$ ***
	June-July 1977 to November 1978	$F_{(6,137)} = 15.10$ ***

*** Significant at 0.1% level.

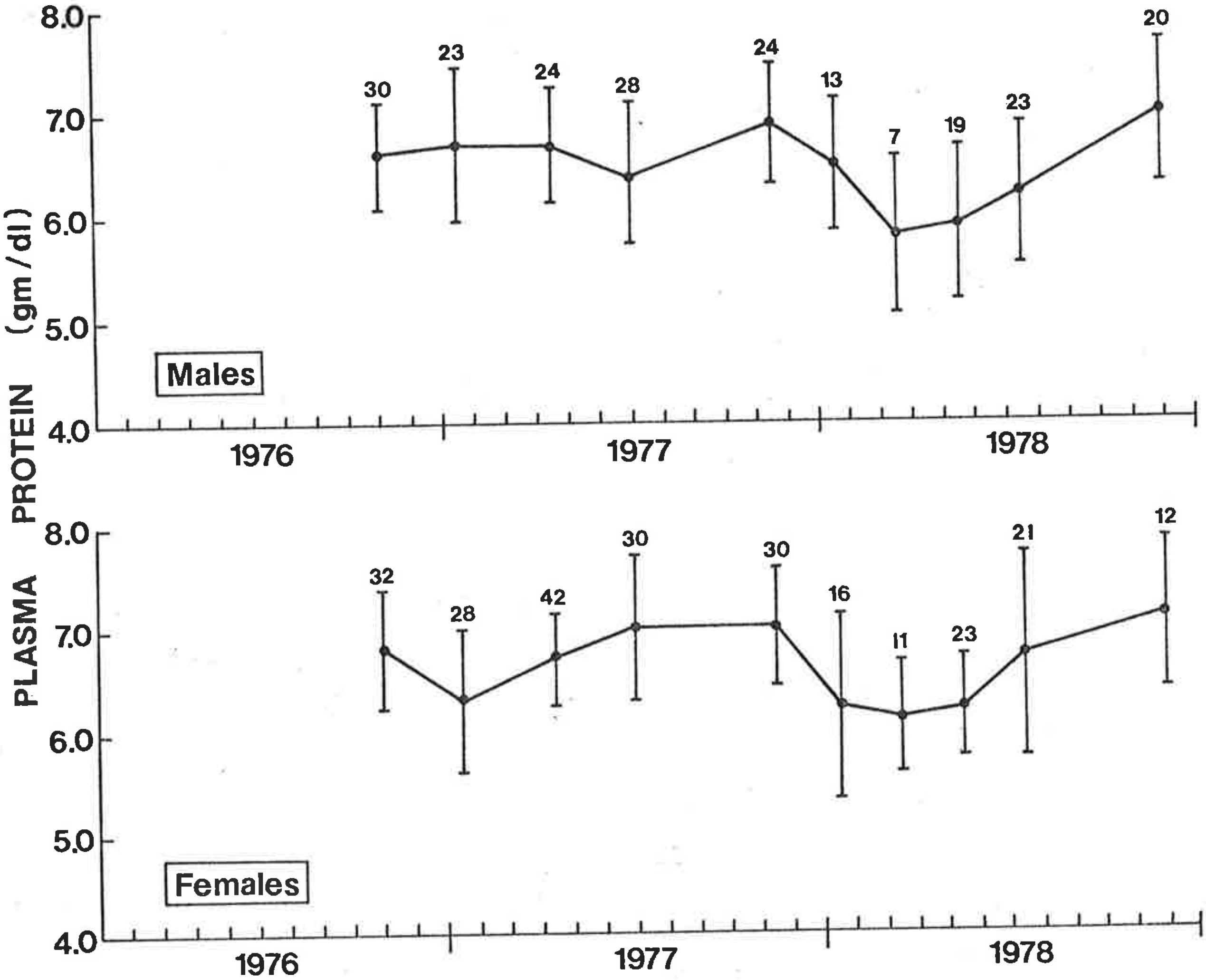
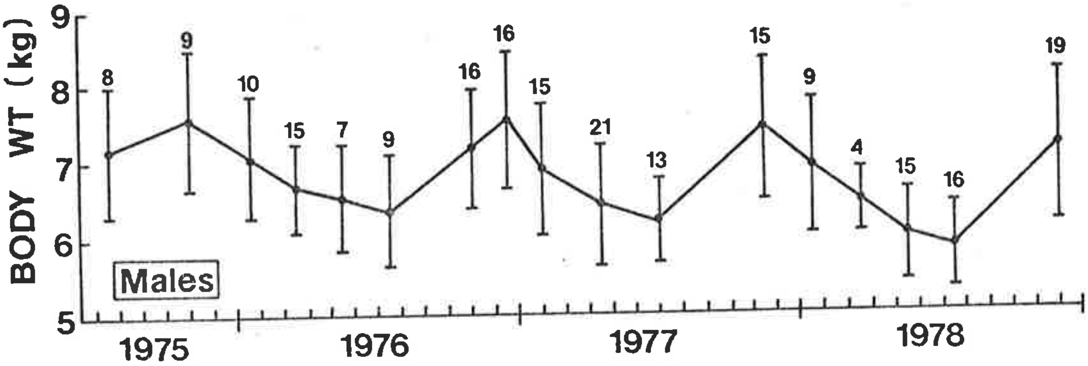


Figure 7.4 Seasonal changes in the plasma protein concentration of Kangaroo Island Wallabies in Flinders Chase National Park. Symbols as for Figure 7.1.

Analysis of Variance

Males	Oct.-Nov. 1976 to November 1977	$F_{(4,124)}=1.87$ N.S.
	November 1977 to November 1978	$F_{(5,100)}=9.51$ ***
Females	Oct.-Nov. 1976 to November 1977	$F_{(4,157)}=5.59$ ***
	November 1977 to November 1978	$F_{(5,107)}=5.99$ ***

N.S. Not significant at 5% level.
*** Significant at 0.1% level.



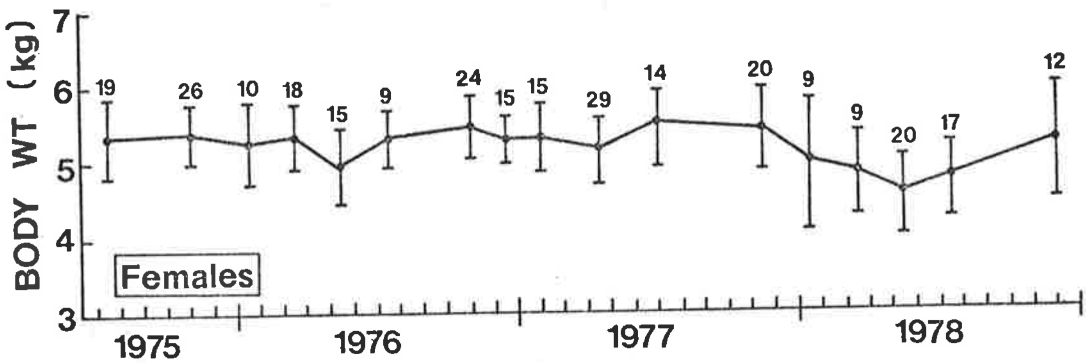


Figure 7.5 Seasonal changes in body weight of adult Kangaroo Island Wallabies in Flinders Chase National Park.
Symbols as for Figure 7.1.

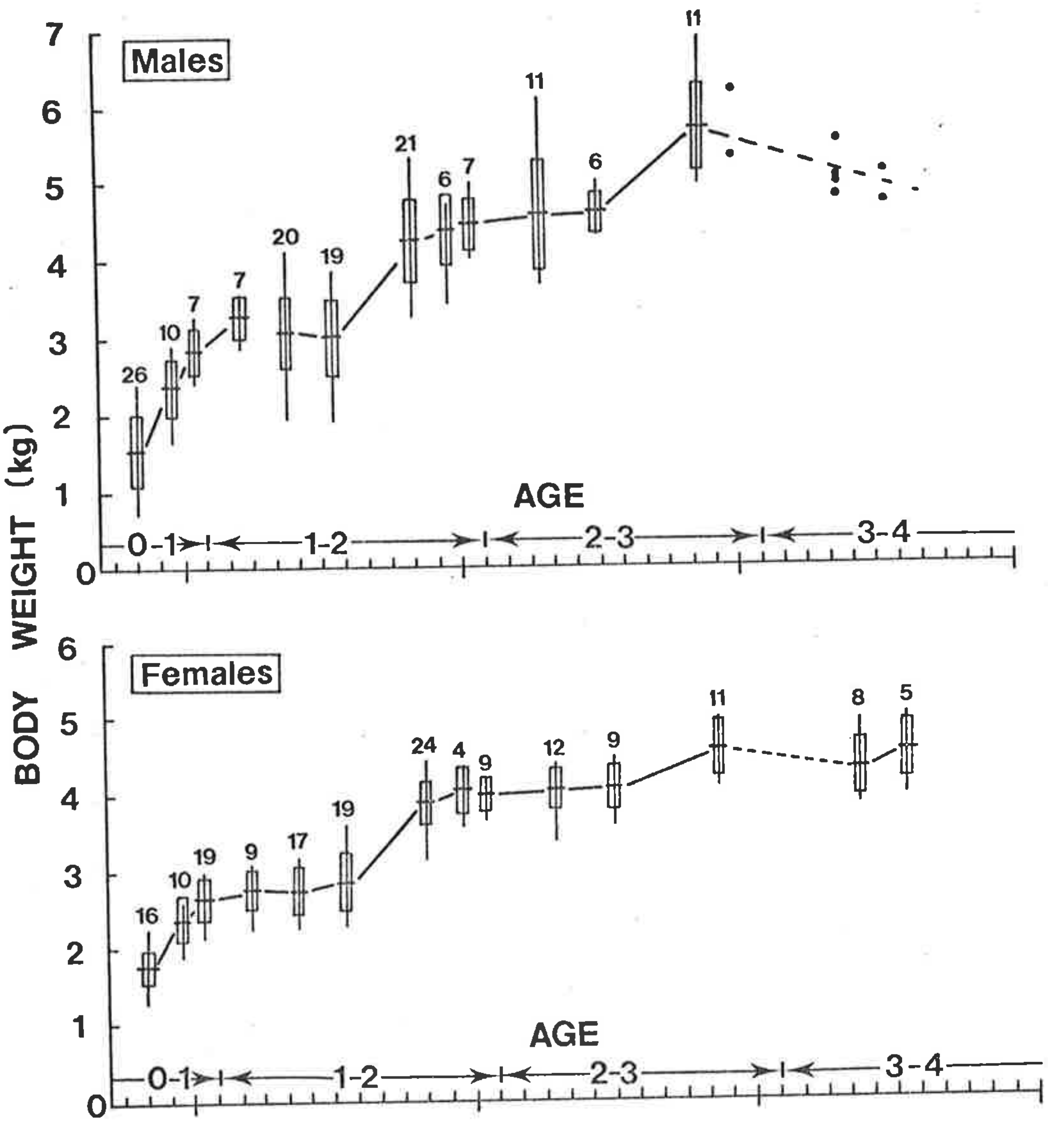


Figure 7.6 Growth pattern of young Kangaroo Island Wallabies in Flinders Chase National Park. Horizontal bars represent mean values obtained over the whole study period (July 1975 - November 1978), vertical lines represent the range and the open rectangle represents the standard deviation.
Numbers above vertical lines represent the sample size.

8.0 GENERAL DISCUSSION

Attempts have been made by ecologists to determine a single theory which could explain population regulation in all species of animals. This has resulted in three quite different theories.

Nicholson (1933, 1954), Nicholson and Bailey (1935) and Smith (1935) put foward a model based on evidence that controlling factors will act more severely against an individual when the density of animals is high. This has become known as desity-dependent population regulation. It was suggested that the controlling factors are food, predators, parasites and pathogens. These factors act by increasing the mortality rate and/or reducing the reproductive rate as the population increases.

Andrewartha and Birch (1954) criticized the density-dependent model because they believed that no special importance should be given to either density-dependent or density-independent regulating mechanisms. They suggested that the numbers of animals in a natural population may be limited by shortage or inaccessibility of material resources, or a shortage of time during which conditions are favourable for an increase in the population. They proposed that the components of the environment, weather, food, other animals and organisms causing disease, and a place in which to live all influence an animal's chance to survive and multiply. Such factors will operate regardless of the density of the population.

Since then other workers have developed a theory which regards intrinsic factors, such as social behaviour and genetic polymorphism, as being the important factors regulating population size. These could increase mortality, reduce fertility or change the dispersal rate such that the population is kept at a level below which resources would become limiting. The intrinsic factors may be in part physiological, such as the 'stress-syndrome' caused by exhaustion of the adreno-pituitary system (Christian, 1950, 1961; Christian, Lloyd and Davis, 1965) or could act through spacing mechanisms such as territoriality (Wynne-Edwards, 1962; Watson and Moss, 1970) or by dispersal of individuals (Lidicker, 1962; Krebs, Keller and Tamarin, 1969). Genetic changes which influence an animals 'fitness' may also be important although there is little information available on this aspect (Chitty, 1960; Krebs, 1972; Krebs and Myers, 1974).

It is apparent that these theories of population regulation are not mutually exclusive. When different populations are examined the evidence points to multiple causes rather than a single cause. Thus Kikkawa (1977) and Lidicker (1978) have expressed the view that a general theory of population regulation is unattainable. Instead they suggest the use of a multi-factorial model. In this model there is a network of extrinsic and intrinsic factors interacting with the subject population and with each other. This approach seems to be the most useful as it takes into account all of the ideas put forward in the previous models. It has therefore been used in interpreting the results of the present study. In this study the size, age structure and annual fluctuations of a natural population of the Kangaroo Island Wallaby has been established and their reproductive pattern, movements and water metabolism studied and related to the environmental conditions. In this way I hoped to gain some insight into the factors influencing the size of the population. Each factor can only operate by influencing one or more of the birth rate, the death rate or dispersal. In this study there was no evidence that dispersal was a significant factor at any time. Hence, in this section I will discuss how natality and mortality combine to cause the observed regular annual fluctuation in population size.

Natality

The Macropodidae are monovular and polyoestrous, and also exhibit the phenomenon known as embryonic diapause (Tyndale-Biscoe, Hearn and Renfree, 1974). In the Kangaroo Island Wallaby there is a post-partum oestrous and mating that results in the formation of a unilaminar blastocyst which remains quiescent for the duration of pouch life. Among polyoestrous mammals the birth rate may be influenced by several components, such as age at sexual maturity, litter size, pregnancy rate, length of the breeding season and the sex ratio (Krebs and Myers, 1974). Sadleir (1969) has also given numerous examples of how climatic, nutritive and social factors may change the reproductive performance of many species of mammals.

The female Kangaroo Island Wallaby reaches sexual maturity and first mates just after leaving the pouch in October-November, at around 9 months of age (see Chapter 4.0). However, they do not give birth until the usual breeding season in late January and February. Hence, because of the strict seasonal breeding pattern, and the fact that the young remain in the pouch for 8 - 9 months, each female is effectively limited to producing only one young each year.

The birth rate was calculated from the proportion of females that were carrying a pouch young when examined as soon as possible after the breeding season had finished. In this study the number of adult females with pouch young was 100% in July 1975, 88% in March 1976, 100% in April 1977 and 96% in May 1978. This high fecundity was also shown in the records of animals caught during the years 1966 to 1969. It was 100% in August 1966 and 97% in May 1967, May 1968 and March 1969. Although the number of juveniles examined was small it appeared that the birth rate for this group was also high except in 1977 and 1978. In 1978 none of the juveniles examined at any time during the year showed signs of having given birth.

The practical problem in relating the birth rate to changes in the population size is to determine how many individuals survive after birth to actively enter the population. The marsupials are born in a very immature state but remain within the mother's pouch for a considerable time. By examining the proportion of females with pouch young later in the year and comparing this to the proportion with young just after the breeding season the extent of any significant loss of young could be determined. In this study it was found that the only time when there was a significant loss of pouch young in adult females was in the latter half of 1978. The proportion of females with a pouch young had fallen from 96% in May to 46% by the time the young were ready to leave the pouch in November. When the records for the years 1966 - 1969 were examined further evidence that mortality among pouch young occurs occasionally was obtained. In 1968 the proportion of adult females with pouch young had fallen from 97% in May to 76% in December.

A high mortality of pouch young has been observed in other macropods during periods of lowered rainfall and poor nutrition. Ealey (1963) and Sadleir (1965) reported losses of the larger pouch young of euros in the north-west of Western Australia during an extended dry season. After a succession of dry seasons female fecundity dropped to 47% (Sadleir, 1965). In a study of the red kangaroo in inland New South Wales, Frith and Sharman (1964) found that significant mortality of pouch young only occurred in drought areas at about the time they were leaving the pouch. In these dry areas 83% failed to reach maturity compared to 15% in the more favourable areas. Similarly, Newsome (1965c, 1966) working on red kangaroos in central Australia found that poor nutrition was the likely cause of a reduction of both the proportion of mature females in breeding condition and the rate of development and survival of pouch young. A drought period in southern Queensland also resulted in the death of all the pouch young of the eastern grey kangaroo born in this period (Kirkpatrick and McEvoy, 1966).

Thus for some species of macropods it is apparent that recruitment is determined by the way in which climatic factors and the food supply influence female fecundity and survival of pouch young. For animals living in the arid zone the population size and structure depends very much on the occurrence of a few good years. Newsome (1977) found an inverted age structure in a population of red kangaroos in central Australia and estimated that periods of two or more good years every 15 - 20 years was necessary to prevent the population declining to extinction. For species such as the grey kangaroos and the Kangaroo Island Wallaby, which live in seasonal and more favourable environments, the birth rate and survival of pouch young is high in most years but may be reduced during an extended dry period.

Mortality

Following the influx of juvenile animals into the population in October - November there is a continual decline in population size over the following year.

Mortality rates varied from year to year and also with the season in any one year.

Juvenile animals tended to have the highest mortality rate, particularly over summer, while young adults had the lowest. Over winter the juvenile females had a low mortality rate while juvenile males and old adult males had the highest.

A high mortality of juvenile animals also occurs in other macropod populations. Frith and Calaby (1969) reported that for female red kangaroos the average mortality over the first year was 38.5% while 46% failed to reach two years of age and 90% died before 10 years. During periods of extended drought, not only is there a high mortality of pouch young and young-at-foot, but many adults also succumb. Thus population 'crashes' are known to occur in both red kangaroos (Newsome, Stephens and Shipway, 1967) and euros (Ealey, 1967a).

In South Australia the summer of 1978 was longer and drier than in previous years. Over the period November 1977 to May 1978 there was a high mortality in all age groups. The total population size was reduced by 35%, compared to 25% for October-November 1975 to May 1976. For juvenile animals the mortality rate was 46% for males and 44% for females. The young adults showed a higher mortality than previous years as it was 41% for males and 34% for females while for the old adults it was 40% for males and 32% for females. Although it was not possible to measure mortality over the winter it was evident that it was very high as many dead animals were observed in the study area. By collecting the skulls of the dead animals it was found that mainly old animals were affected.

A high mortality was also observed in 1968. From November - December 1967 to May 1968 the total population declined by 33% whereas from November-December 1966 to May 1967 it had declined by only 18%. Murphy (1970) reported a die-off of wallabies in Flinders Chase during July 1968 when high rainfall in early winter followed a hot, dry summer.

It is apparent that the abundance and quality of food, and access to water, are the major factors regulating the size of populations of the red kangaroo (Frith and Sharman, 1964; Newsome, 1965a, 1966; Bailey, 1971; Bailey, Martenz and Barker, 1971), the euro (Ealey, 1967b; Ealey and Main, 1967) and the quokka (Barker, 1974). Such factors are also known to be limiting in many other mammal populations.

Sinclair (1974) has shown that for the African buffalo (*Syncerus caffer*) the availability of plant nitrogen was the most important component of the environment limiting their abundance. The influence of weather on the abundance of food and/or shortage of plant nitrogen have also been implicated in the regulation of populations of rabbits, *Oryctolagus cuniculus*, (Myers and Poole, 1963; Stoddart and Myers, 1966), squirrels, *Tamiasciurus hudsonicus, Sciurus carolensis* and *S. niger*, (Kemp and Keith, 1970; Nixon, McClain and Donohoe, 1975) and elephants, *Loxodonta africana*, (Hanks and McIntoch, 1963; Phillipson, 1975). Undernutrition is also known to be a major cause of mortality in many species of ungulates (Rosen and Bischoff, 1952; Taber and Dasman, 1954; Klein and Olson, 1960; Hirst, 1969).

For the Kangaroo Island Wallaby there was no evidence that nitrogen was a limiting factor at any time of the year (Barker, 1971) as it is for the same species on East Wallabi Island in the Abrolhos archipelago, Western Australia (Kinnear and Main, 1975). The Kangaroo Island Wallaby may obtain nitrogen from the seeds of *Acacia retinodes* during the summer as it was observed by Andrewartha and Barker (1969) that the wallabies were foraging beneath these trees. The radio-tracking data indicates that during the summer the wallabies are moving around more and have expanded the size of their home-ranges. This is probably due to animals searching for better quality food as the grass on the cleared area dries off over summer. Their diet seems to be much more indigestible during summer as there is more faecal dry matter excreted at this time. It is possible that they are suffering from an inadequate energy intake over the late summer and early winter. The greater movements that take place at this time may place an extra burden on animals.

With regard to their water metabolism, although the wallabies are conserving water during the summer, as indicated by the low water turnovers and low urine volumes of high concentration, they were not suffering from dehydration.

The other factors which could contribute to mortality are predation, disease or social stress.

Predation is unlikely to be a major factor as the only large predator is the Wedge-tailed Eagle (*Aquila audax*). One adult male was apparently killed by a pair of eagles during the study. However this animal was obviously out in the open on the cleared-area when attacked. It was not known whether the eagles directly killed the wallaby or if it was panicked and stunned itself trying to get through the fence-line. A similar instance was reported by Andrewartha and Barker (1969) where eagles killed a young wallaby that had entered a fence-trap during daylight. However, these are unusual occurrences as wallabies normally spend the day in dense scrub where it would be extremely difficult for them to be captured by eagles. It is probable that eagles are opportunistic predators and hence have no great affect on the population. Feral cats (*Felis catus*) could prey upon young animals just out of the pouch but as cats are not abundant in this area it is doubtful that they cause many deaths.

The influence of social factors in determining abundance is unknown except that the radio-tracking data has shown that the wallabies have over-lapping home-ranges. Some stress could occur during the breeding season when males are competing for oestrous females or if the population reached a high density. Neither natality nor mortality could be shown to be density-dependent although the time period of the study was too short to determine whether this may occur in the long term. It is possible that if the population did build up to a high density this would have drastic affects on their food supply. Although the abundance of food was not measured it was not obvious that the size of the population observed in the present study was having an adverse affect on the abundance of food.

Thus, the most likely influences on mortality are through food quality over summer and possibly parasites and/ or pathogens in winter. The amount of rainfall obviously influences pasture growth. According to Burrows (1979) the growing season on Kangaroo Island begins, on average, in the second week of April and ends in the third week of October. However, in some years the growing season may end earlier and start later. I suggest that it is in these years, such as 1968 and 1978, that the highest mortality will occur. Mortality over the following winter could also be influenced by the drier summer. Being stressed by the energy shortage over summer the animals cannot cope with the cold, wet conditions of winter. There may be further problems due to heavy parasite loads and the the possibility of disease. Undernutrition is known to impair the immune response and affects the endocrine system, which in turn allows existing diseases to become pathogenic (Scrimshaw, Taylor and Gordon, 1968).

The total worm burdens of the gastro-intestinal tract of Kangaroo Island Wallabies fluctuates seasonally and from year to year (Smales and Mawson, 1978) with a tendency for low levels of infestation in summer and highest in winter. This is typical of strongyle infections in sheep where there is a pronounced winter rainfall (Anderson, 1972; Gordon, 1958; Parnell, 1963). These results are also consistent with those reported by Arundel, Barker and Beveridge (1977) suggesting that juvenile eastern grey kangaroos begin to pick up nematodes in autumn at about 14 - 16 months of age, about 4 months after leaving the pouch.

Although there is little information available on the pathogenicity of helminths in natural populations a winter mortality in the eastern grey kangaroo has been associated with the blood-sucking nematode *Globocephaloides trifidospicularis* (Arundel, Barker and Beveridge, 1977). Mortality with associated anaemia occurred each year in July and August when animals had low haematocrits, haemoglobin and plasma protein concentrations. Although all animals were heavily infected with gastro-intestinal parasites, *Globocephaloides* appeared to be the only serious pathogen. This parasite is also found in the Kangaroo Island Wallaby (Smales and Mawson, 1978) although it does not appear to be abundant. Despite the fact that low haematocrits and plasma protein concentrations were observed in the Kangaroo Island Wallaby over winter, and particularly in 1978, it was not possible to relate this to the presence of any particular parasites or disease state.

During May and July 1978 when many dead wallabies were observed on the study area 3 males and 1 female, which were in very poor condition, were collected from Flinders Chase and autopsied at the Institute of Medical and Veterinary Science, Adelaide. All of these animals had large numbers of nematodes in the gastro-intestinal tract which were often associated with granuloma formations on the gastric mucosa. These very heavy parasite loads could have contributed to the poor state of health of these animals. There was histological evidence that these wallabies were also suffering from sporozoan infections, both *Toxoplasma* and *Coccidia* were detected (R. Giesecke, pers. comm.) and it is likely that this was the cause of death.

It seems likely that poor quality forage over summer, combined with heavy parasite loads and cold, wet conditions in early winter stress the animals severely so that the weaker individuals die. The delicate balance of this survival pattern is indicated by the fact that a much higher mortality in the population often follows a long dry summer.

Control Measures on Farms

The Kangaroo Island Wallaby is regarded as a pastoral pest by many farmers as it competes with domestic animals for the introduced pasture species. This has led to the illegal use of the poison 1080 to control wallabies, particularly on the eastern end of the island. Indescriminate use of this poison has undoubtedly affected numbers of many native vertebrates. This pest problem is enhanced by the large areas of pasture which adjoin tracts of uncleared scrub. The scrub acts as an excellent daytime refuge for the wallaby.

The aim of a management programme is to reduce the animal population to a level which causes least damage to the farmland without completely exterminating it.

Before control measures can be properly instigated it is necessary to determine the abundance of wallabies. The most appropriate method for estimating density in this situation is the line-transect spotlight count. This method has the advantage that it is not time consuming and gives a reliable density measurement. Johnson (1977) found this method suitable for Bennetts wallaby, pademelon and the brush-tailed possum in Tasmania. He has outlined the use of the method and the calculation of densities.

To estimate the proportion of animals to be removed from a pest population it is first necessary to establish an acceptable level for the population density. Then, if a census reveals that the population size is above this level a number of animals must be removed. To maintain the population at this level will require that an annual census be made to determine the rate of increase. If the rate of increase is positive then more animals will have to be culled from the population. Because environmental conditions fluctuate from year to year so will the fecundity and survival rates, as seen in the present study, and thus the rate of increase and the number to be culled will vary.

The time of year when the census is made must be taken into consideration as high populations will be encountered when young leave the pouch and lower numbers will be seen over summer and winter, following natural mortality. The best time of year to census the population and to remove that proportion which will keep the rate of increase at zero would be just after young animals leave the pouch, around November.

9.0 APPENDICES

APPENDIX I

PLANTS OCCURRING ON THE STUDY AREA

Identifications from Black, J.M. (1943 - 1957) 'Flora of South Australia' 2nd. Edn. Vols. I - IV Govt. Printer, Adelaide, and Eichler, H. (1965) 'Supplement to J.M. Black's Flora of South Australia (2nd. Ed., 1943 - 1957)' Govt. Printer, Adelaide. Identification of Bryophytes by L.D. Williams, Ecological Survey Section, Dept. of the Environment.

A. Within the Scrub

LILIACEAE

Thysanotus dichotomus (Labill.) R.Br.

Xanthorrhoea tateana F.v.M.

CASUARINACEAE

Casuarina striata Macklin

PROTEACEAE

Isopogon ceratophyllus R.Br.

Adenanthos sericea var. *brevifolia* Benth.

Hakea rostrata F.v.M. ex Meisn.

Banksia marginata Cav.

B. ornata F.v.M. ex Meisn.

DROSERACEAE

Drosera auriculata Backh. ex Planch.

MIMOSACEAE

Acacia armata R.Br. ex Ait.

A. retinodes Schldl.

FABACEAE

Pultenaea daphnoides Wendl.

RUTACEAE

Boronia filifolia F.v.M.

Correa pulchella Mackay ex Sweet

RHAMNACEAE

Spyridium phylicoides Reiss.

STERCULIACEAE

Lasiopetalum schulzenii (F.v.M.) Benth.

DILLENIACEAE

Hibbertia sericea (R.Br. ex DC.) Benth.

MYRTACEAE

Leptospermum juniperinum Sm.

Melaleuca lanceolata Otto

Eucalyptus obliqua L'Herit.

E. diversifolia Bonpl.

EPACRIDACEAE

Epacris impressa Labill.

B. On the Cleared Area

MUSCI

Barbula pseudopilifera C. Muell. & Hampe

Triquetrella papillata (Hook. f. & Wils.) Broth.

Bryum billardieri Schwaegr.

PTERIDOPHYTA

Pteridium esculentum (Forst. f.) Nakai

LILIACEAE

Arthropodium strictum R.Br.

GRAMINEAE

Agrostis avenacea Gmel.

Danthonia pilosa R.Br.

* *Vulpia myuros* (L.) Gmel.

V. bromoides (L.) S.F. Gray

CARYOPHYLLACEAE

* *Cerastium glomeratum* Thuill.

FABACEAE

* *Trifolium dubium* Sibth.

* *Trigonella ornithopodioides* (L.) DC.

(* Represents introduced plants.)

APPENDIX II

SKULL MEASUREMENTS (FROM THOMAS 1888)

Basal Length :	From the basion, or lower front edge of the foramen magnum, to the gnathion, or most anterior point of the premaxilla.
Nasal Length :	Greatest length.
Nasal Width :	Greatest breadth of the two nasals together.
Inter-orbital Width :	Least breadth between the two orbito-temporal fossae.
Palate Length :	From the back of the bony palate to the gnathion.
Diastema :	From the back of the alveolus of the last incisor to the front of that of the most anterior of the cheek-teeth.

APPENDIX III

HISTORY OF TRANSMITTER ANIMALS

MALE 1

First captured 29/5/76 Born 1972

Last captured 6/7/78

Total number of times caught - 7

Transmitter (U.A.) placed on animal 7/12/76. Position of animal recorded at intervals of 2 - 4 hours from 1400 hrs. 7/12/76 to 2400 hrs. 9/12/76. Transmitter was removed. A second transmitter (C.S.I.R.O.) placed on animal 13/4/77. Position of animal noted at irregular intervals during April 1977 (14/4/77 - 17/4/77); at 3 - 5 hour intervals in May 1977 (22/5/77 - 25/5/77); at irregular time intervals in June - July 1977 (28/6/77 - 5/7/77) and in August 1977 (3/8/77 - 5/8/77). The transmitter signal was getting weaker in August 1977 and could not be picked up in September 1977. Transmitter was removed 8/11/77.

A third transmitter (A.V.M.) placed on animal 30/1/78. Position of animal recorded at 4-hourly intervals in January - February 1978 (31/1/78 - 3/2/78), March - April 1978 (30/3/78 - 2/4/78) and May 1978 (9/5/78 - 11/5/78). Four measurements at irregular time intervals were made in July 1978 (13/7/78 - 14/7/78). Transmitter signal was getting weak at this time. The transmitter was not recovered.

MALE 2

First captured 22/1/76 Born 1974

Last captured 12/7/78

Total number of times caught - 4

Transmitter (C.S.I.R.O.) placed on animal 7/4/77. Position of animal recorded at irregular intervals during April 1977 (10/4/77 - 17/4/77); at intervals of 3 - 5 hours in May 1977 (22/5/77 - 24/5/77) and at irregular intervals in August 1977 (3/8/77 - 4/8/77). Transmitter signal could not be heard in September 1977 and was removed 5/11/77.

A second transmitter (A.V.M.) was placed on animal 12/12/77. Position of animal was recorded at 4 - hourly intervals in December 1977 (14/12/77 - 17/12/77), January - February 1978 (31/1/78 - 3/2/78), March - Arpil 1978 (30/3/78 - 2/4/78) and May 1978 (9/5/78 - 11/5/78). Transmitter was removed 12/7/78 when signal was getting weak.

MALE 3

First captured 27/ 5/76 Born 1975

Last captured 8/11/77

Total number of times caught - 8

Transmitter (C.S.I.R.O.) placed on animal 9/4/77. Measurements of the animal's position were recorded at irregular intervals in April 1977 (10/4/77 - 17/4/77); at regular intervals of 3 - 5 hours in May 1977 (22/5/77 - 25/5/77) and at irregular intervals in June - July 1977 (28/6/77 - 5/7/77) and August 1977 (3/8/77 - 5/8/77). Transmitter apparently not working in September 1977 and was removed 3/11/77.

MALE 4

First captured 6/11/77 Born 1977

Last captured 11/12/77

Total number of times caught - 2

Transmitter (A.V.M.) placed on animal 12/12/77. Position of animal recorded at regular intervals of 4 hours in December 1977 (14/12/77 - 17/12/77), January - February 1978 (31/1/78 -

3/2/78), March - April 1978 (30/3/78 - 2/4/78) and May 1978 (9/5/78 - 11/5/78). Four measurements of position were taken at irregular time intervals in July 1978 (13/7/78 - 14/7/78). Transmitter signal was getting weaker in July 1978.
Transmitter not recovered.

<u>MALE 5</u>

First captured 16/3/76 Born 1975
Last captured 6/7/78
Total number of times caught - 8
Found dead September 1978
Transmitter (A.V.M.) placed on animal 12/12/77. Position of animal followed at regular intervals of 4 hours in January - February 1978 (31/1/78 - 3/2/78) and March - April 1978 (30/3/78 - 2/4/78). Weak signal heard from main feeding area in May 1978 but position of animal in scrub could not be found.
Transmitter recovered from dead animal September 1978.

<u>MALE 6</u>

First captured 24/ 1/76 Born 1973
Last captured 11/12/77
Total number of times caught - 5
Transmitter (A.V.M.) placed on animal 12/12/77. Position of animal recorded at 4-hourly intervals in December 1977 (14/12/77 - 17/12/77).
Transmitter signal not heard again and transmitter not recovered.

MALE 7

First captured 3/11/77 Born 1976

Last captured 30/ 1/78

Total number of times caught - 2

Transmitter (A.V.M.) placed on animal 25/1/78. Position of animal measured at 4-hourly intervals January - February 1978 (31/1/78 - 3/2/78) and March - April 1978 (30/3/78 - 2/4/78). Transmitter signal weak in May 1978, position of animal not recorded.

Transmitter was not recovered.

MALE 8

First captured 16/3/76 Born 1974

Last captured 8/7/78

Total number of times caught - 4

Transmitter (A.V.M.) placed on animal 1/2/78. Position of animal recorded at regular intervals of 4 hours in February 1978 (2/2/78 - 3/2/78), March - April 1978 (30/3/78 - 2/4/78) and May 1978 (9/5/78 - 11/5/78). Four measurements were taken at irregular time intervals in July 1978 (13/7/78 - 14/7/78).

FEMALE 1

First captured 6/11/76 Born 1973

Last captured 13/ 7/78

Total number of times caught - 8

Carried a female pouch young in 1977 and had female pouch young in 1978 which was present in May 1978 but had been lost by 13/7/78.

Transmitter (C.S.I.R.O.) placed on animal 6/4/77. Position of animal recorded at irregular intervals in April 1977 (11/4/77 - 17/4/77); at regular spaced intervals of 3 - 5 hours in May 1977 (22/5/77 - 25/5/77); at irregular intervals in June - July 1977 (28/6/77 - 5/7/77) and August 1977 (3/8/77 - 5/8/77).

Transmitter was removed 13/8/77.

FEMALE 2

First captured 7/11/75 Born 1973

Last captured 13/7/78

Total number of times caught - 10

Carried pouch young (sex unknown) in 1976, female pouch young in 1977 and a male pouch young in 1978.

Transmitter (C.S.I.R.O.) placed on animal 7/4/77. Position of animal recorded at irregular time intervals in April 1977 (10/4/77 - 17/4/77); at regular intervals of 3 - 5 hours in May 1977 (22/5/77 - 25/5/77) and at irregular intervals in June - July 1977 (28/6/77 - 5/7/77) and August 1977 (4/8/77 - 5/8/77). Transmitter signal was getting weaker in August and could not be heard in September 1977.

Transmitter was removed 2/11/77.

A second transmitter (A.V.M.) placed on animal 25/1/78. Position of animal recorded at regular intervals January-February 1978 (31/1/78 - 3/2/78) and March - April 1978 (30/3/78 - 2/4/78).

Transmitter was not heard in May 1978 and was removed on 11/7/78.

FEMALE 3

First captured 31/10/75 Born 1975

Last captured 8/ 7/78

Total number of times caught - 12

Carried a male pouch young in 1976, a female pouch young in

1977 which was lost by 28/6/77, a male pouch young in 1978. Transmitter (C.S.I.R.O.) placed on animal 7/4/77. Position of animal recorded at irregular intervals in April 1977 (10/4/77 - 17/4/77); at regular time intervals of 3 - 5 hours in May 1977 (22/5/77 - 25/5/77) and at irregular intervals in June - July 1977 (28/6/77 - 5/7/77).
Transmitter found to have flat batteries in August 1977 and removed 4/8/77.
Second transmitter (A.V.M.) placed on animal 12/12/77.
Position of animal recorded at regular time intervals of 4 hours in December 1977 (14/12/77 - 17/12/77). January - February 1977 (31/1/78 - 3/2/78), March - April 1978 (30/3/78 - 2/4/78) and May 1978 (9/5/78 - 11/5/78). Transmitter was not working in July 1978 and was removed 11/7/78.

FEMALE 4

First captured 6/4/77 Born 1973
Last captured 4/8/77
Total number of times caught - 3
Carried a female pouch young in 1977.
Transmitter (C.S.I.R.O.) placed on animal 7/4/77. Position of animal recorded at irregular intervals in April 1977 (10/4/77 - 17/4/77) and May 1977 (22/5/77 - 24/5/77).
Transmitter signal could not be heard in June 1977 and transmitter was removed 4/8/77.

FEMALE 5

First captured 5/11/76 Born 1976
Last captured 6/11/77
Total number of times caught - 3
Did not appear to have carried a pouch young in 1977.

Transmitter (A.V.M.) placed on animal 12/12/77. Position of animal recorded at 4 - hourly intervals in December 1977 (14/12/77 - 17/12/77), January - February 1978 (31/1/78 - 3/2/78) and March - April 1978 (30/3/78 - 2/4/78). Transmitter could not be heard in May 1978 and was not recovered.

FEMALE 6

First captured 3/11/75 Born 1973

Last captured 1/12/78

Total number of times caught - 6

Had been lactating when caught in 1975 and 1976, carried a male pouch young in April 1977, which was killed during capture, and subsequently produced and reared a female pouch young. Carried a female pouch young in 1978.

Transmitter (A.V.M.) placed on animal 13/12/77. Position of animal recorded at regular intervals of 4 hours in December 1977 (14/12/77 - 17/12/77), January - February 1978 (31/1/78 - 3/2/78) and in March - April 1978 (30/3/78 - 2/4/78). Transmitter was weak in May 1978 and was removed 10/7/78.

FEMALE 7

First captured 24/1/76 Born 1975

Last captured 6/7/78

Total number of times caught - 8

Carried a male pouch young in 1976, a male pouch young in 1977 and a female pouch young in 1978.

Transmitter (A.V.M.) placed on animal 1/2/78. Position of animal recorded at regular 4 - hourly intervals in February 1978 (2/2/78 - 3/2/78), March - April 1978 (30/3/78 - 2/4/78) and May 1978 (9/5/78 - 11/5/78). Four measurements at irregular time intervals were taken in July 1978. Transmitter was not recovered.

FEMALE 8

First captured 12/12/77 Born 1977

Last captured 8/ 5/78

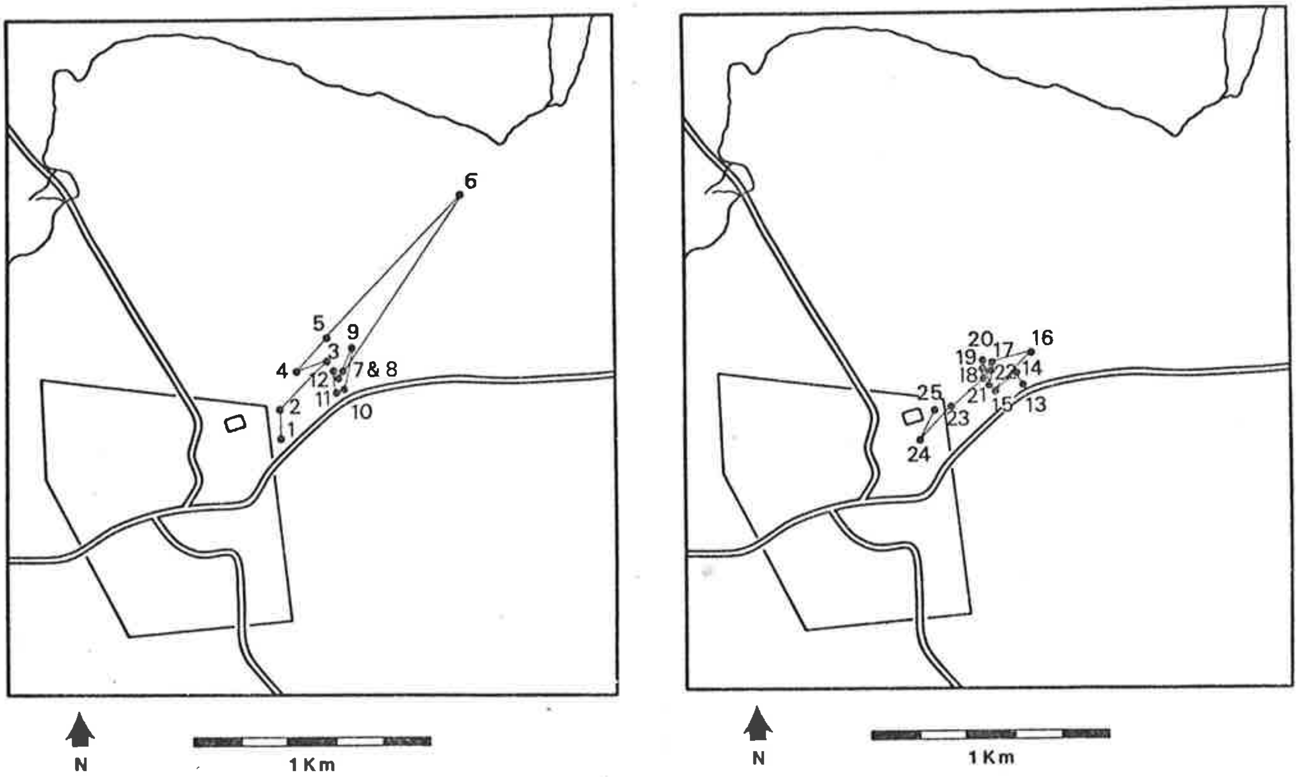
Total number of times caught - 3

Did not carry a pouch young in 1978.

Transmitter (A.V.M.) placed on animal 8/5/78. Position of animal recorded at regular 4-hourly intervals in May 1978 (9/5/78 - 11/5/78). Signal could not be heard in July 1978 and the transmitter was not recovered.

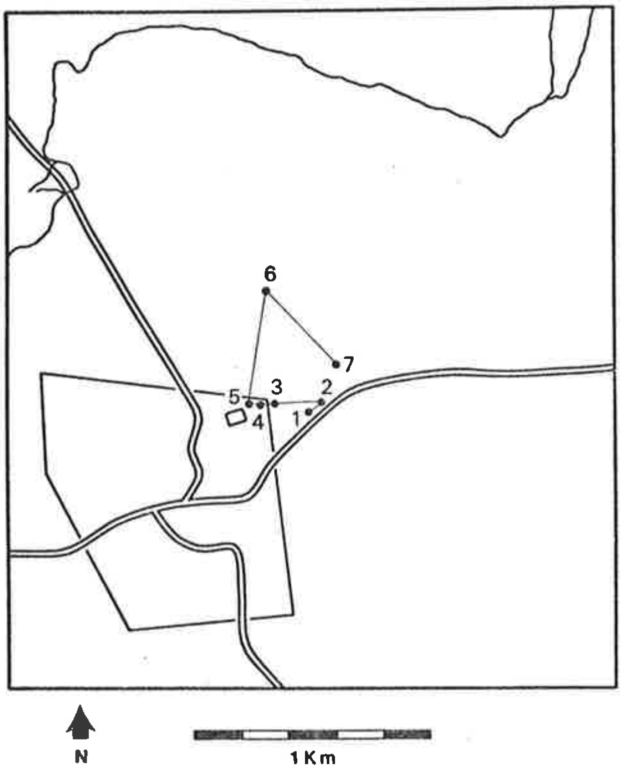
APPENDIX IV

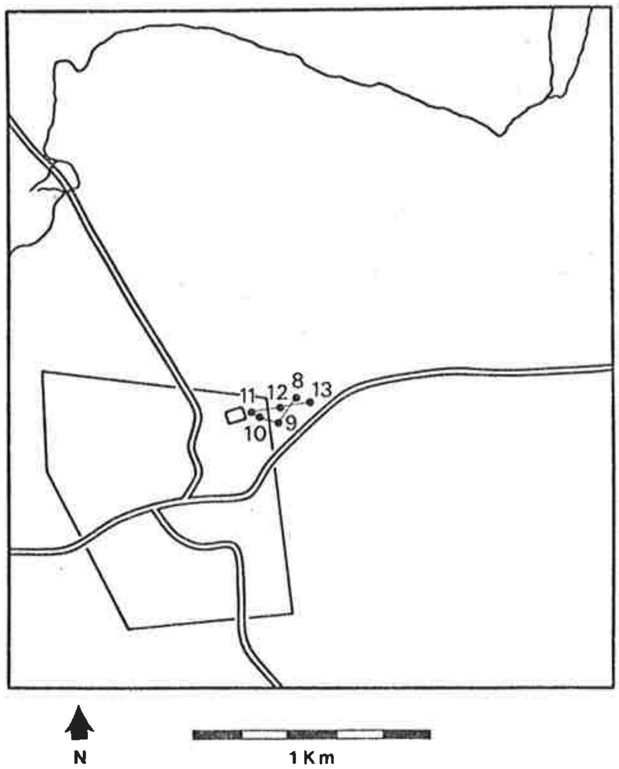
The daily movement patterns of each wallaby at different times of the year are presented in the following maps, together with the dates on which the observations were made and the times when each measurement was taken.

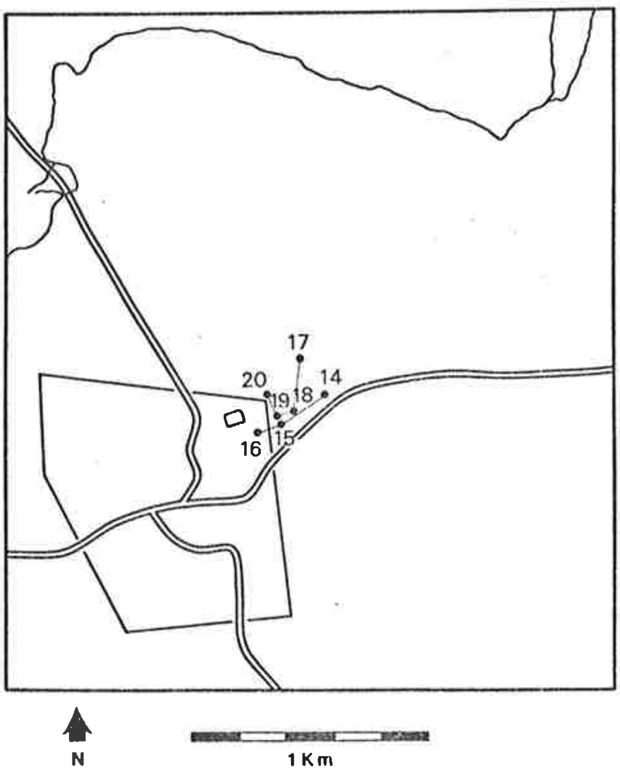


Male 1 December 1976

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	7/12/76	1400	13	8/12/76	1630
2		1830	14		1830
3		2100	15		2030
4		2200	16		2130
5	8/12/76	0030	17	9/12/76	0230
6		0230	18		0730
7		0430	19		1200
8		0700	20		1400
9		0830	21		1600
10		1030	22		1800
11		1230	23		2000
12		1430	24		2200
			25		2400

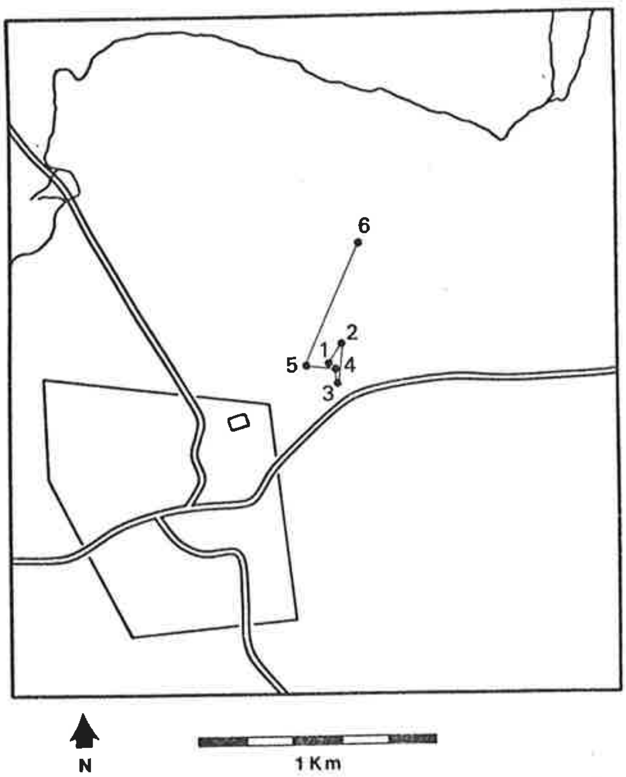


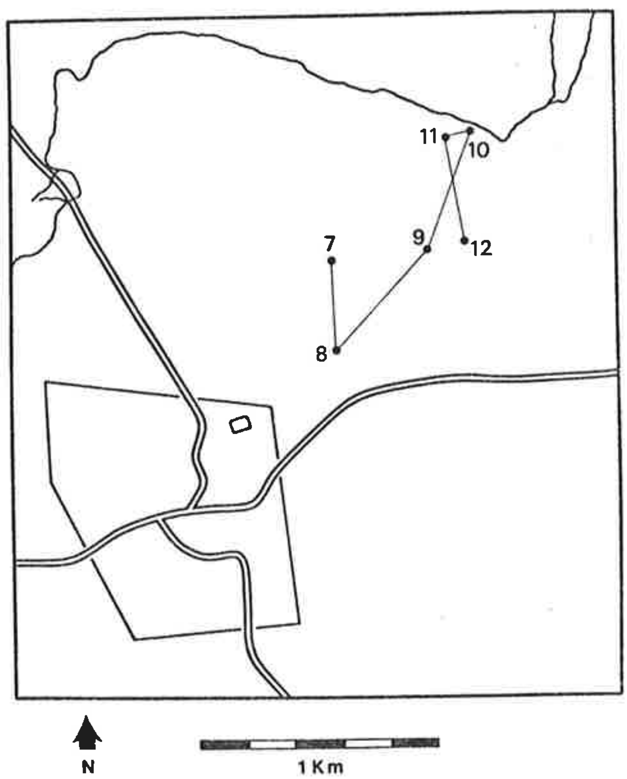


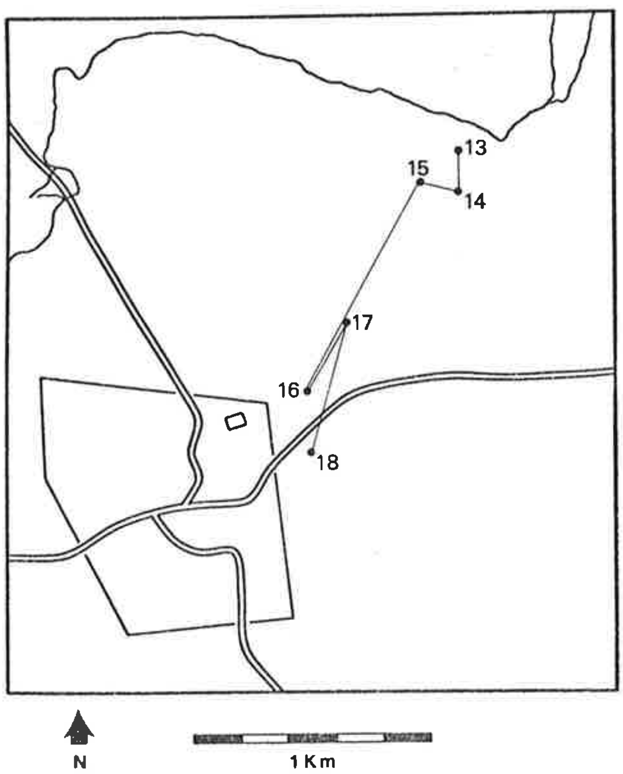


Male 1 May 1977

Reference	Date	Time (hrs)
1	22/5/77	1100
2		1500
3		1800
4		2200
5	23/5/77	0100
6		0700
7		1100
8		1500
9		1800
10		2200
11	24/5/77	0200
12		0600
13		1100
14		1500
15		1800
16		2200
17	25/5/77	1100
18		1500
19		1800
20		2200

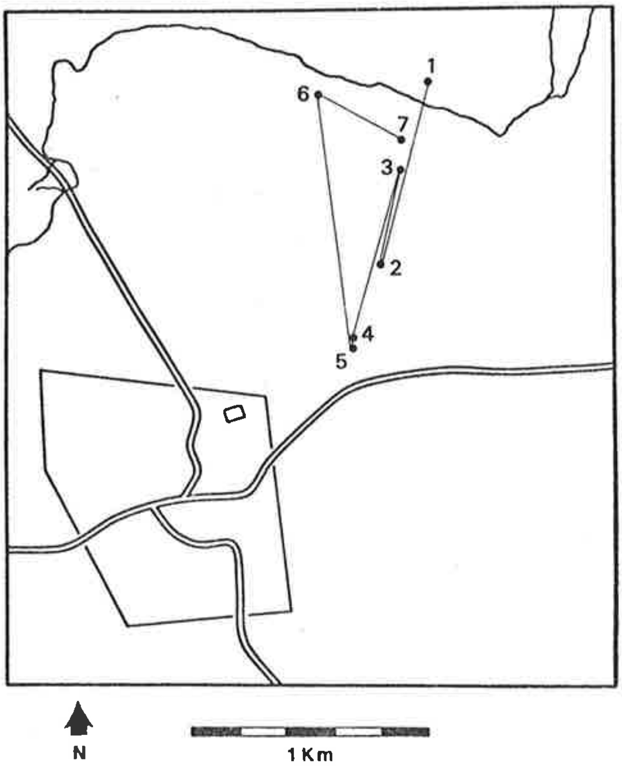


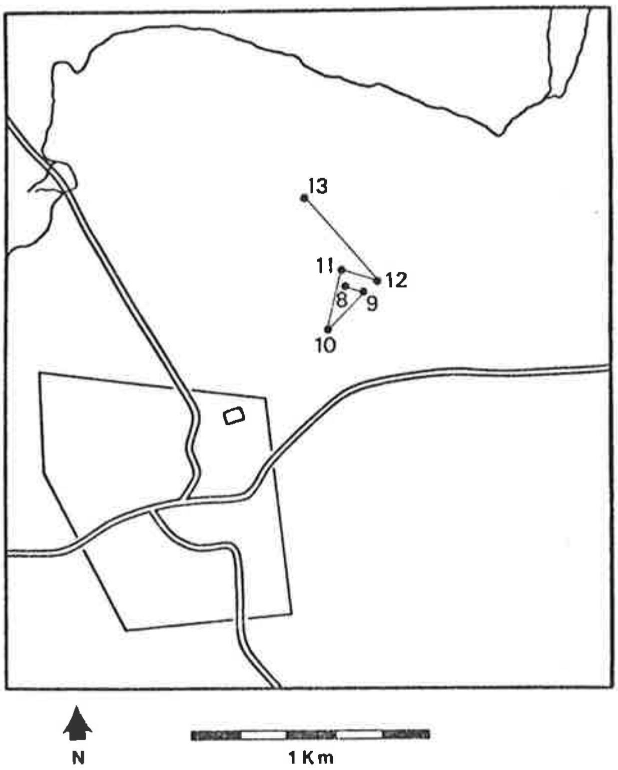


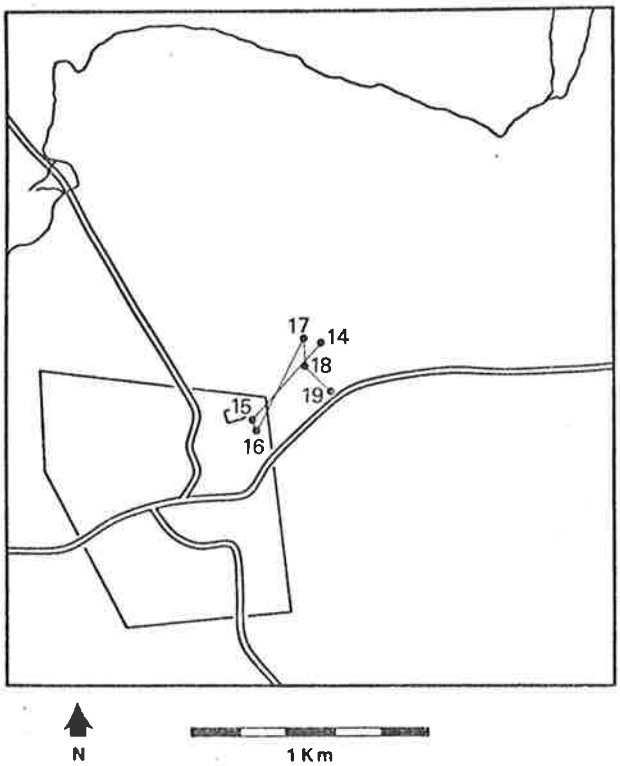


Male 1 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0800
6		1200
7		1600
8		2000
9		2400
10	2/2/78	0400
11		0800
12		1200
13		1600
14		2000
15		2400
16	3/2/78	0400
17		0800
18		1200

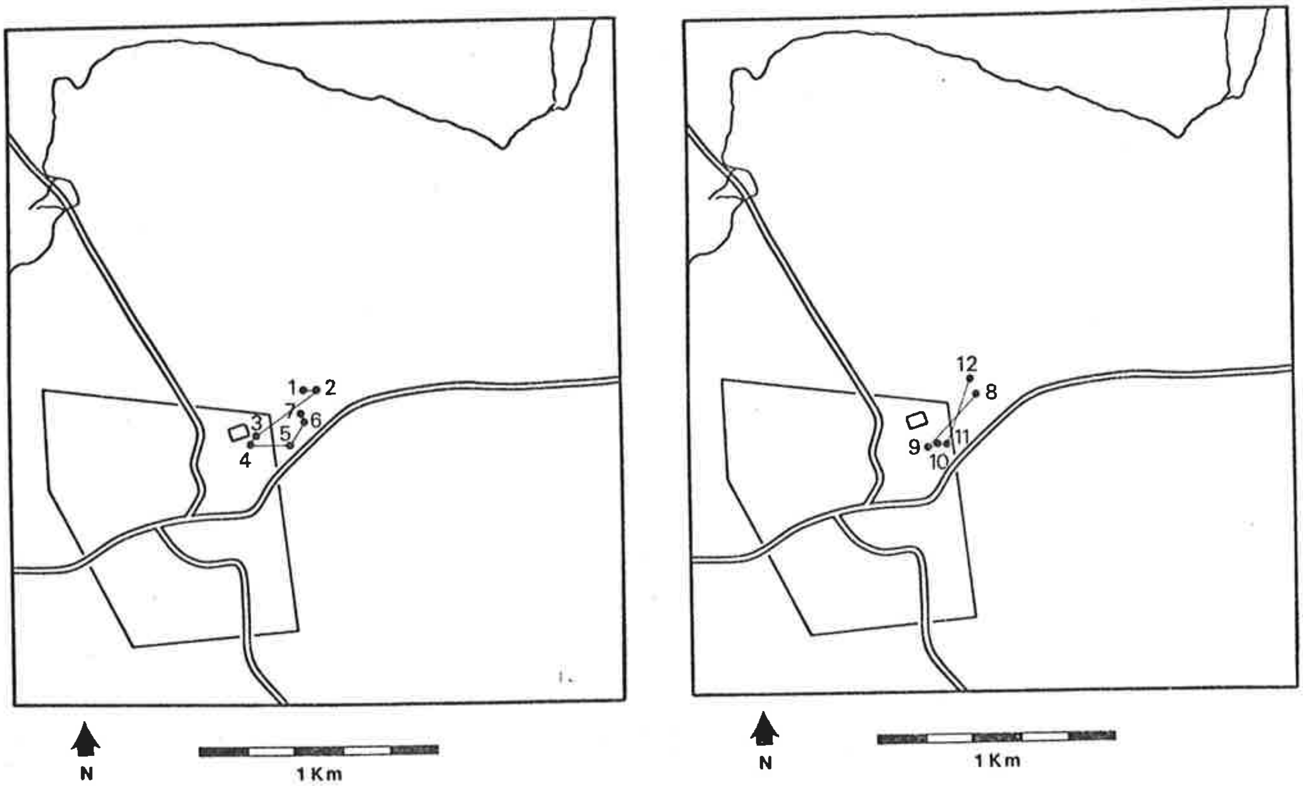






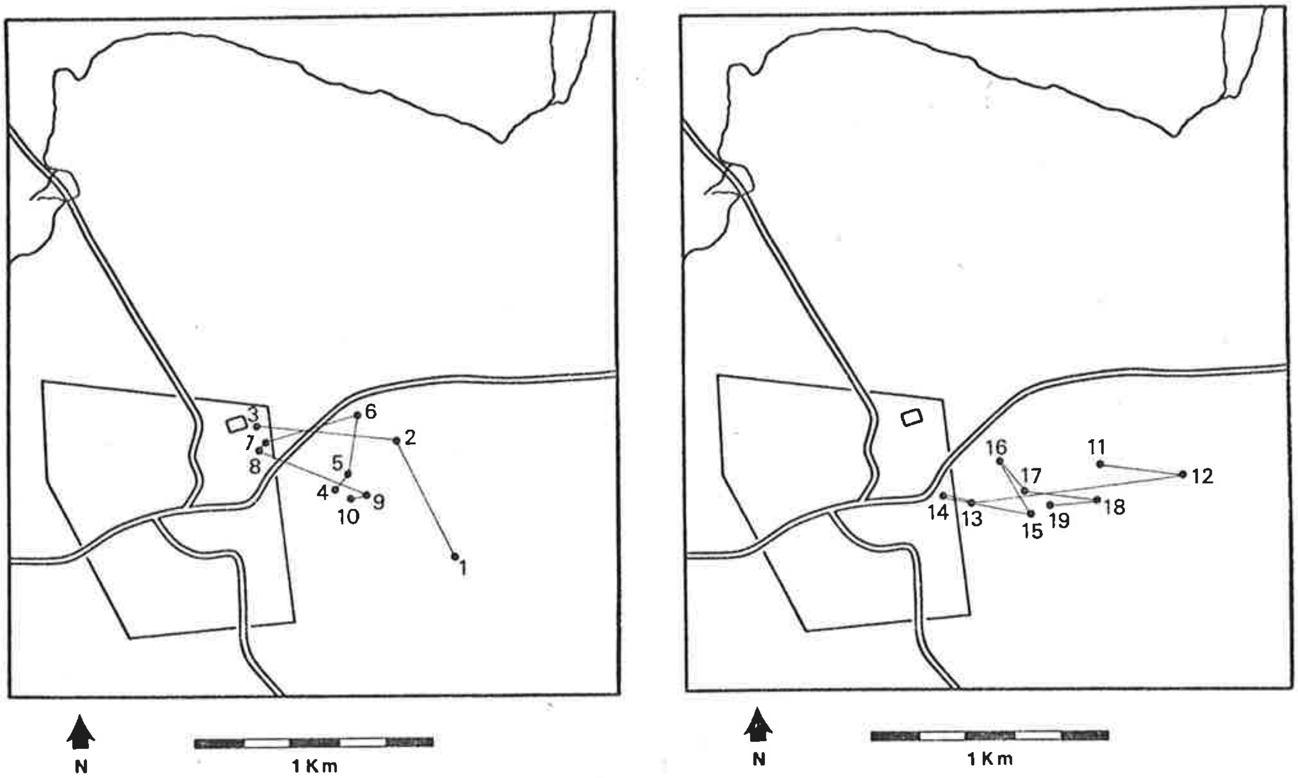
Male 1 March/April 1978

Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200



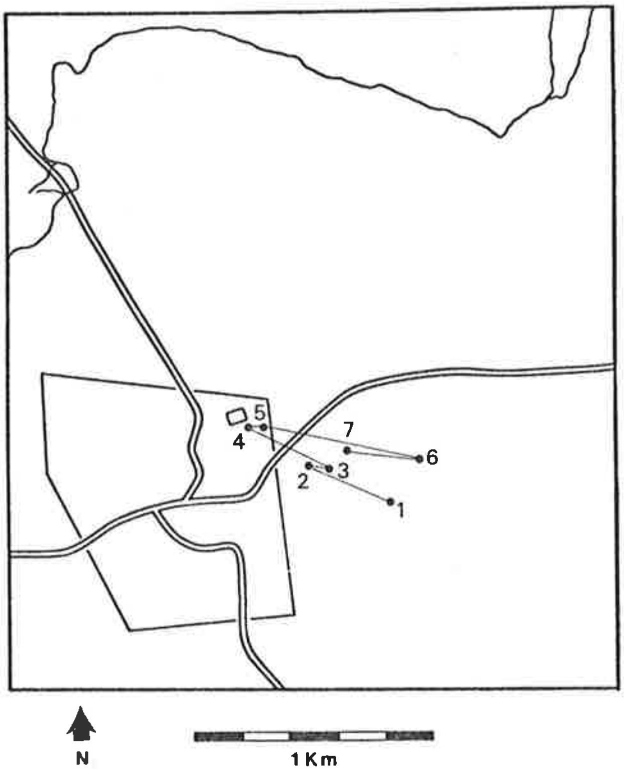
Male 1 May 1978

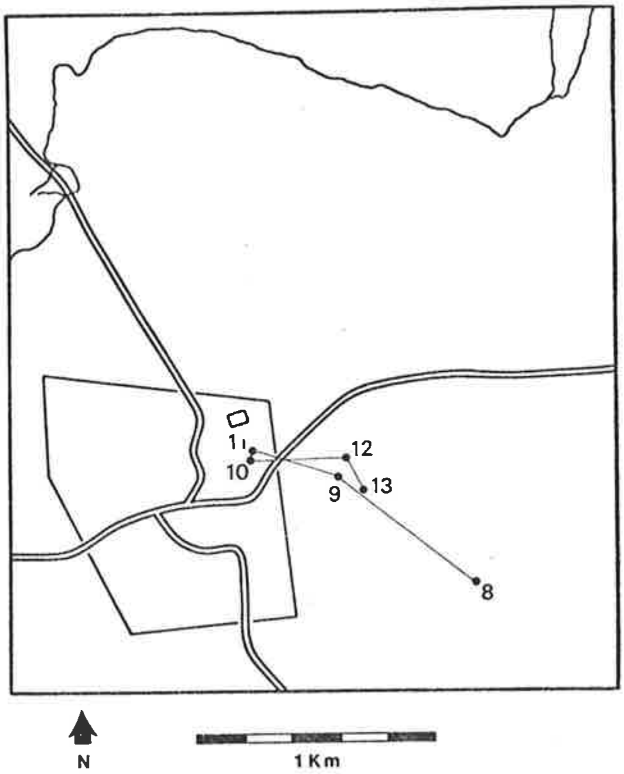
Reference	Date	Time (hrs)
1	9/5/78	1200
2		1600
3		2000
4		2400
5	10/5/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	11/5/78	0400
12		0800

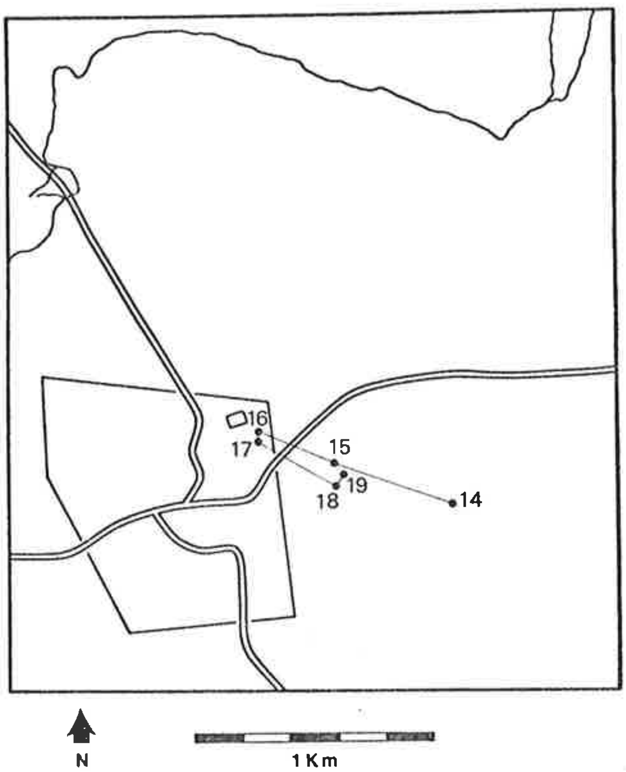


Male 2 December 1977

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	14/12/77	1200	11	16/12/77	1600
2		1700	12		2000
3		2400	13		2300
4	15/12/77	1200	14	17/12/77	0400
5		1600	15		0800
6		2000	16		1200
7		2300	17		1600
8	16/12/77	0400	18		2000
9		0800	19		2300
10		1200			

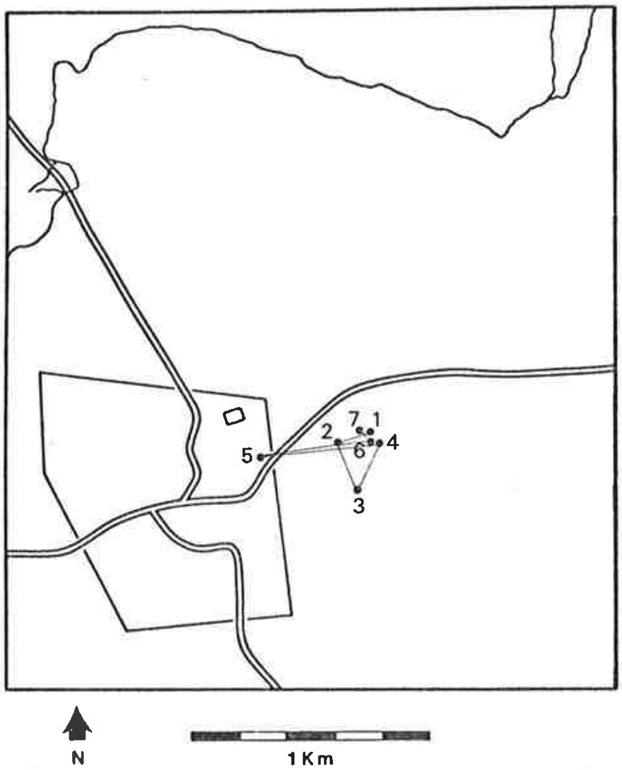


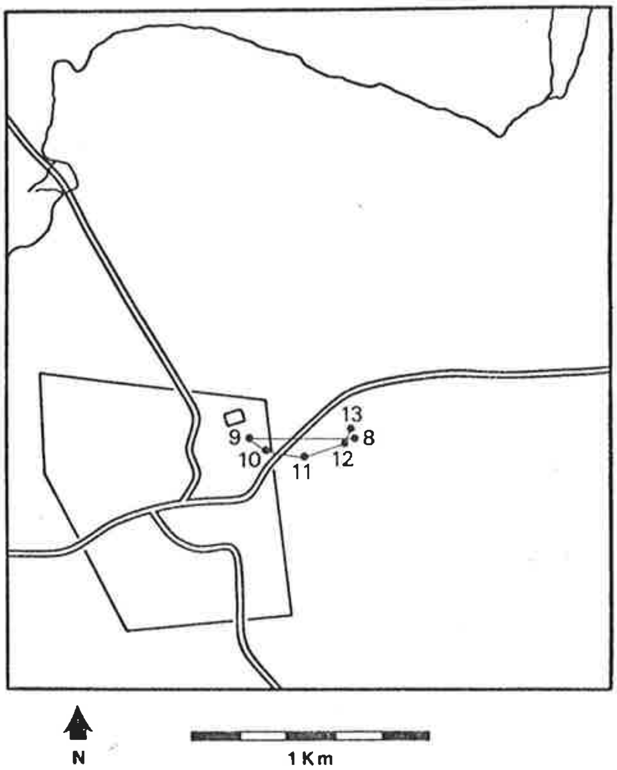


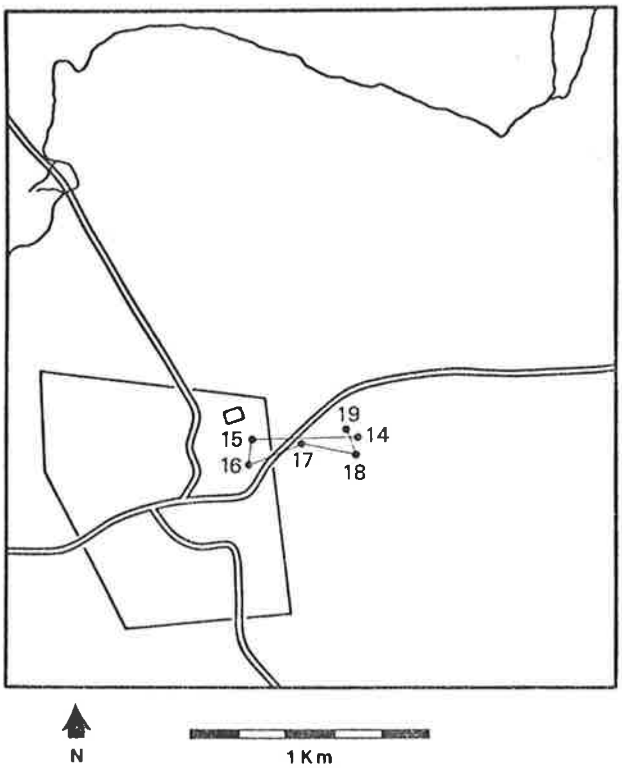


Male 2 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

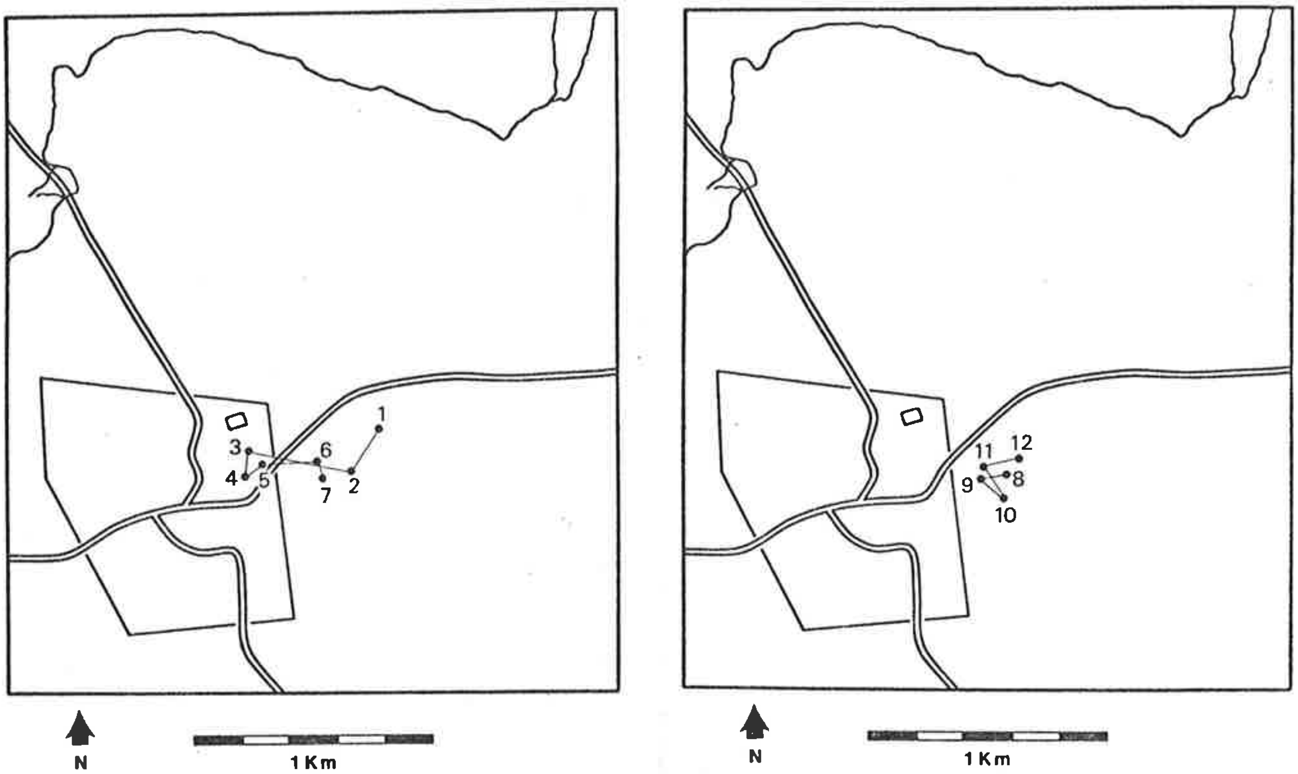






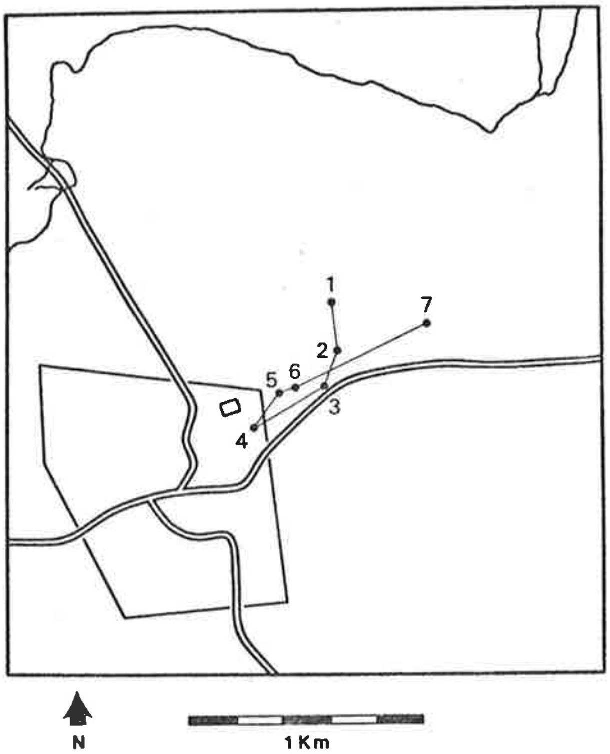
Male 2 March/April 1978

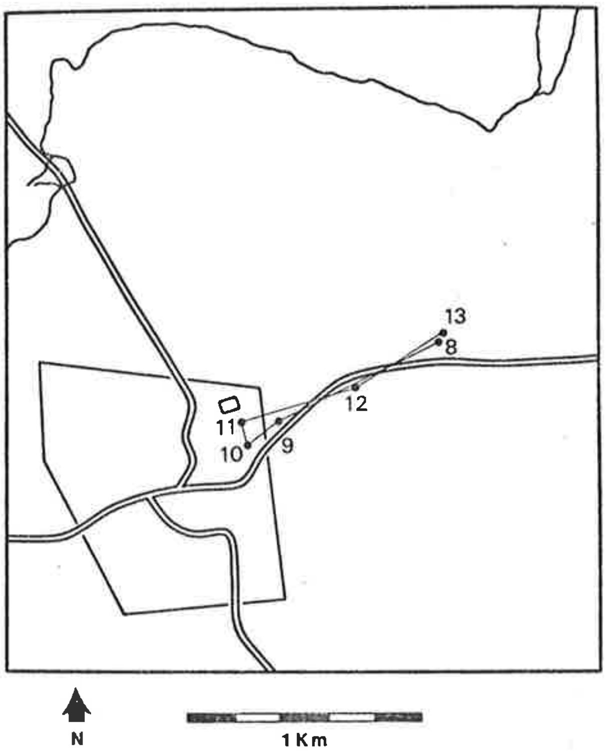
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

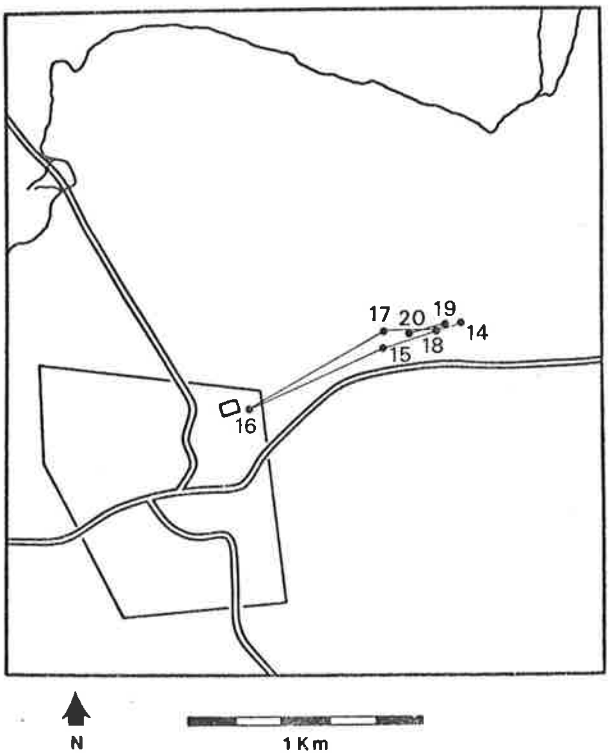


Male 2 May 1978

Reference	Date	Time (hrs)
1	9/5/78	1200
2		1600
3		2000
4		2400
5	10/5/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	11/5/78	0400
12		0800

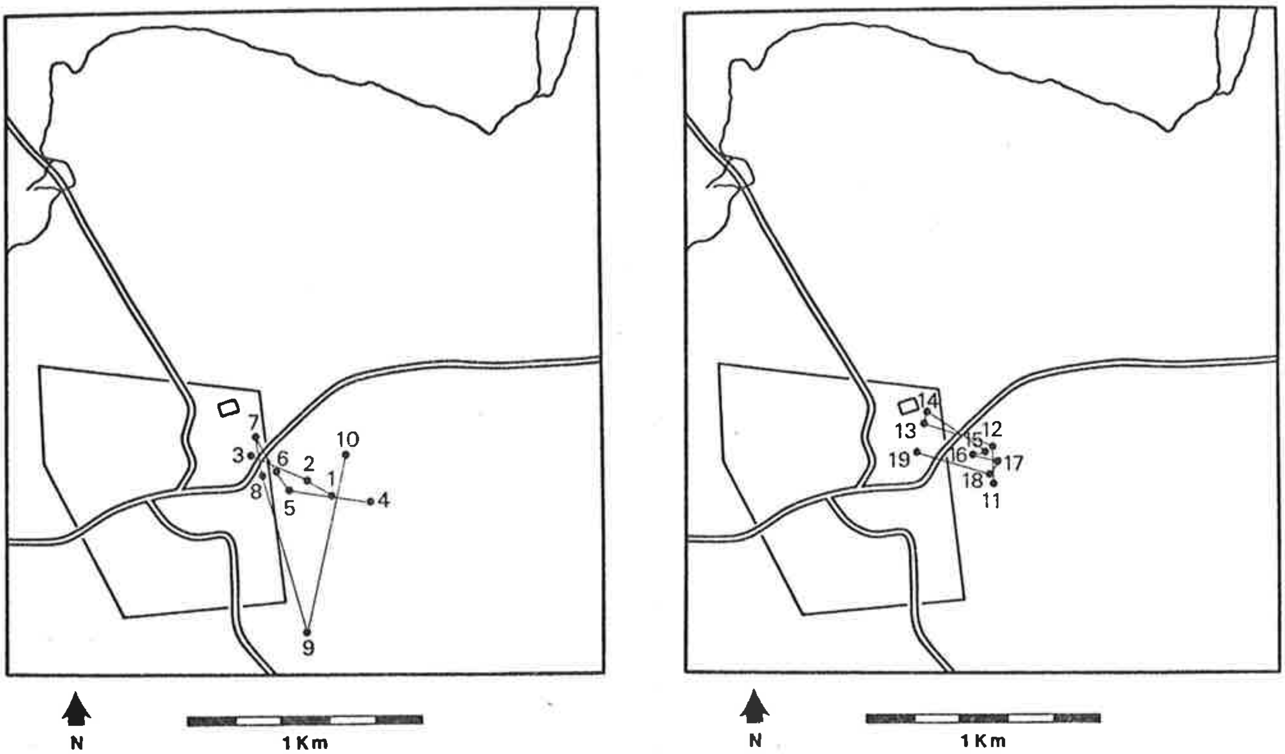






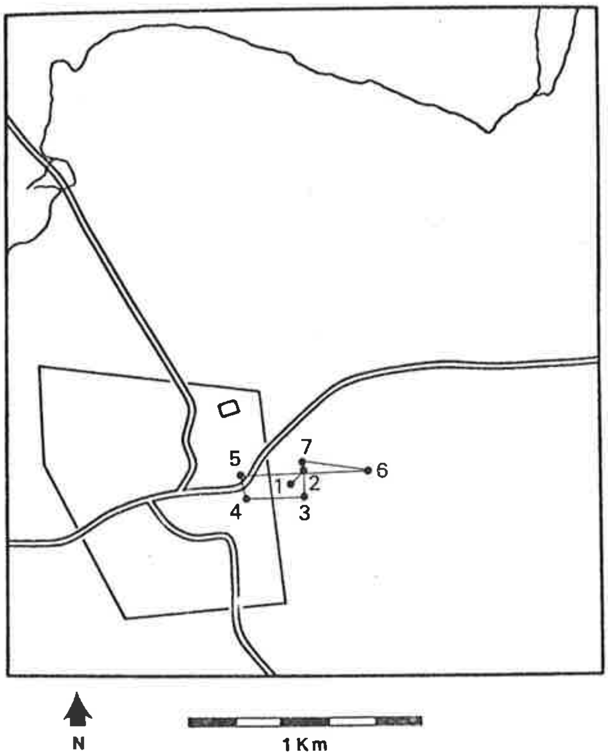
Male 3 May 1977

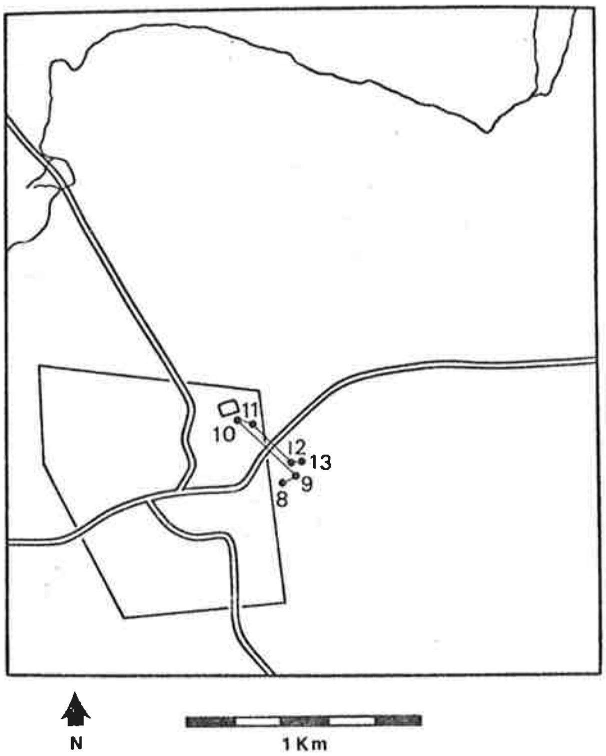
Reference	Date	Time (hrs)
1	22/5/77	1100
2		1500
3		1800
4		2200
5	23/5/77	0100
6		0600
7		1100
8		1500
9		1800
10		2200
11	24/5/77	0200
12		0600
13		1100
14		1500
15		1800
16		2200
17	25/5/77	0600
18		1100
19		1500
20		1800

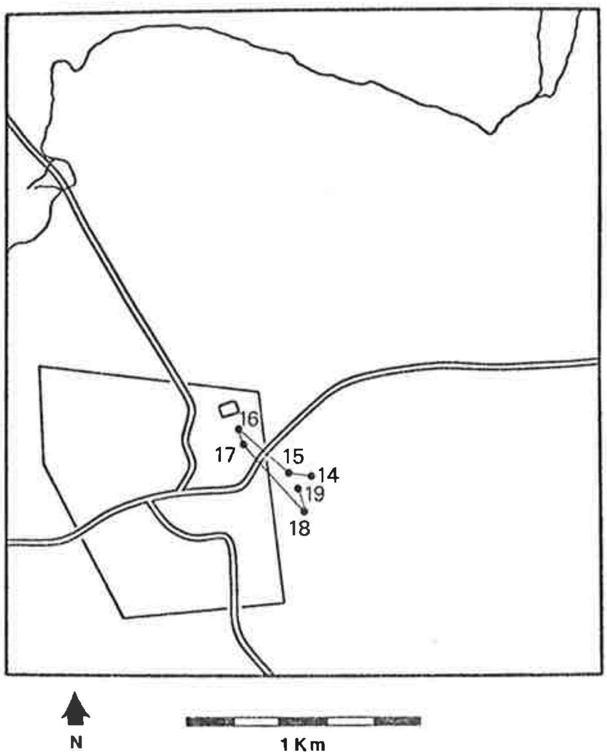


Male 4 December 1977

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	14/12/77	1200	11	16/12/77	1600
2		1700	12		2000
3		2400	13		2300
4	15/12/77	1200	14	17/12/77	0400
5		1600	15		0800
6		2000	16		1200
7		2300	17		1600
8	16/12/77	0400	18		2000
9		0800	19		2300
10		1200			

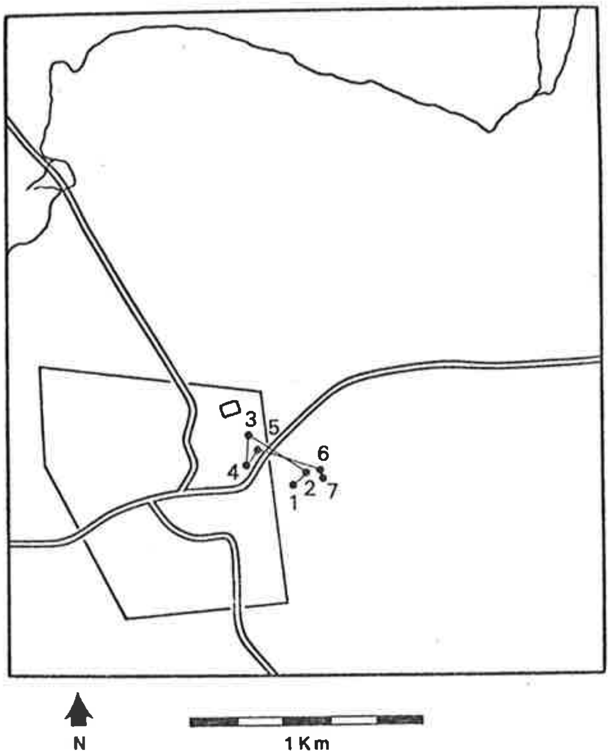


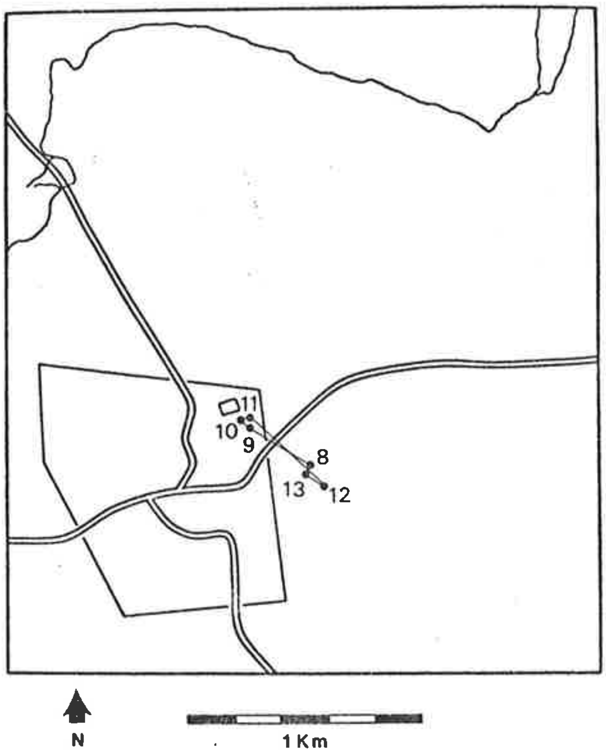


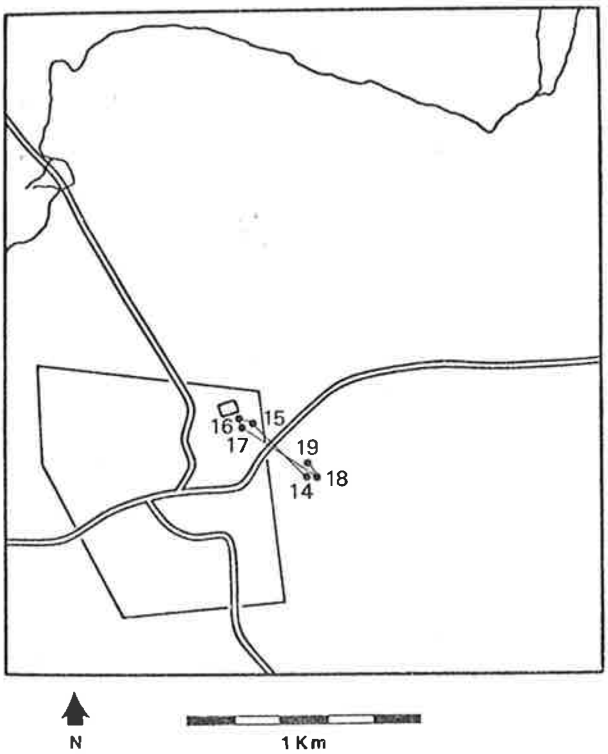


Male 4 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

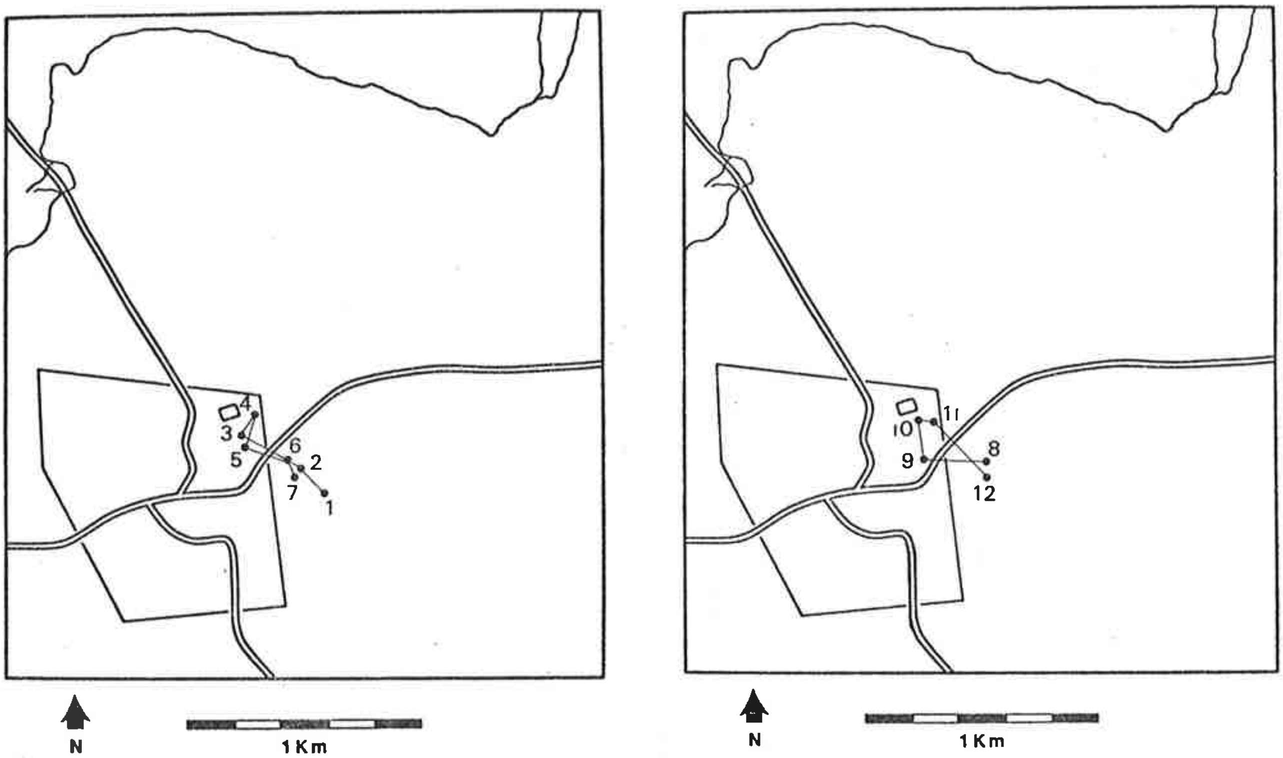






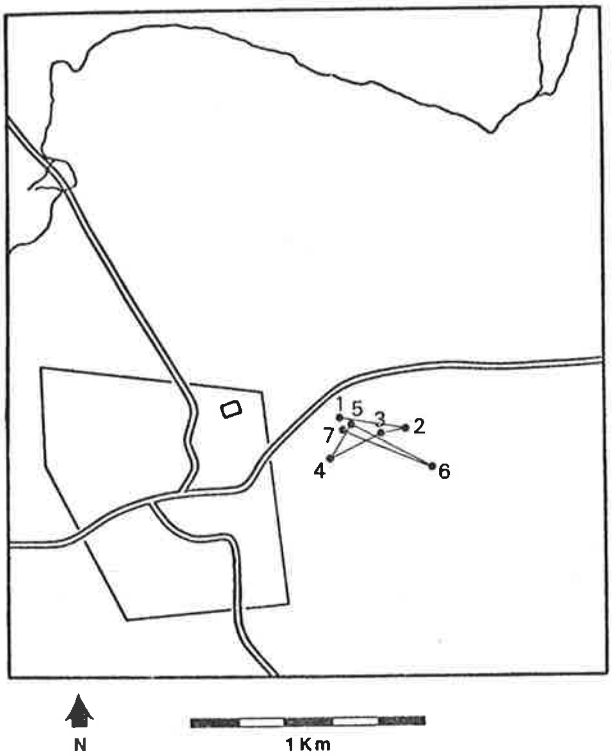
Male 4 March/April 1978

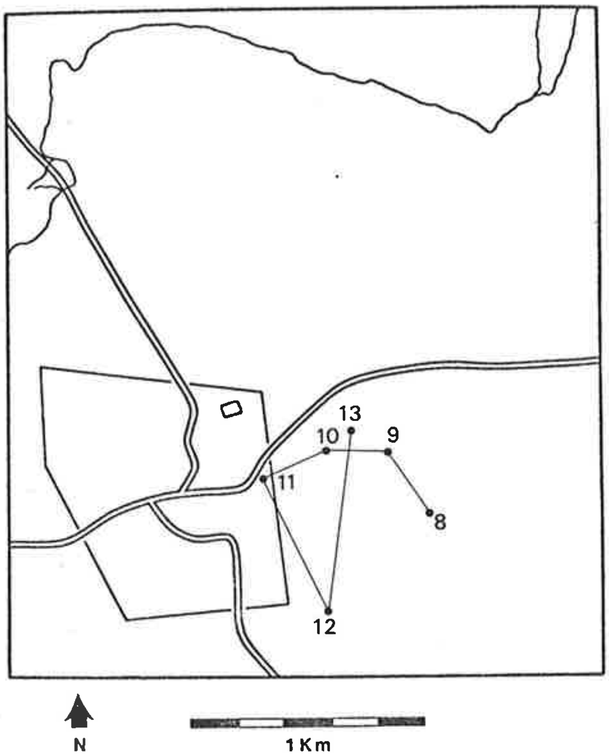
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

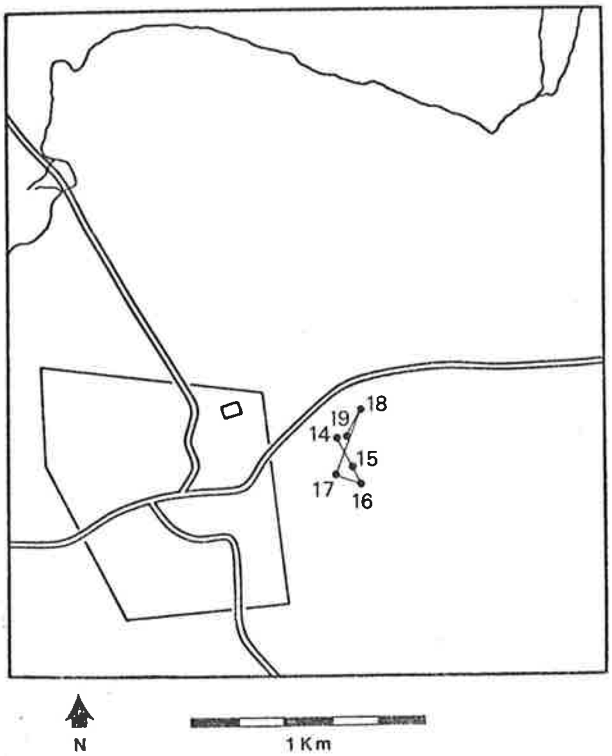


Male 4 May 1978

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	9/5/78	1200	8	10/5/78	1600
2		1600	9		2000
3		2000	10		2400
4		2400	11	11/5/78	0400
5	10/5/78	0400	12		0800
6		0800			
7		1200			

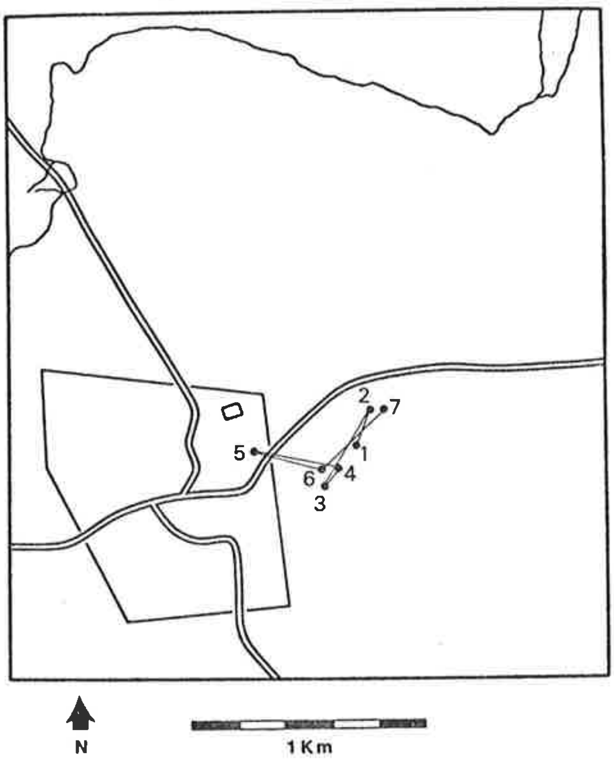


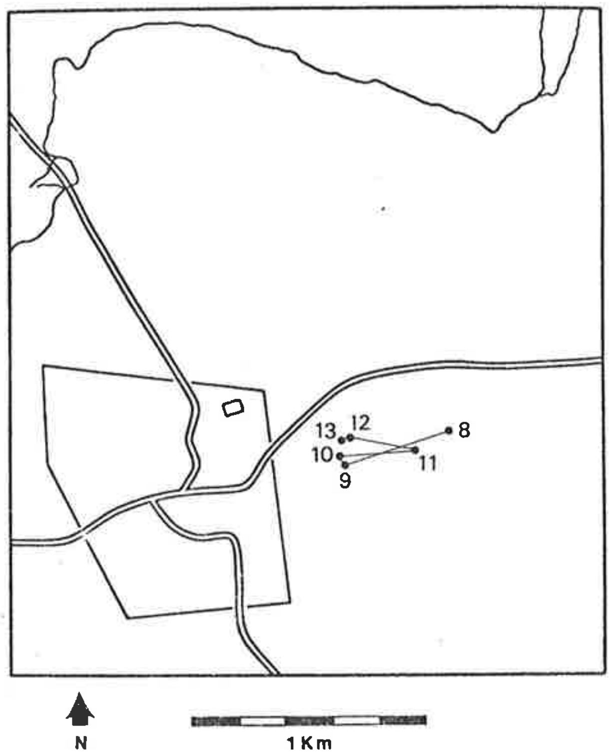


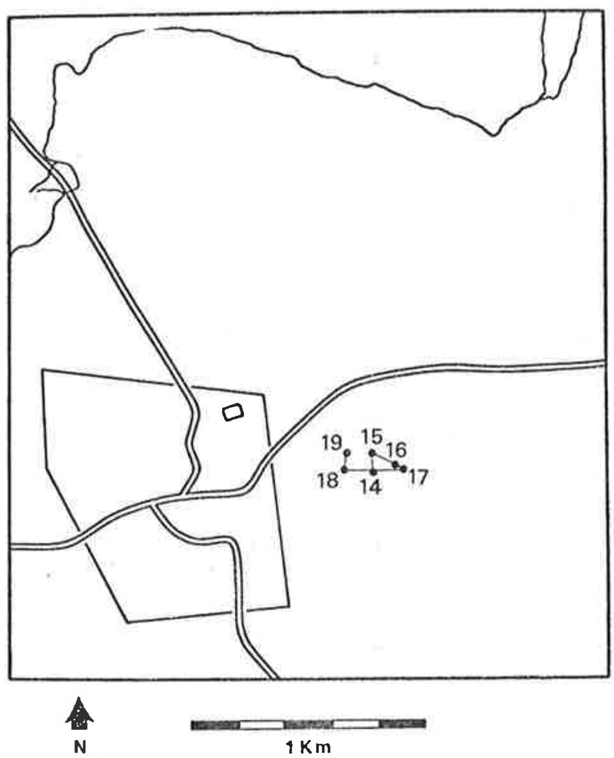


Male 5 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200







Male 5 March/April 1978

Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
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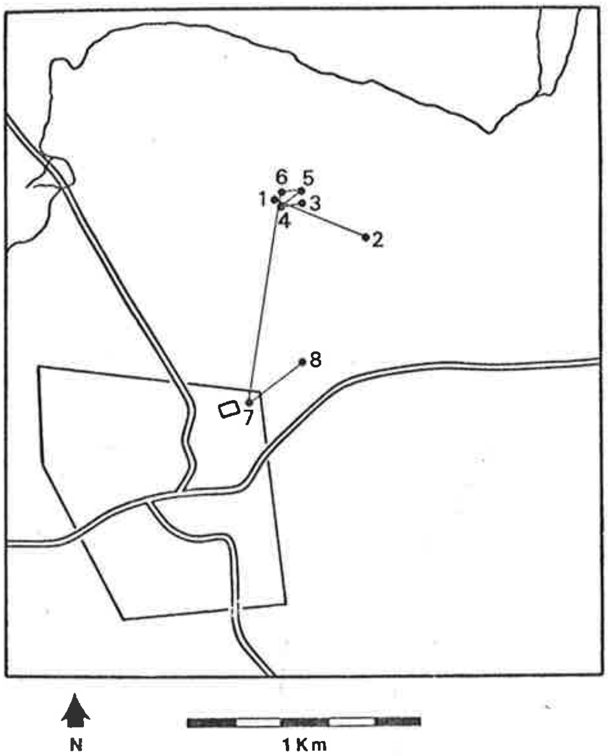
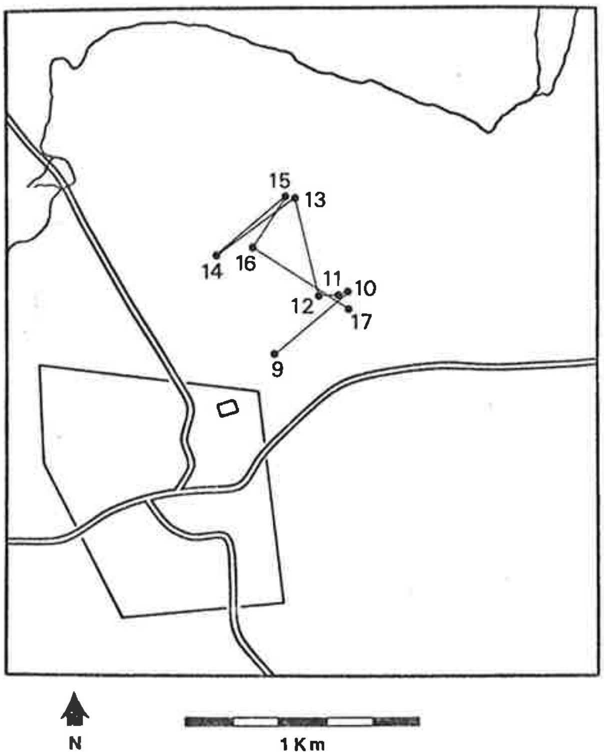
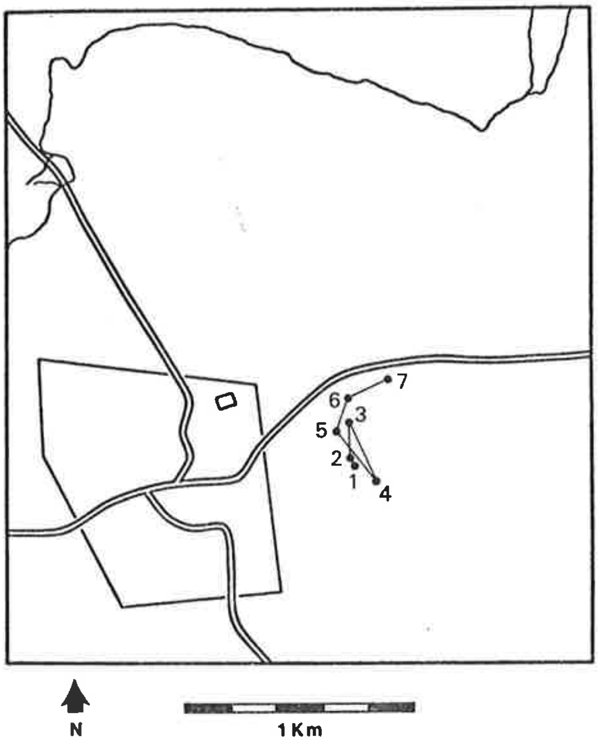
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

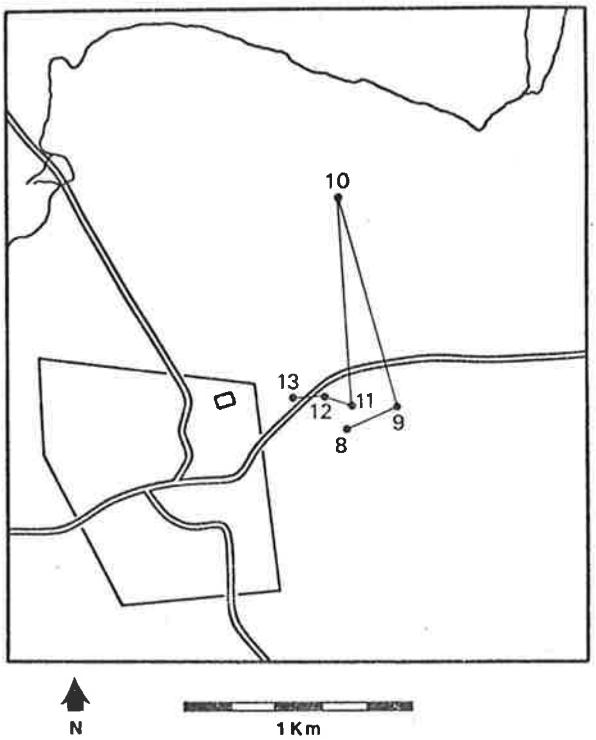


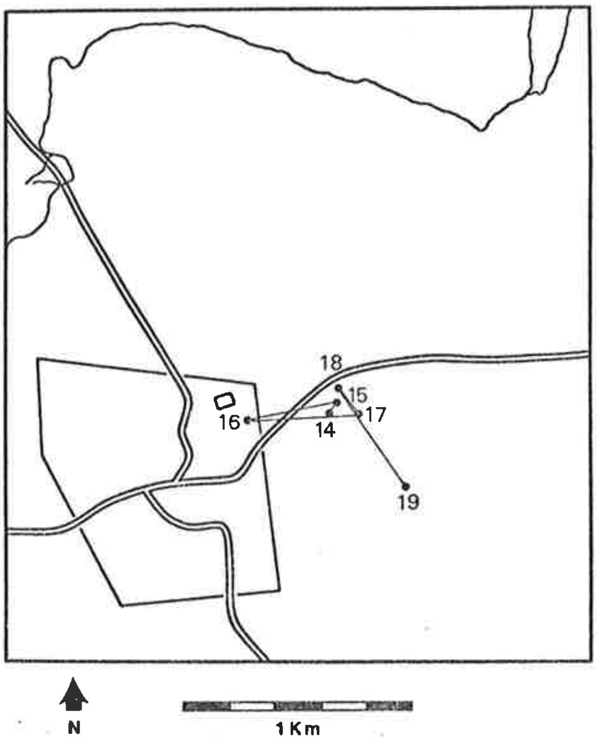


Male 6 December 1977

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	14/12/77	1200	9	16/12/77	1600
2		1700	10		2000
3	15/12/77	1200	11		2300
4		1600	12	17/12/77	0400
5		2000	13		0800
6		2300	14		1200
7	16/12/77	0400	15		1600
8		1200	16		2000
			17		2300

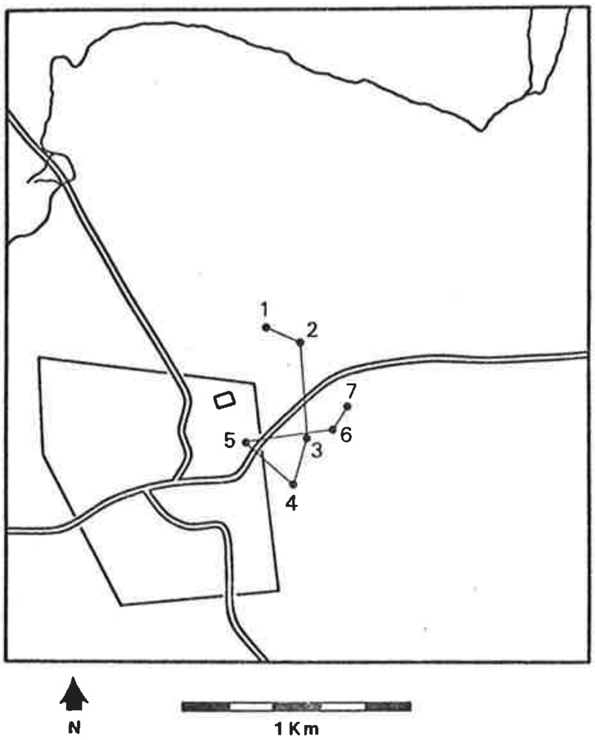


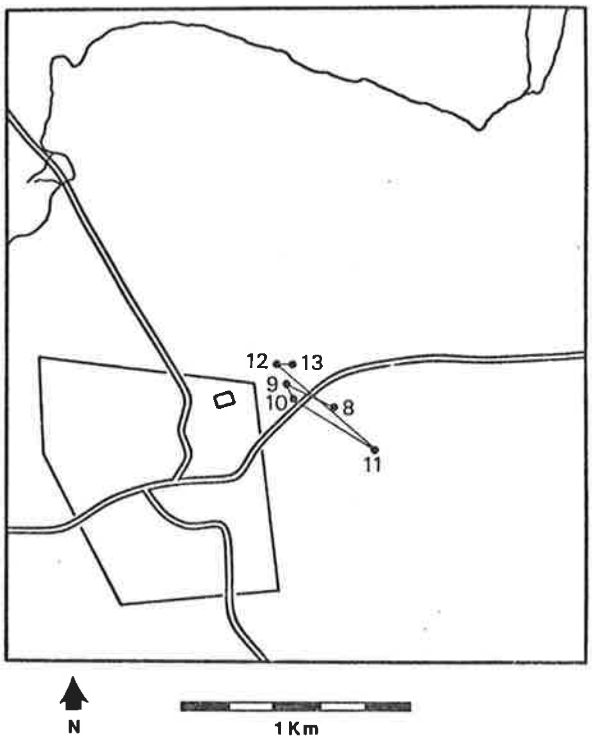


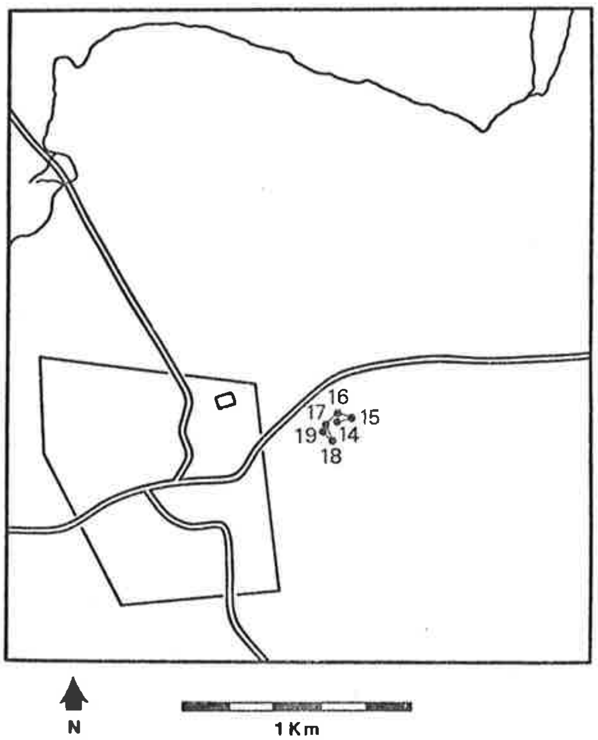


Male 7 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

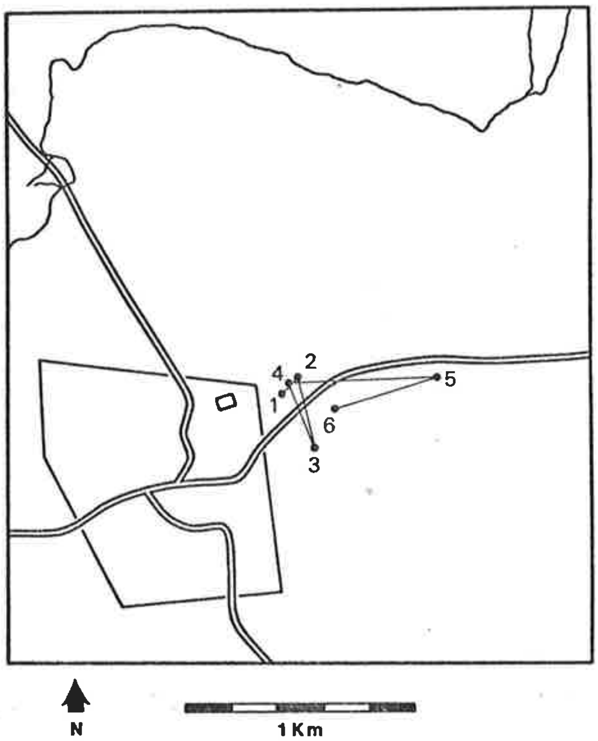






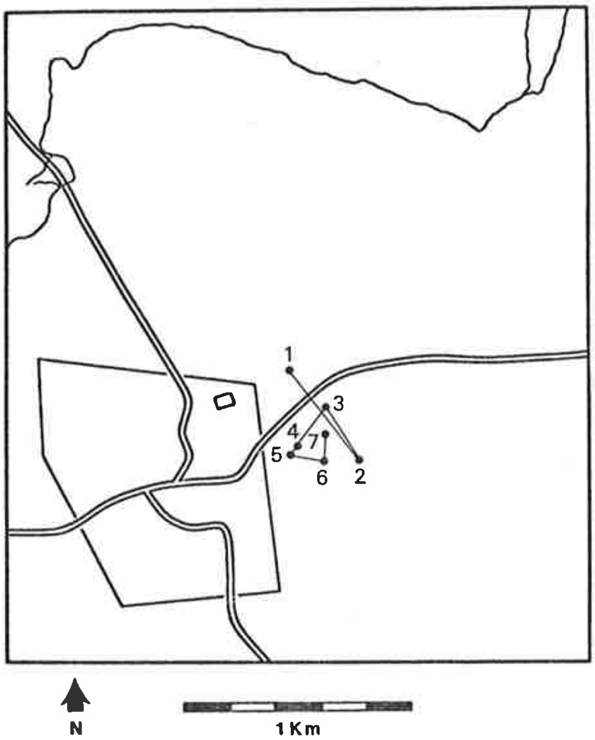
Male 7 March/April 1978

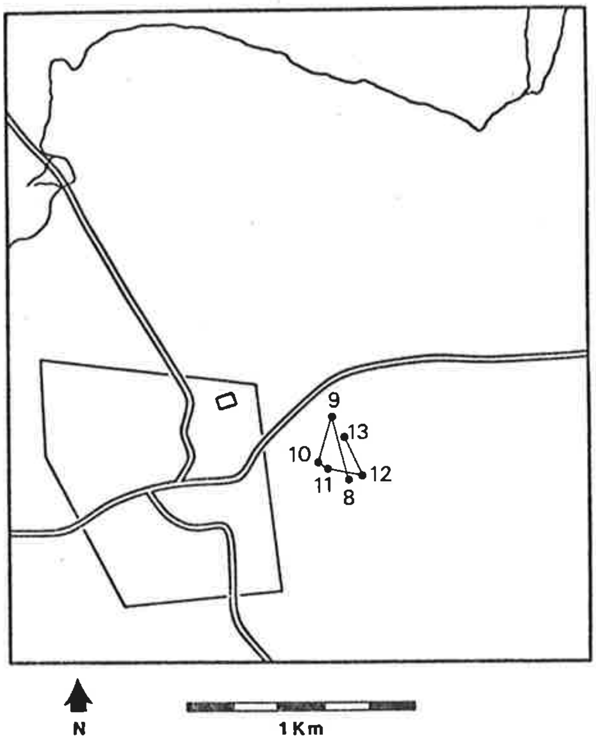
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

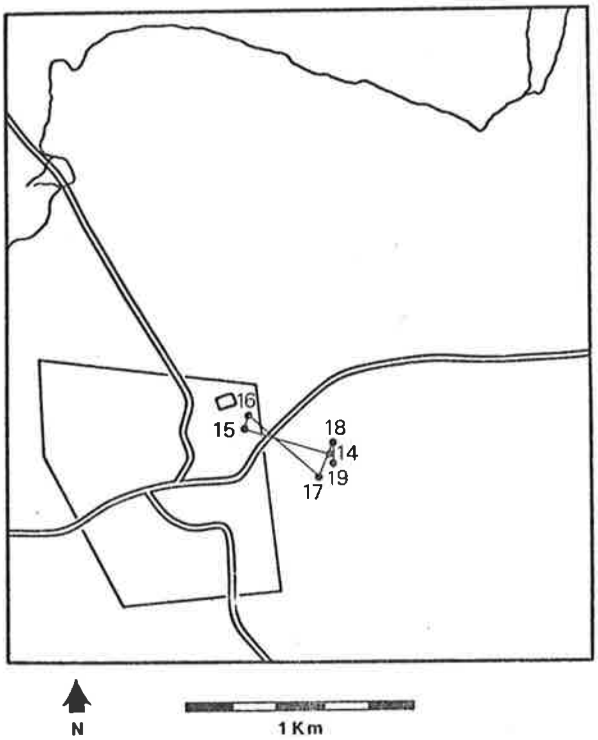


Male 8 February 1978

Reference	Date	Time (hrs)
1	2/2/78	1600
2		2000
3		2400
4	3/2/78	0400
5		0800
6		1200







Male 8 March/April 1978

Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
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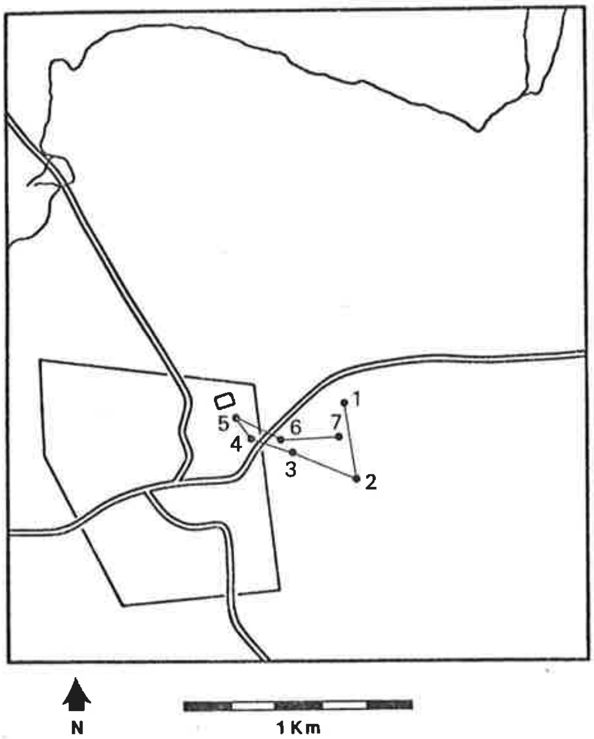
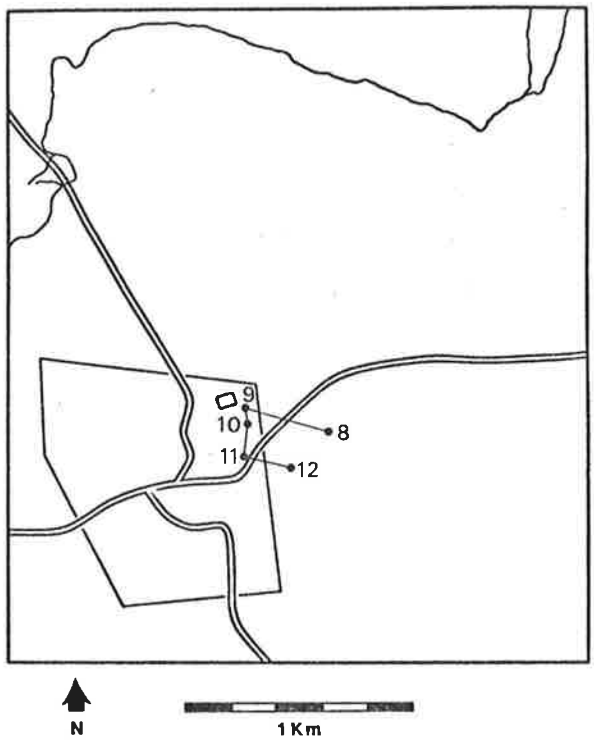
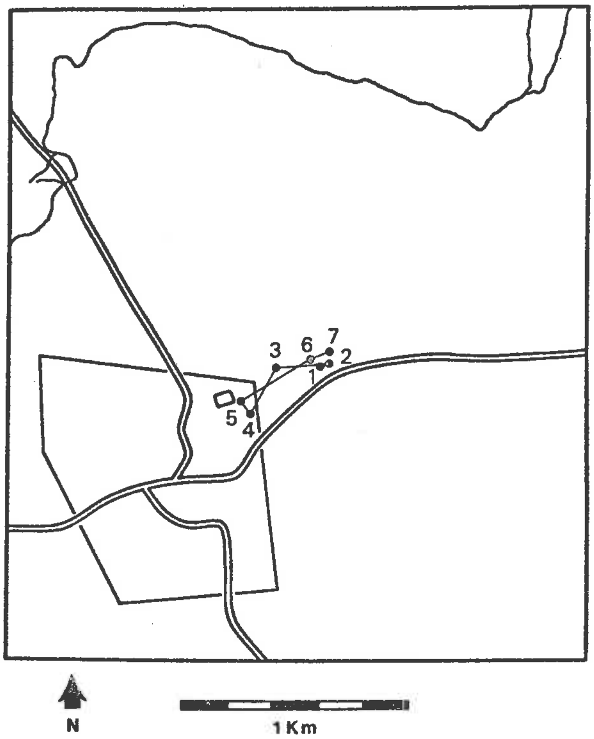
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

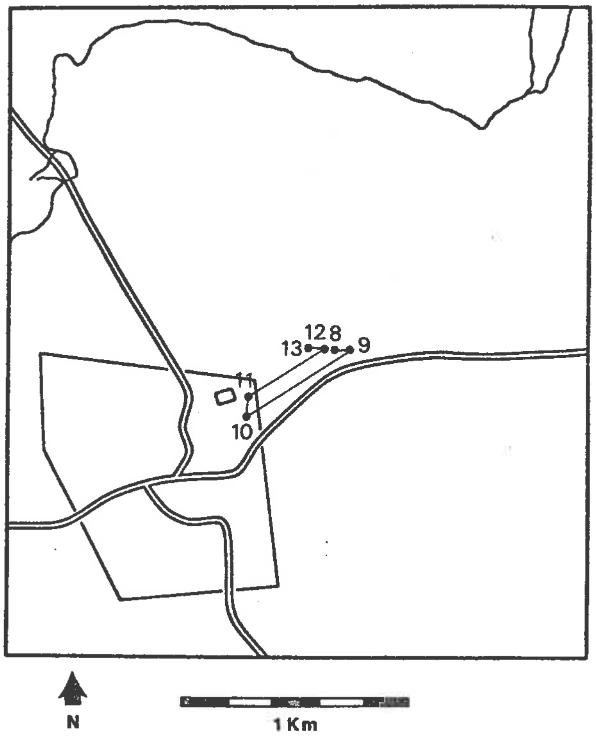


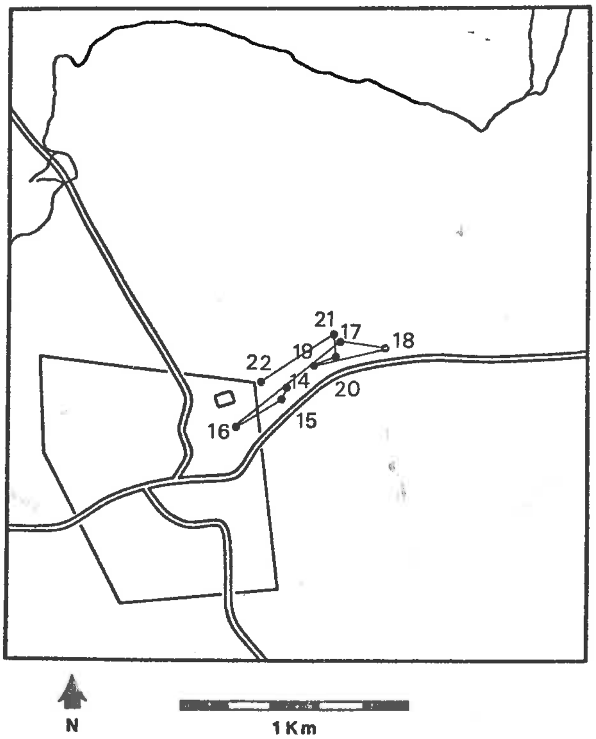


Male 8 May 1978

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	9/5/78	1200	8	10/5/78	1600
2		1600	9		2000
3		2000	10		2400
4		2400	11	11/5/78	0400
5	10/5/78	0400	12		0800
6		0800			
7		1200			

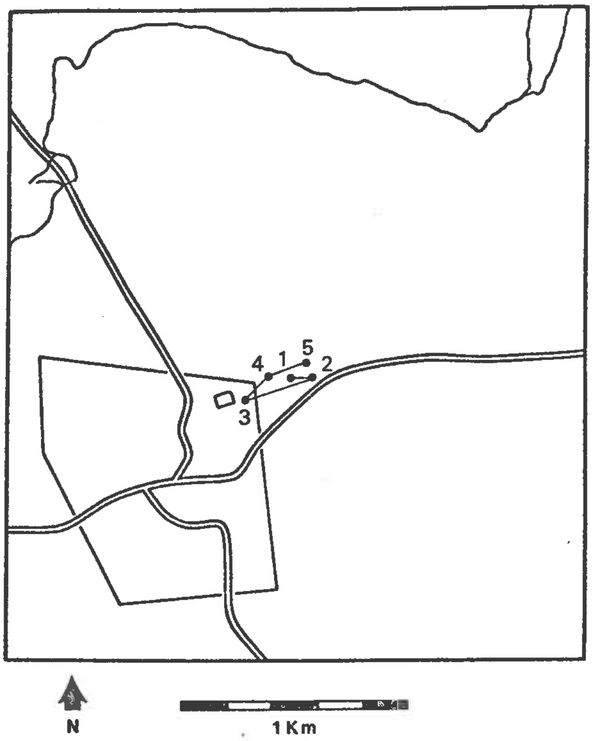


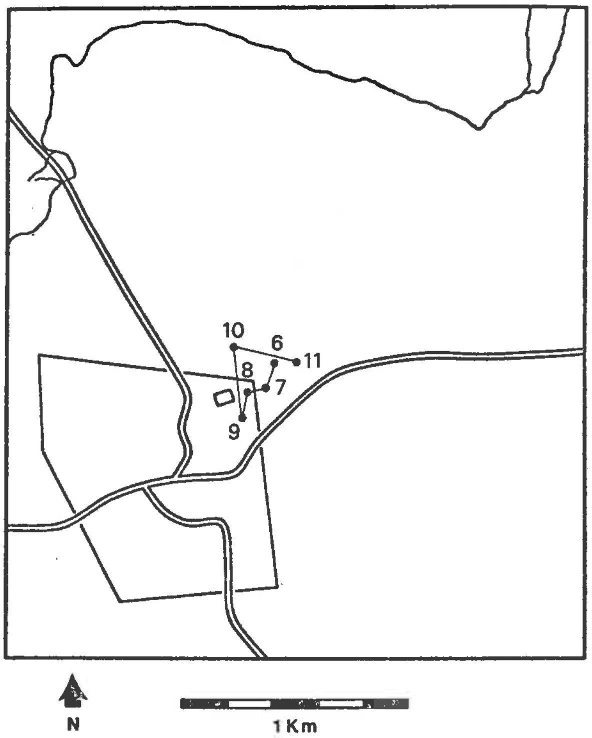


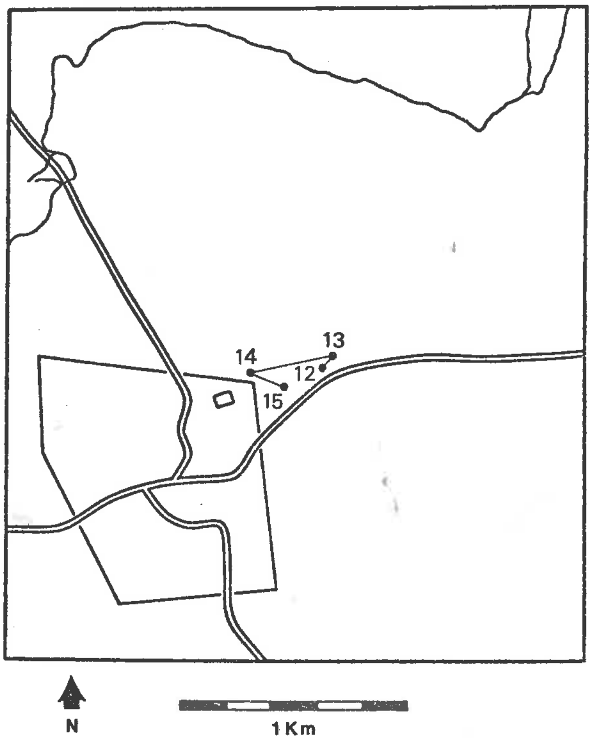


Female 1 May 1977

Reference	Date	Time (hrs)
1	22/5/77	1100
2		1500
3		1800
4		2200
5	23/5/77	0100
6		0700
7		1100
8		1500
9		1800
10		2200
11	24/5/77	0200
12		0600
13		1100
14		1500
15		1800
16		2200
17	25/5/77	0200
18		0600
19		1100
20		1500
21		1800
22		2200

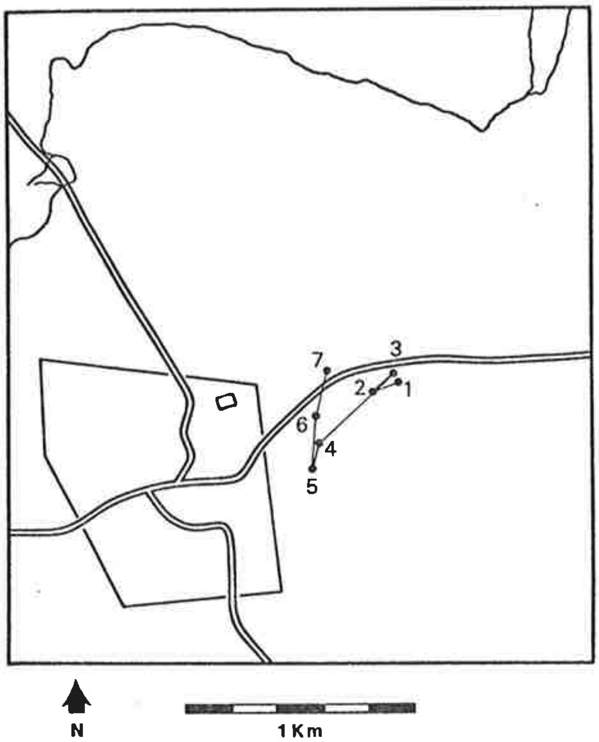


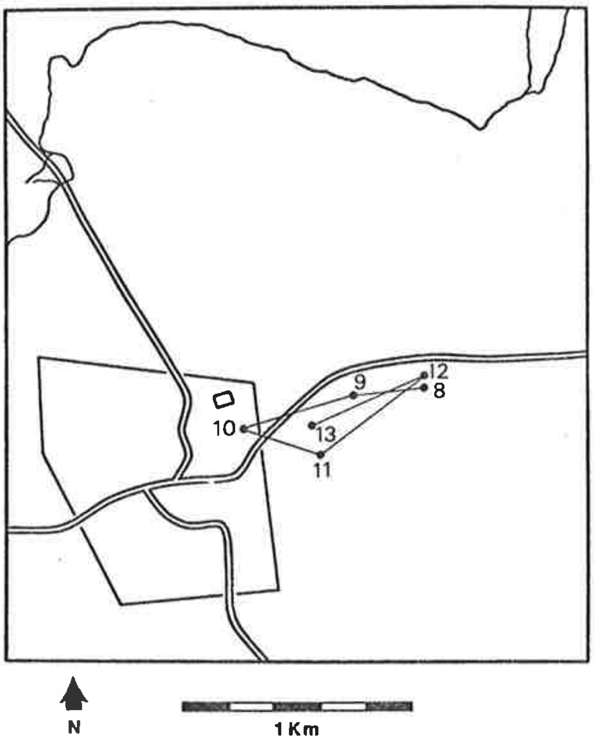


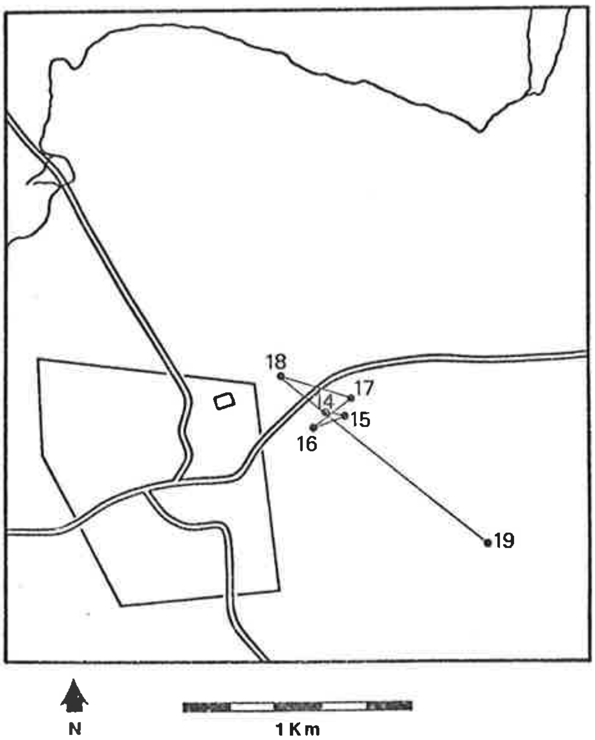


Female 2 May 1977

Reference	Date	Time (hrs)
1	22/5/77	1100
2		1800
3		2200
4	23/5/77	0100
5		0600
6		1500
7		1800
8		2200
9	24/5/77	0200
10		0600
11		1100
12		1500
13		1800
14		2200
15	25/5/77	1100

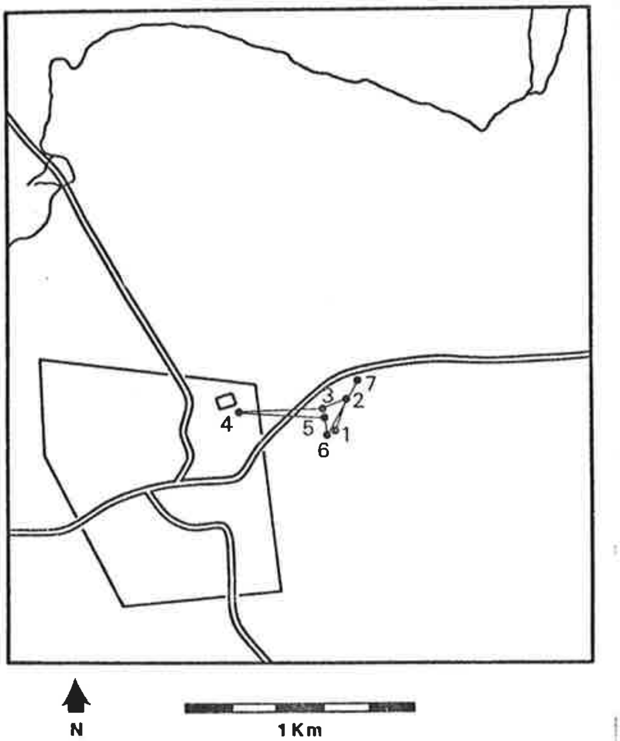


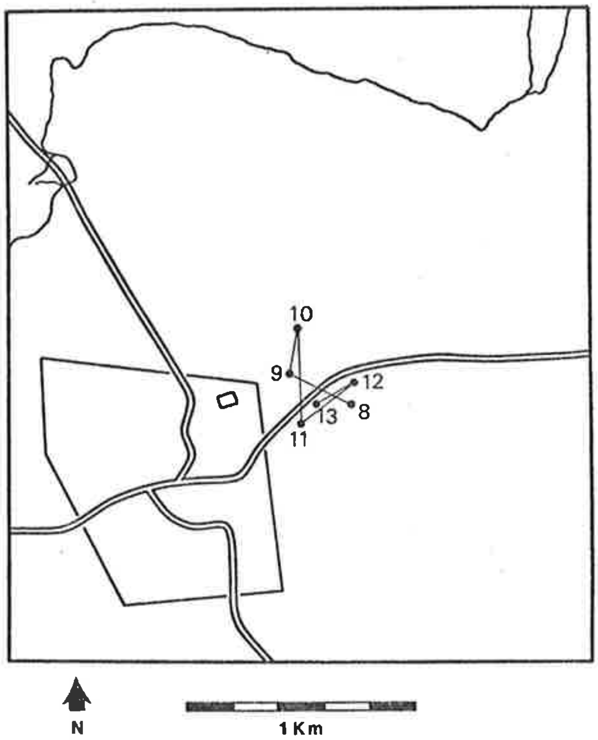


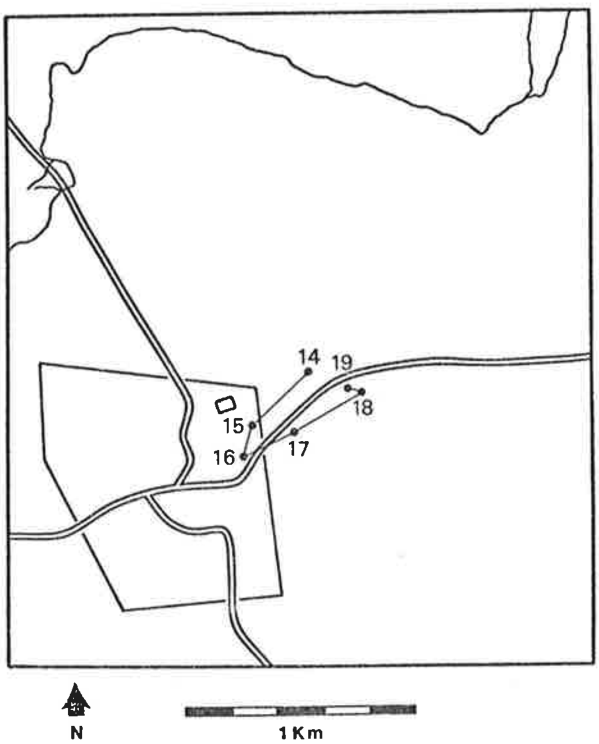


Female 2 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

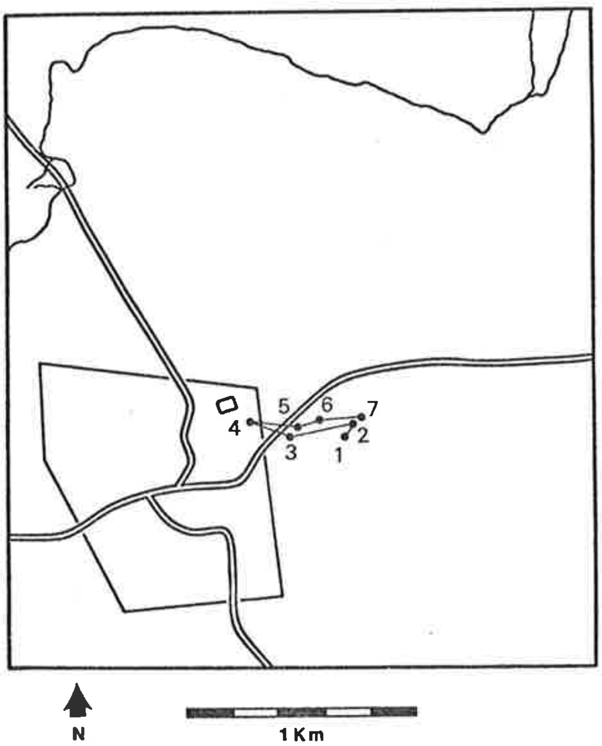


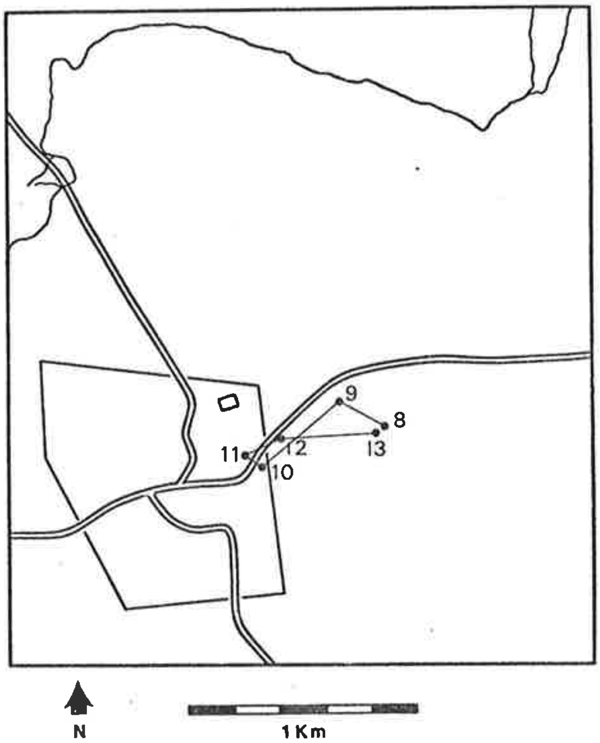


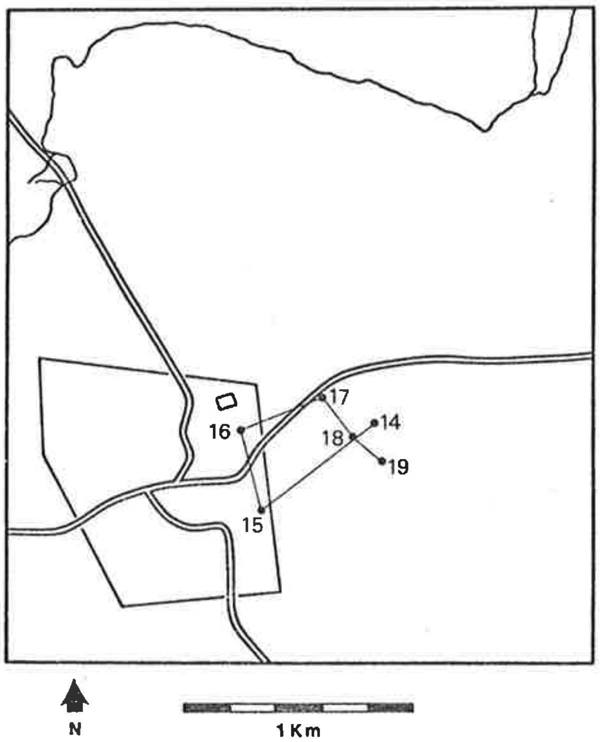


Female 2 March/April 1978

Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

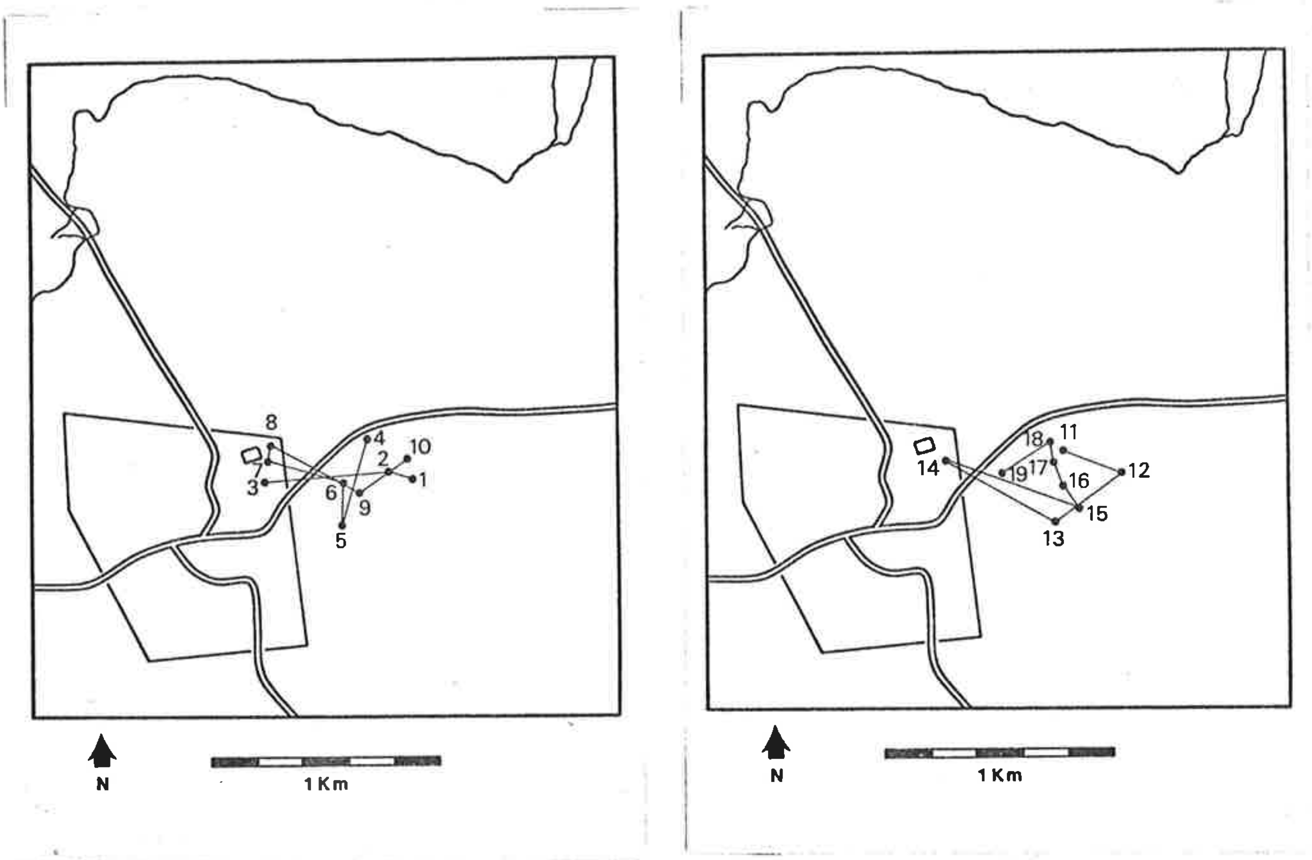






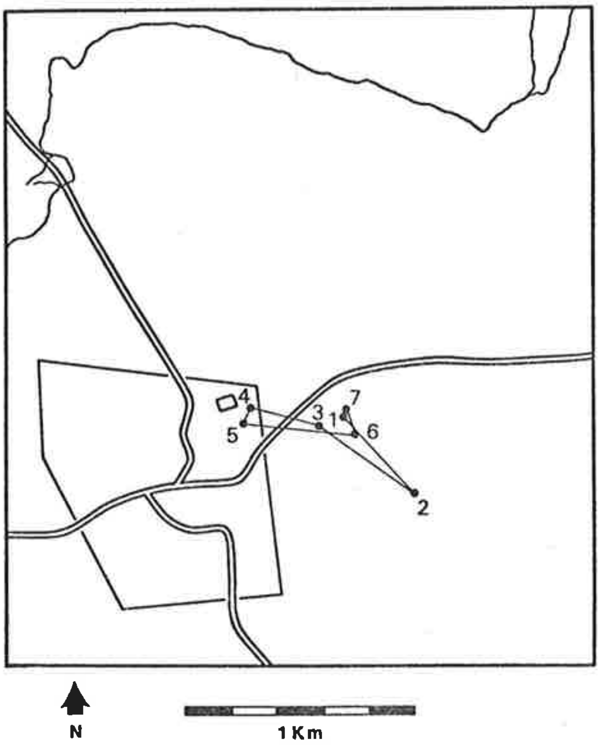
Female 3 May 1977

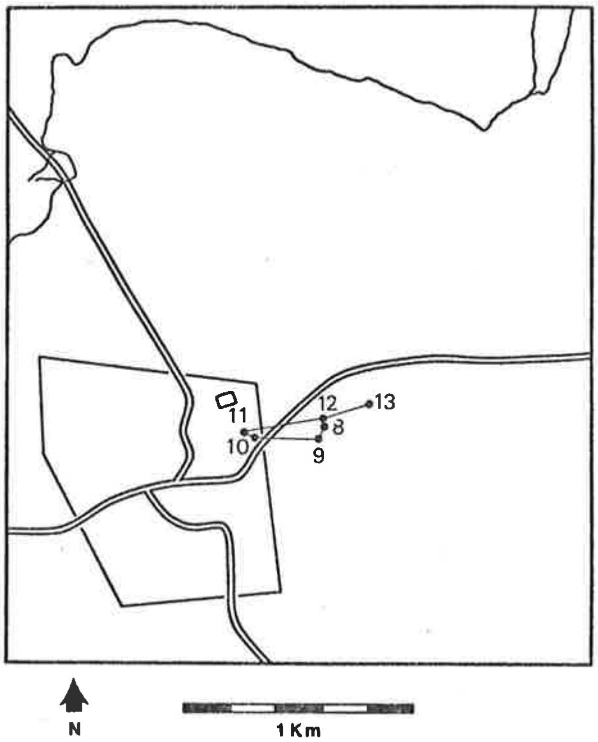
Reference	Date	Time (hrs)
1	22/5/77	1100
2		1500
3		1800
4		2200
5	23/5/77	0100
6		0600
7		1100
8		1500
9		1800
10		2200
11	24/5/77	0200
12		0600
13		1100
14		1500
15		1800
16		2200
17	25/5/77	0200
18		1100
19		1800

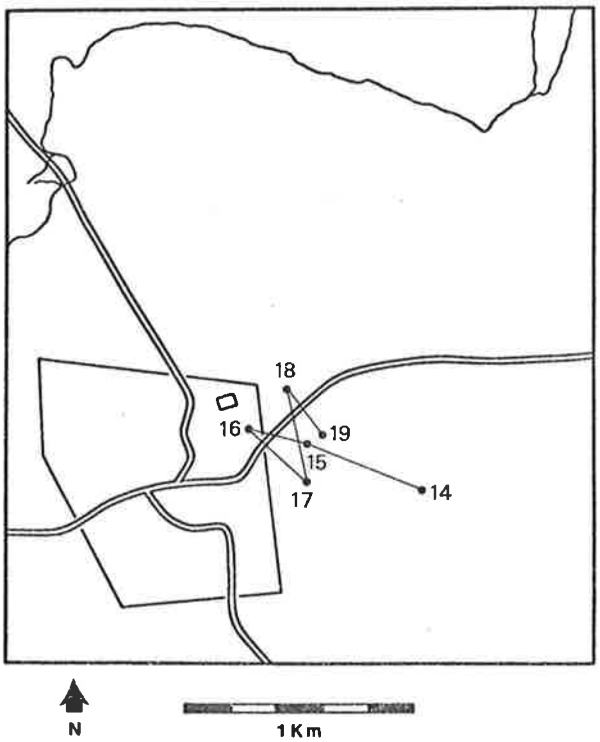


Female 3 December 1977

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	14/12/77	1200	11	16/12/77	1600
2		1700	12		2000
3		2400	13		2300
4	15/12/77	1200	14	17/12/77	0400
5		1600	15		0800
6		2000	16		1200
7		2300	17		1600
8	16/12/77	0400	18		2000
9		0800	19		2300
10		1200			

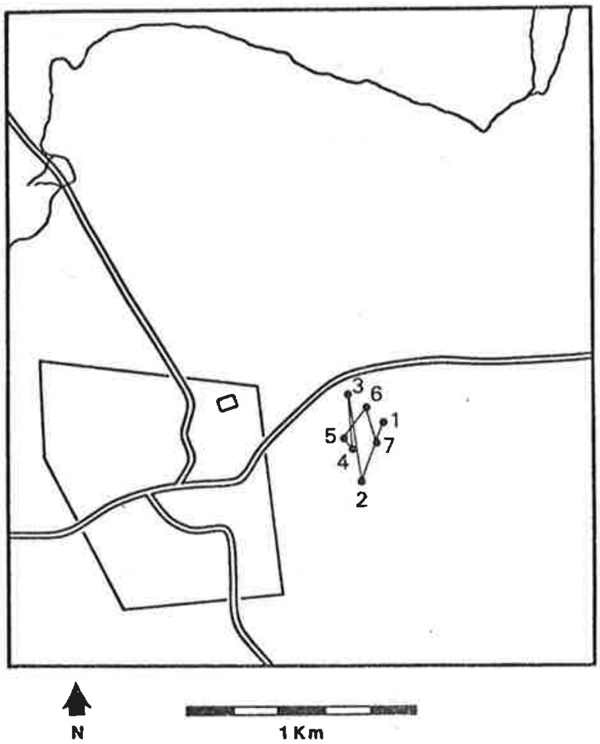


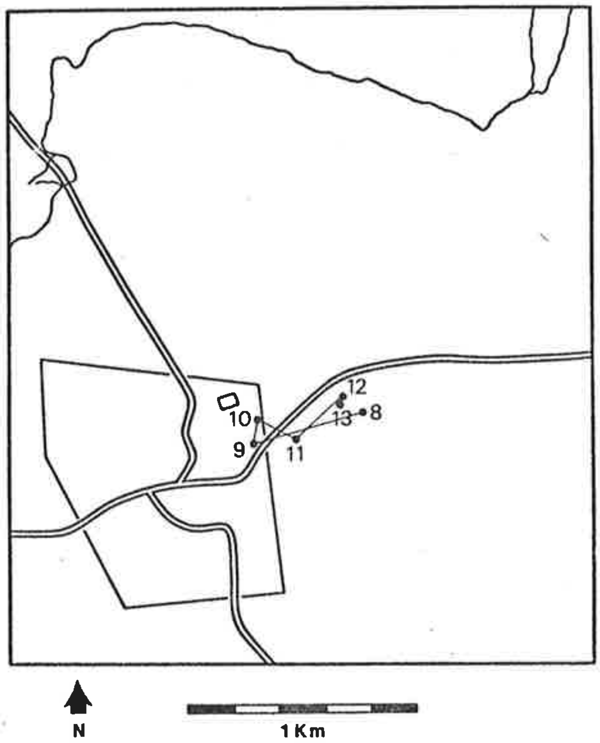


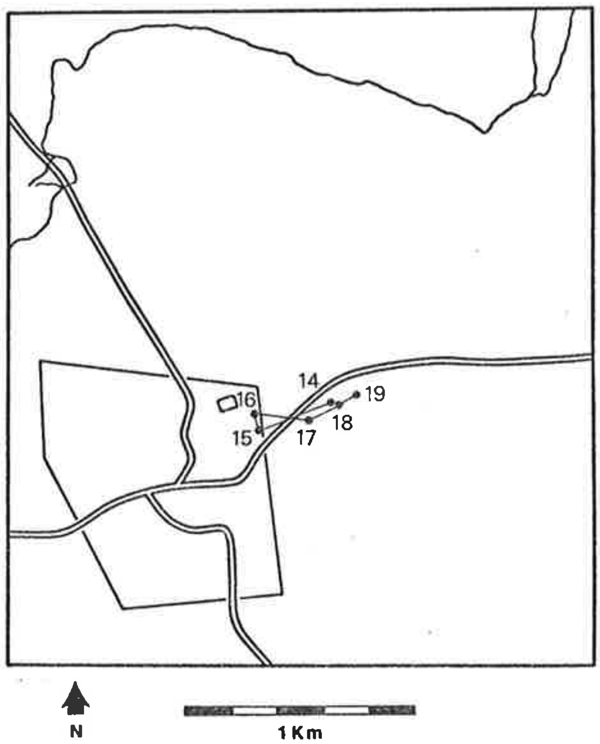


Female 3 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

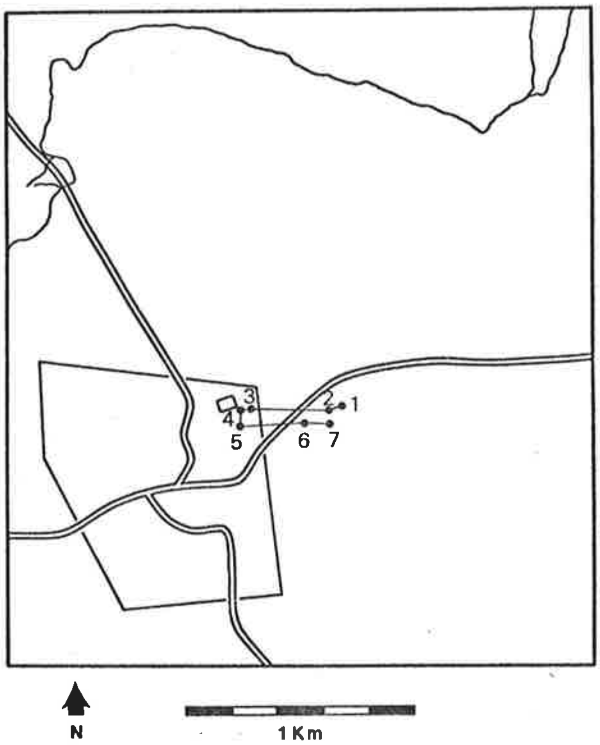


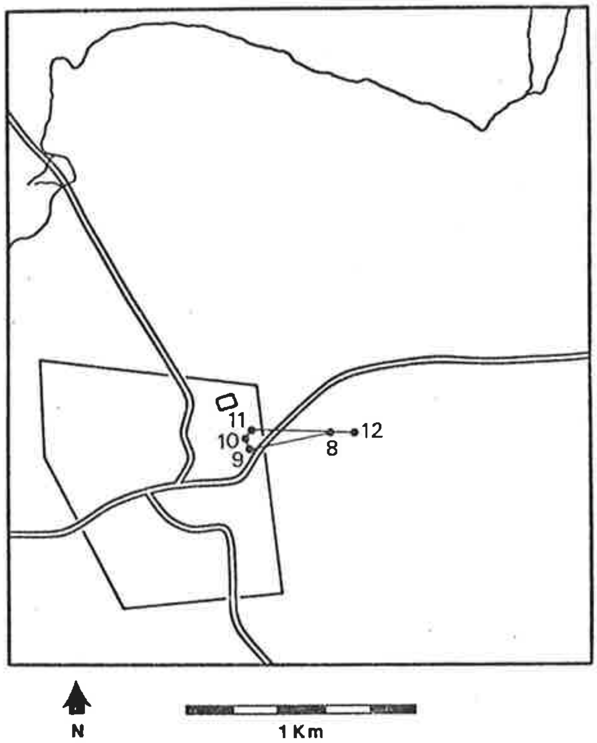




Female 3 March/April 1978

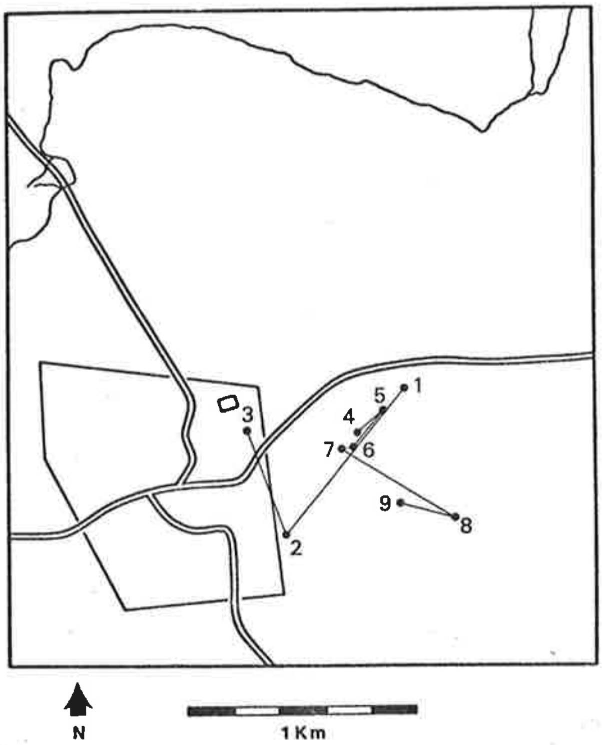
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

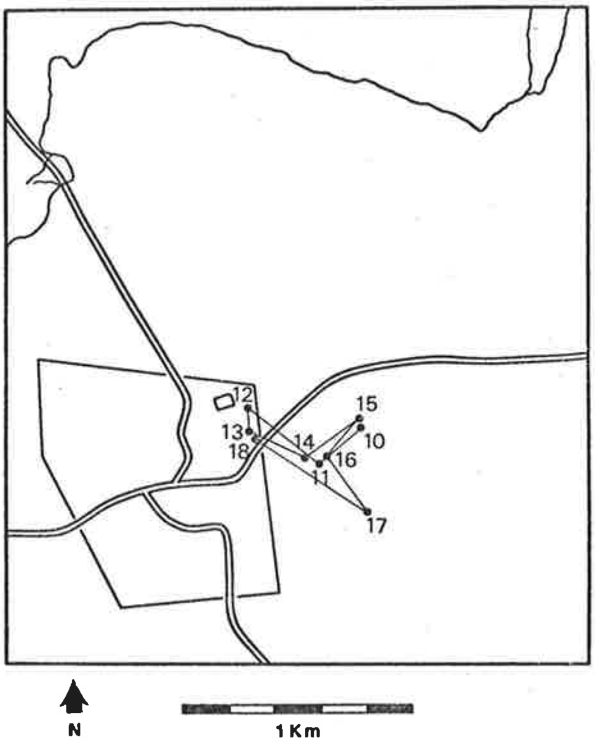




Female 3 May 1978

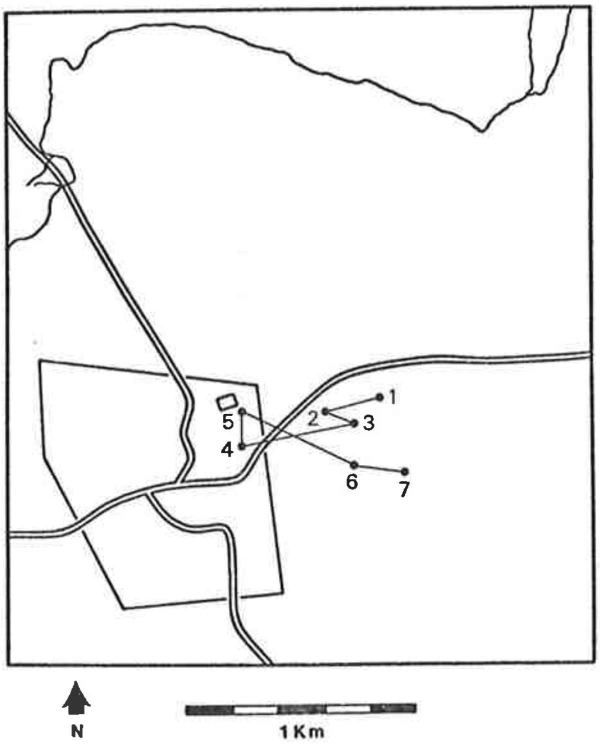
Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	9/5/78	1200	8	10/5/78	1600
2		1600	9		2000
3		2000	10		2400
4		2400	11	11/5/78	0400
5	10/5/78	0400	12		0800
6		0800			
7		1200			

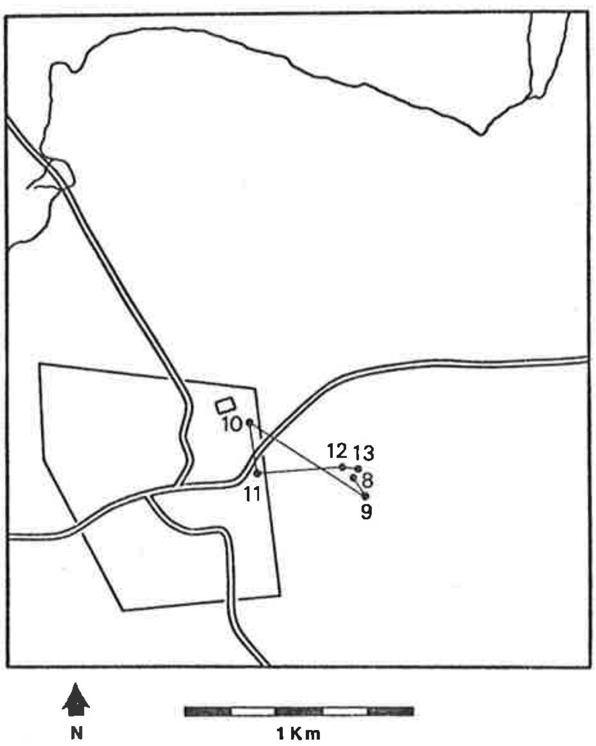


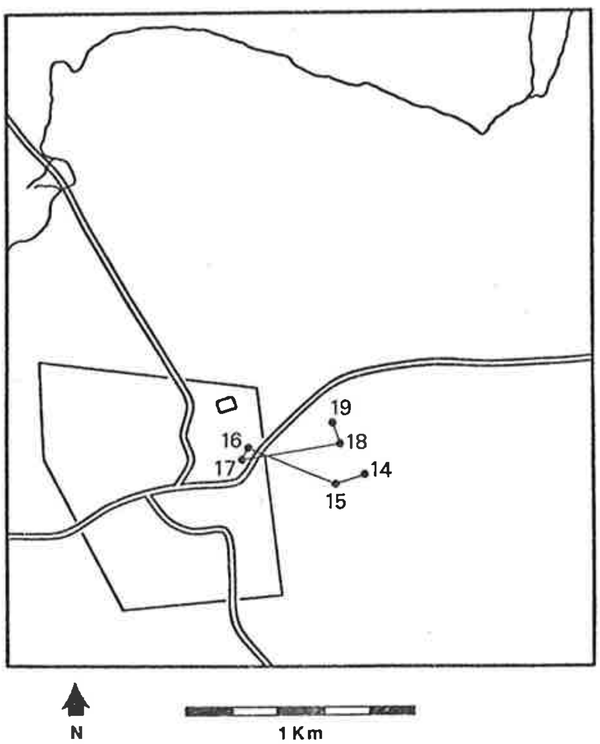


Female 5 December 1977

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	14/12/77	1200	10	16/12/77	1600
2		1700	11		2000
3		2400	12		2300
4	15/12/77	1200	13	17/12/77	0400
5		2000	14		0800
6		2300	15		1200
7	16/12/77	0400	16		1600
8		0800	17		2000
9		1200	18		2300

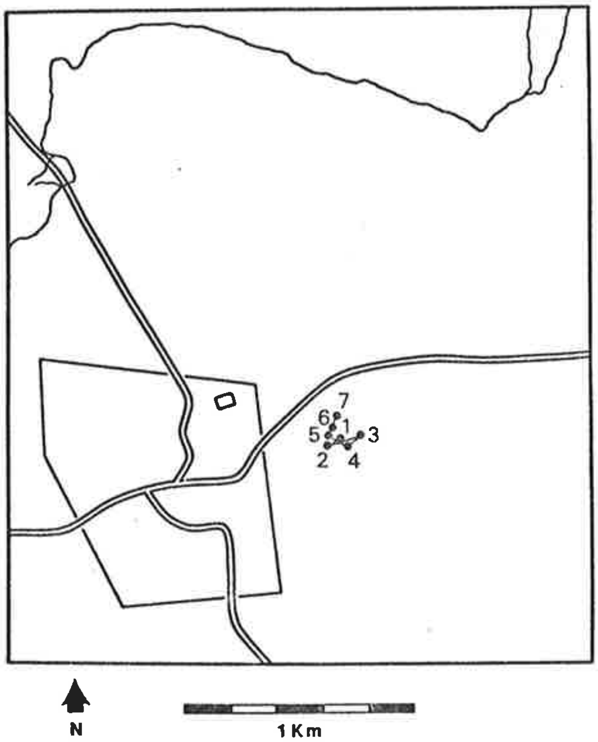


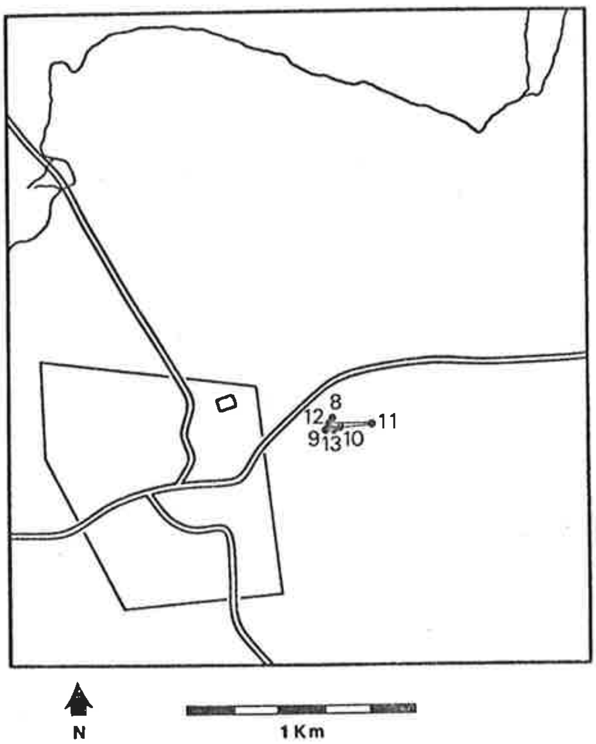


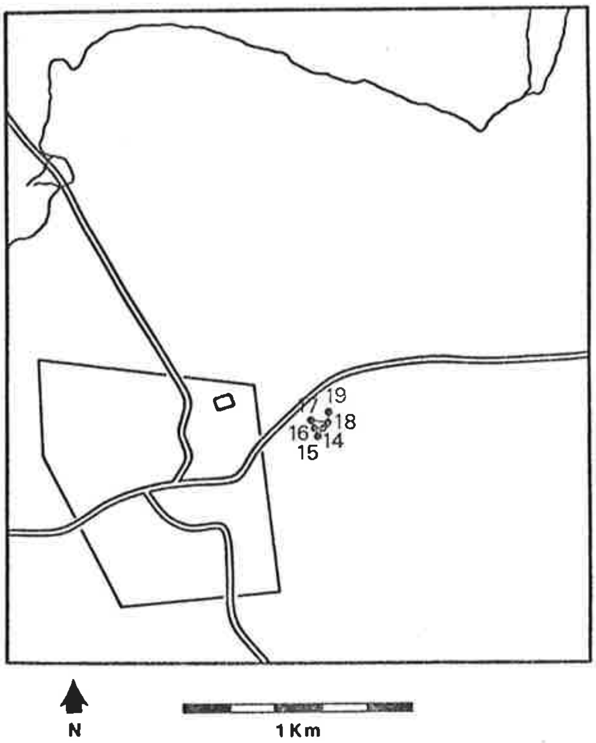


Female 5 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

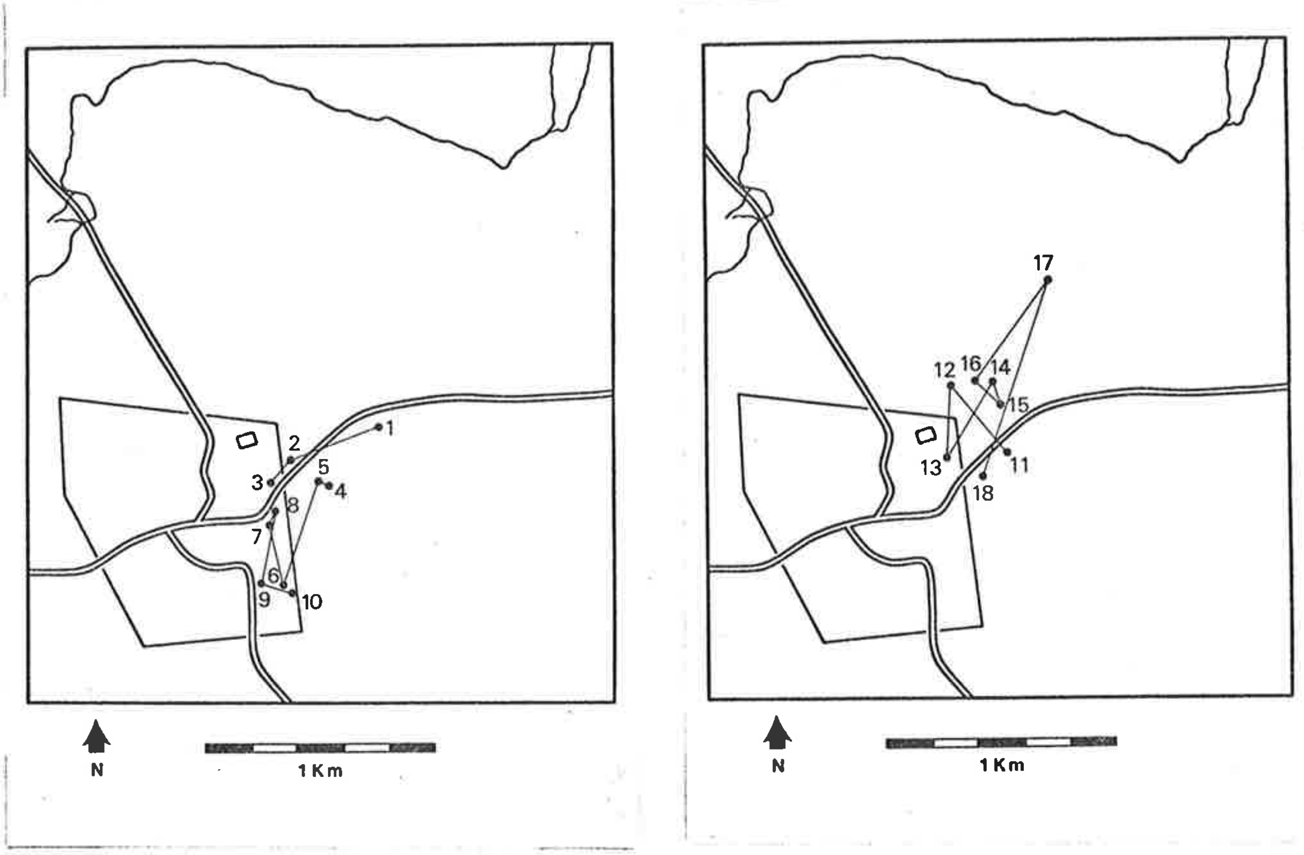






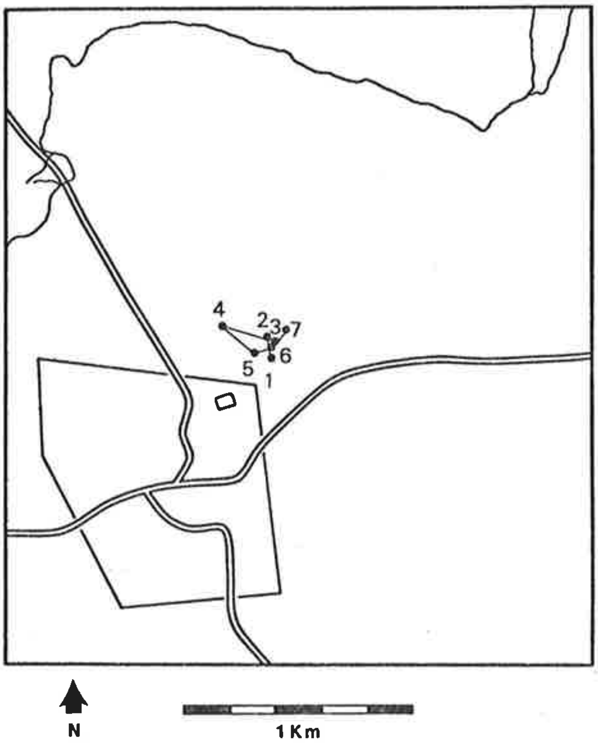
Female 5 March-April 1978

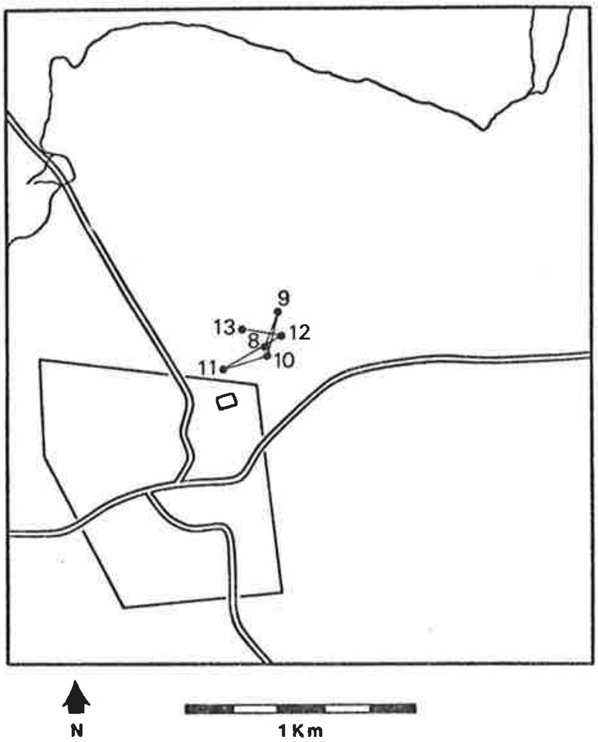
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

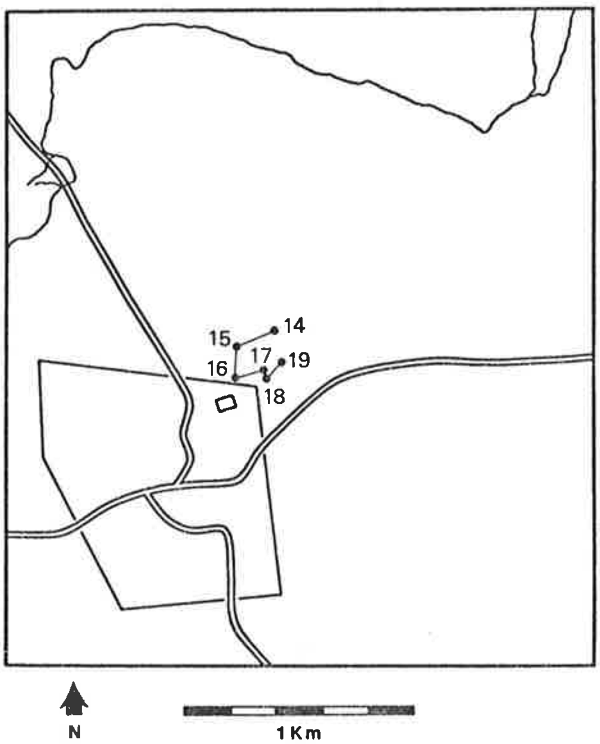


Female 6 December 1977

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	14/12/77	1200	11	16/12/77	1600
2		1700	12		2300
3		2400	13	17/12/77	0400
4	15/12/77	1200	14		0800
5		1600	15		1200
6		2000	16		1600
7		2300	17		2000
8	16/12/77	0400	18		2300
9		0800			
10		1200			

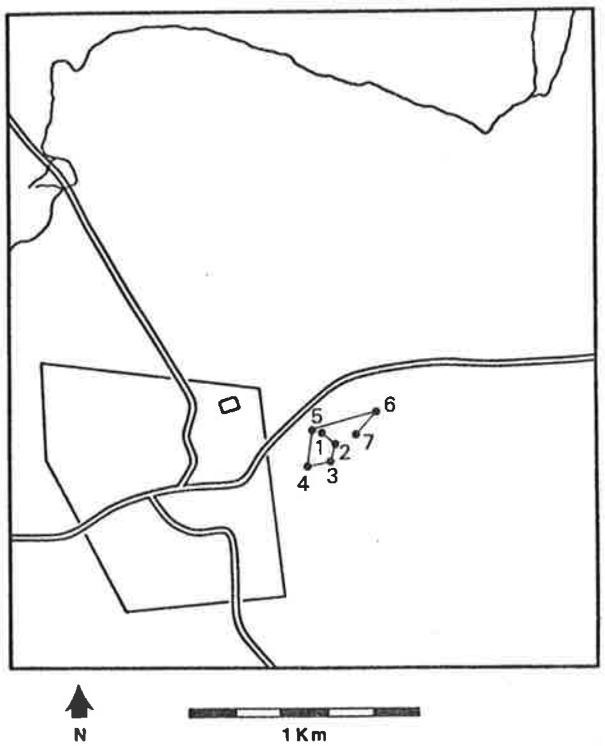


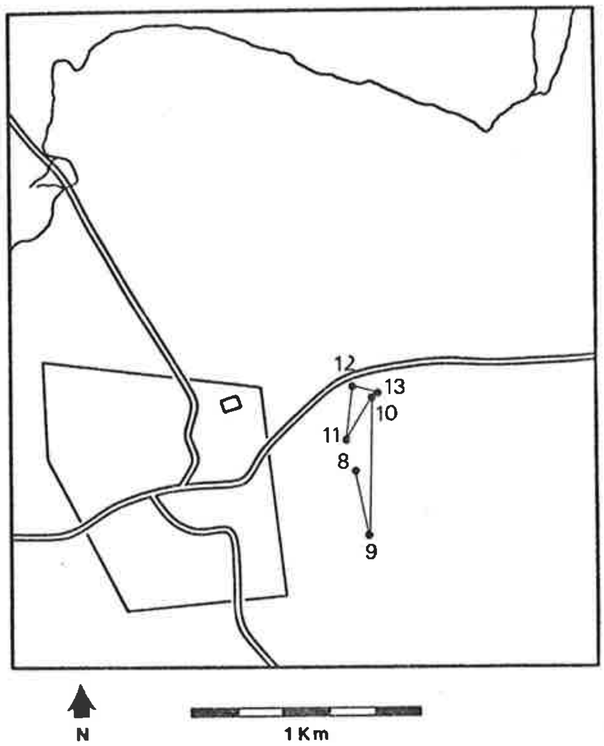


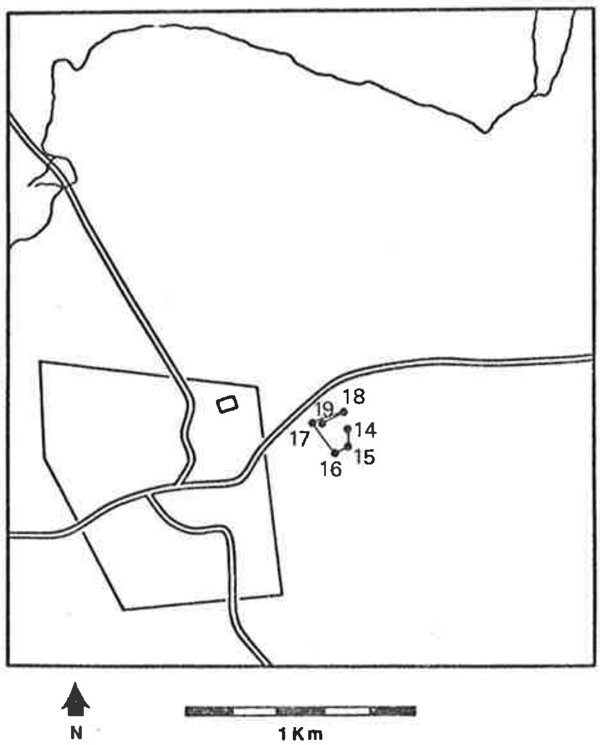


Female 6 Jan./Feb. 1978

Reference	Date	Time (hrs)
1	31/1/78	1200
2		1600
3		2000
4		2400
5	1/2/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	2/2/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	3/2/78	0400
18		0800
19		1200

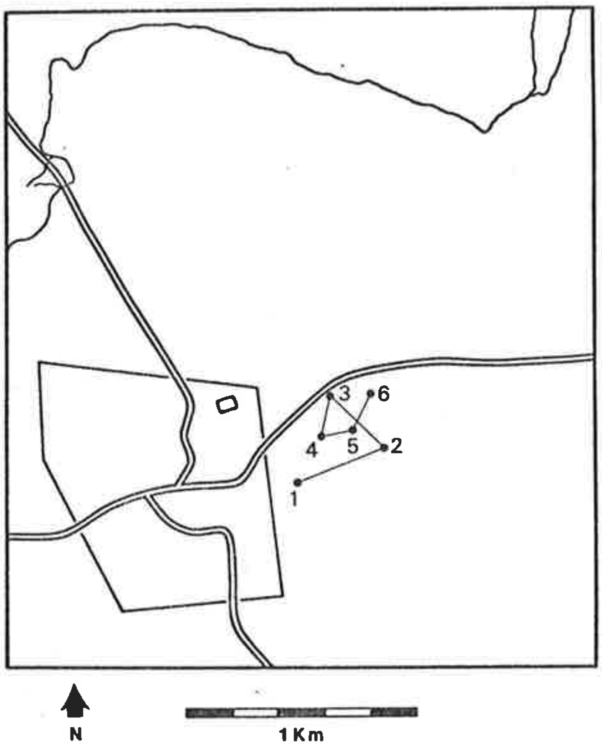






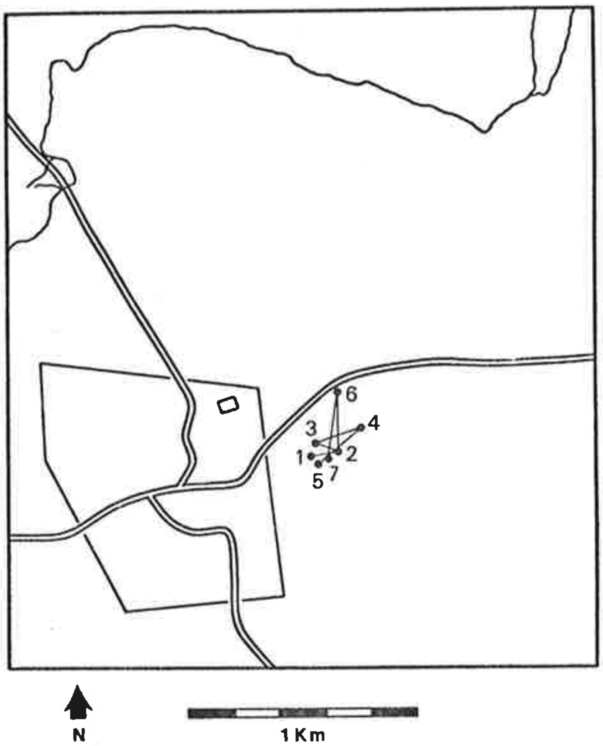
Female 6 March/April 1978

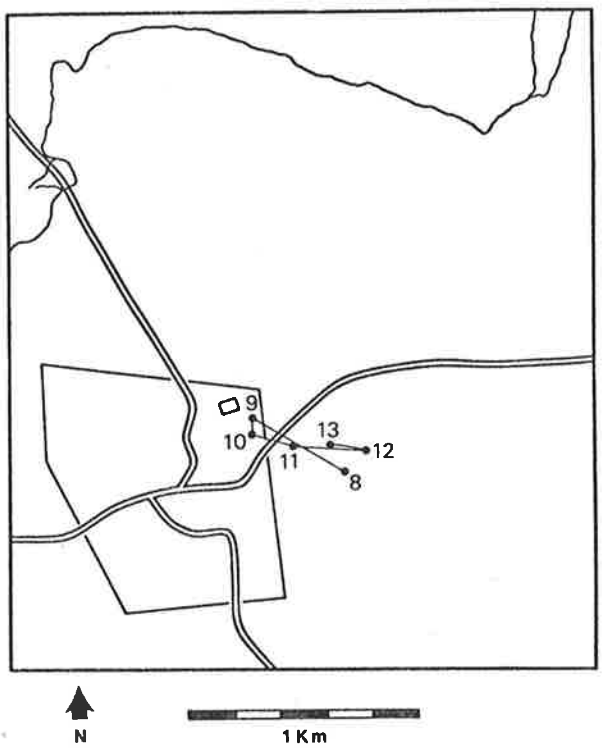
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

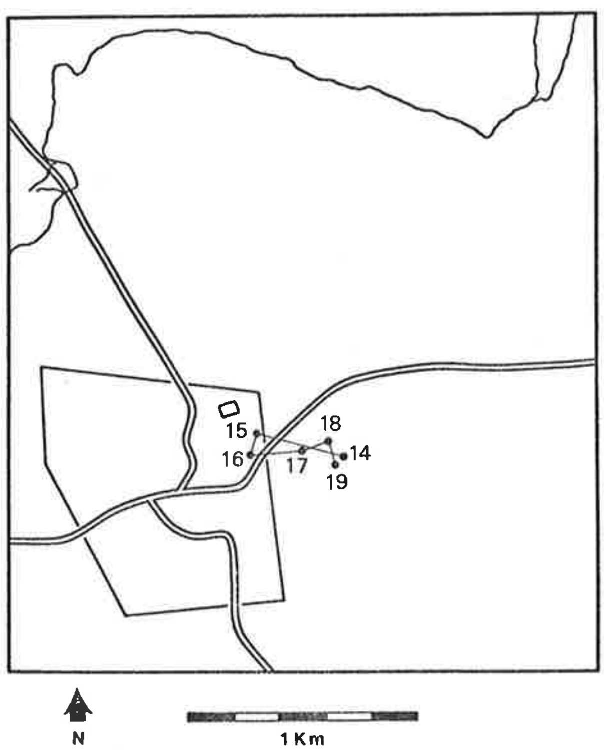


Female 7 February 1978

Reference	Date	Time (hrs)
1	2/2/78	1600
2		2000
3		2400
4	3/2/78	0400
5		0800
6		1200

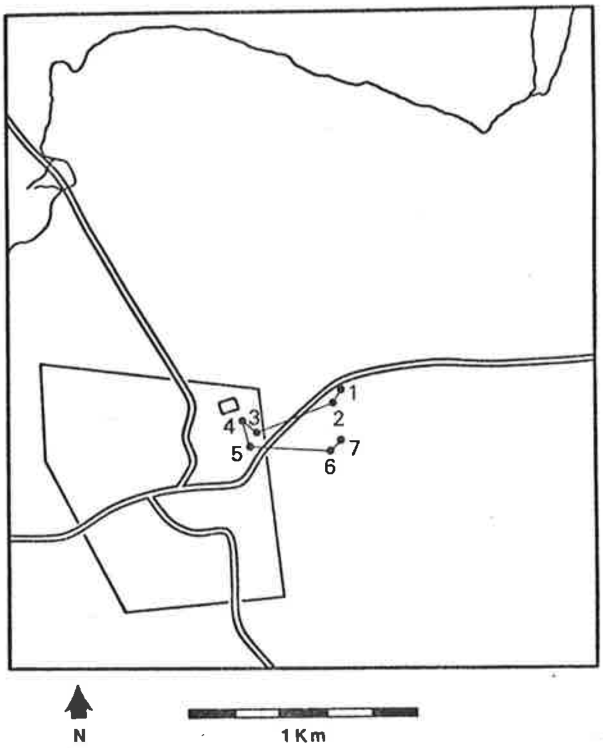


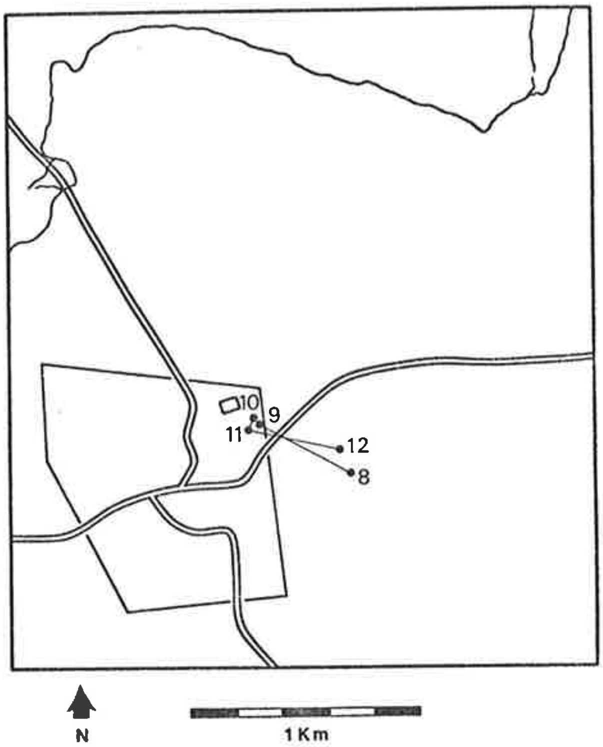




Female 7 March/April 1978

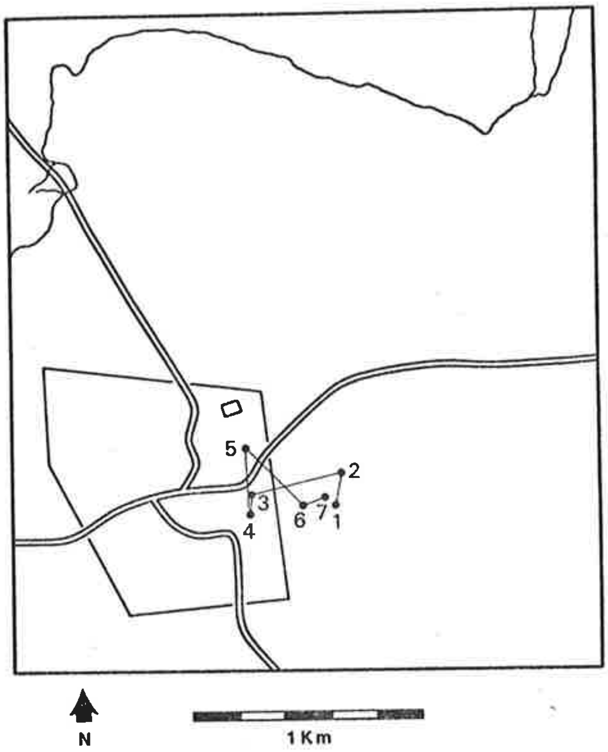
Reference	Date	Time (hrs)
1	30/3/78	1200
2		1600
3		2000
4		2400
5	31/3/78	0400
6		0800
7		1200
8		1600
9		2000
10		2400
11	1/4/78	0400
12		0800
13		1200
14		1600
15		2000
16		2400
17	2/4/78	0400
18		0800
19		1200

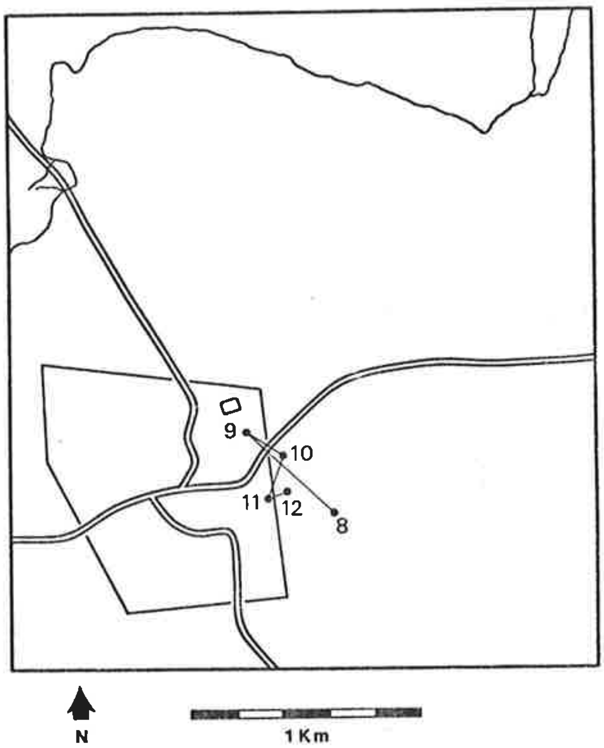




Female 7 May 1978

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	9/5/78	1200	8	10/5/78	1600
2		1600	9		2000
3		2000	10		2400
4		2400	11	11/5/78	0400
5	10/5/78	0400	12		0800
6		0800			
7		1200			





Female 8 May 1978

Reference	Date	Time (hrs)	Reference	Date	Time (hrs)
1	9/5/78	1200	8	10/5/78	1600
2		1600	9		2000
3		2000	10		2400
4		2400	11	11/5/78	0400
5	10/5/78	0400	12		0800
6		0800			
7		1200			

APPENDIX V

The number of animals caught during each trip for the present study, and the number ear-tagged in each trip from November 1963 to July 1972.

The total number of wallabies caught in each trip for the Main Study Area from July 1975 to November 1978.

Field Trip Date	Total Number Caught			Mean No.	Range	Deaths During Capture		
	F	M	T	Caught/Night	Caught/Night	F	M	T
July 1975	25	18	43	7.2	5-11	0	1	1
October-November 1975	50	23	73	7.3	1-12	2	0	2
January 1976	24	19	43	7.2	4-11	0	0	0
March 1976	40	30	70	10.0	8-14	0	0	0
May 1976	28	30	58	9.7	8-14	0	1	1
July 1976	21	20	41	10.3	6-16	0	0	0
October-November 1976	56	52	108	18.0	11-24	0	0	0
December 1976	33	37	70	11.7	1-17	0	1	1
January 1977	34	29	63	10.5	6-16	0	0	0
April 1977	78	45	123	12.3	6-20	0	1	1
June-July 1977	41	36	77	9.6	4-16	0	0	0
November 1977	58	47	105	11.7	2-29	1	0	1
December 1977-January 1978	21	26	47	3.9	1-9	1	0	1
May 1978	30	32	62	7.8	3-14	0	1	1
July 1978	27	27	54	7.7	1-15	0	0	0
November 1978	28	36	64	8.0	2-15	0	0	0

The number of wallabies caught in the Goose Paddock and Bottom Paddock traps.

Goose Paddock

Field Trip Date	Total Number Caught		
	F	M	T
May 1975	15	42	57
July 1975	4	8	12
October-November 1975	0	2	2
January 1976	2	2	4
*March 1976	1	6	7
May 1976	11	9	20
July 1976	6	12	18
December 1976	0	1	1

Bottom Paddock

Field Trip Date	Total Number Caught		
	F	M	T
July 1975	5	1	6
October-November 1975	5	6	11
March 1976	1	0	1

* 1 Male died during capture, March 1976.

The number of wallabies ear-tagged for each trip from November 1963 to July 1972. Data from Dr. S. Barker, Zoology Department, University of Adelaide.

Field Trip Date	Number of Animals Ear-Tagged		
	Females	Males	Total
November 1963	3	4	7
February-March 1964	8	14	22
October-November 1964	7	9	16
May 1965	7	5	12
January 1966	4	8	12
August 1966	30	17	47
November-December 1966	34	15	49
May 1967	28	26	54
November-December 1967	25	28	53
February 1968	23	17	40
May 1968	22	21	43
July 1968	21	11	32
December 1968	21	23	44
March 1969	11	19	30
May 1969	17	11	28
March 1972	19	23	42
July 1972	2	1	3

APPENDIX VI

TABLES FOR THE ANALYSIS OF THE MARK-RECAPTURE DATA FOR 1975 - 1978 AND 1966 - 1969 USING THE JOLLY-SEBER STOCHASTIC MODEL

n_i = number caught in the i th sample.

s_i = number released from the i th sample after marking.

R_i = number of animals released from the i th sample that are caught subsequently.

Z_i = number of animals marked before time i which are not caught in the ith sample but are caught subsequently.

The n_i, S_i and R_i values for Females (1975 - 1978)

i	n_i	S_i	Time of last previous capture															
July 1975	24	24	*1*															
October-November 1975	42	40	7	*2*														
January 1976	19	19	1	4	*3*													
March 1976	31	31	3	9	5	*4*												
May 1976	25	25	4	4	1	8	*5*											
July 1976	19	19	0	2	0	5	7	*6*										
October-November 1976	43	43	2	5	5	7	4	8	*7*									
December 1976	28	28	0	2	0	0	1	1	14	*8*								
January-February 1977	30	30	0	0	0	4	1	1	3	10	*9*							
April 1977	48	48	0	2	2	0	2	5	9	9	12	*10*						
June-July 1977	32	32	0	2	0	0	0	1	5	0	2	18	*11*					
November 1977	40	39	0	0	0	0	1	1	3	0	2	13	15	*12*				
December 1977-January 1978	20	19	0	0	0	1	0	0	0	1	1	1	2	9	*13*			
May 1978	27	27	0	0	1	1	0	0	0	1	2	1	3	7	9	*14*		
July 1978	22	22	1	0	0	0	0	0	0	2	0	2	0	1	4	10	*15*	
November 1978	22	22	0	0	0	0	0	0	0	0	0	0	1	4	0	1	3	*16*
		$R_i =$	18	30	14	26	16	17	34	23	19	35	21	21	13	11	3	

The z_i values for Females (1975 - 1978)

	1															
	7	*2*														
	1	5	*3*													
	3	12	17	*4*												
	4	8	9	17	*5*											
	0	2	2	7	14	*6*										
	2	7	12	19	23	31	*7*									
	0	2	2	2	3	4	18	*8*								
	0	0	0	4	5	6	9	19	*9*							
	0	2	4	4	6	11	20	29	41	*10*						
	0	2	2	2	2	3	8	8	10	28	*11*					
	0	0	0	0	1	2	5	5	7	20	35	*12*				
	0	0	0	1	1	1	1	2	3	4	6	15	*13*			
	0	0	1	2	2	2	2	3	5	6	9	16	25	*14*		
	1	1	1	1	1	1	1	3	3	5	5	6	10	20	*15*	
	0	0	0	0	0	0	0	0	0	0	1	5	5	6	9	*16*
$z_i + 1 =$	11	36	33	42	44	30	46	50	28	35	21	27	15	6		
	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9	Z_{10}	Z_{11}	Z_{12}	Z_{13}	Z_{14}	Z_{15}		

The n_i, S_i and R_i values for Males (1975 - 1978)

Time of last previous capture

i	n_i	S_i																
July 1975	18	17	*1*															
October-November 1975	23	23	2	*2*														
January 1976	17	17	1	1	*3*													
March 1976	25	25	0	0	3	*4*												
May 1976	27	26	2	2	3	5	*5*											
July 1976	20	20	0	0	2	1	7	*6*										
October-November 1976	38	38	0	1	2	3	6	10	*7*									
December 1976	31	30	0	0	2	4	2	0	13	*8*								
January-February 1977	25	25	1	1	0	1	0	1	4	12	*9*							
April 1977	36	35	0	0	0	1	1	1	2	12	12	*10*						
June-July 1977	30	30	0	0	1	0	0	2	2	1	2	11	*11*					
November 1977	37	37	0	0	0	0	0	0	2	0	1	4	10	*12*				
December 1977-January 1978	21	21	0	0	0	1	0	0	1	0	0	3	2	7	*13*			
May 1978	24	23	0	0	0	0	0	0	1	0	1	0	3	7	3	*14*		
July 1978	23	23	0	0	0	0	0	0	0	0	0	2	0	3	4	9	*15*	
November 1978	25	25	0	0	0	1	0	0	1	1	0	1	1	5	0	3	1	*16*
		R_i =	6	5	13	17	16	14	26	26	16	21	16	22	7	12	1	

The z_i values for Males (1975 - 1978)

	1															
	2	*2*														
	1	2	*3*													
	0	0	3	*4*												
	2	4	7	12	*5*											
	0	0	2	3	10	*6*										
	0	1	3	6	12	22	*7*									
	0	0	2	6	8	8	21	*8*								
	1	2	2	3	3	4	8	20	*9*							
	0	0	0	1	2	3	5	17	29	*10*						
	0	0	1	1	1	3	5	6	8	19	*11*					
	0	0	0	0	0	0	2	2	3	7	17	*12*				
	0	0	0	1	1	1	2	2	2	5	7	14	*13*			
	0	0	0	0	0	0	1	1	2	2	5	12	15	*14*		
	0	0	0	0	0	0	0	0	0	2	2	5	9	18	*15*	
	0	0	0	1	1	1	2	3	3	4	5	10	10	13	14	*16*
$z_i + 1$ =	4	7	17	22	28	20	25	31	18	20	19	27	19	13		
	z_2	z_3	z_4	z_5	z_6	z_7	z_8	z_9	z_{10}	z_{11}	z_{12}	z_{13}	z_{14}	z_{15}		

The n_i, S_i and R_i values for Females (1966 - 1969)

i	n_i	S_i	Time of last previous capture									
August 1966	38	38	*1*									
November-December 1966	38	38	4	*2*								
May 1967	44	44	9	4	*3*							
November-December 1967	38	38	6	1	6	*4*						
February 1968	33	33	0	1	2	5	*5*					
May 1968	44	44	3	1	7	5	5	*6*				
July 1968	44	44	3	1	7	3	4	5	*7*			
December 1968	40	40	0	3	0	4	4	2	5	*8*		
March 1969	34	34	0	1	1	1	3	6	4	7	*9*	
May 1969	44	44	0	2	2	2	1	2	4	4	9	*10*
		R_i =	25	14	25	20	17	15	13	11	9	

The Z_i values for Females (1966 - 1969)

	1									
	4	*2*								
	9	13	*3*							
	6	7	13	*4*						
	0	1	3	8	*5*					
	3	4	11	16	21	*6*				
	3	4	11	14	18	23	*7*			
	0	3	3	7	11	13	18	*8*		
	0	1	2	3	6	12	16	23	*9*	
	0	2	4	6	7	9	13	17	26	*10*
$Z_i + 1$ =	21	22	34	46	42	34	29	17		
	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9		

The n_i, S_i and R_i values for Males (1966 - 1969)

Information from November-December 1966 was deleted from the analysis because no animals from this trip were subsequently recaptured.

i	n_i	S_i	Time of last previous capture								
August 1966	21	21	*1*								
May 1967	30	29	1	*2*							
November-December 1967	32	31	1	2	*3*						
February 1968	23	23	1	0	4	*4*					
May 1968	39	38	3	4	6	4	*5*				
July 1968	23	21	2	1	1	0	6	*6*			
December 1968	26	26	1	0	0	1	0	1	*7*		
March 1969	28	28	0	1	2	0	2	3	1	*8*	
May 1969	19	19	0	0	0	1	1	0	2	4	*9*
		R_i =	9	8	13	6	9	4	3	4	

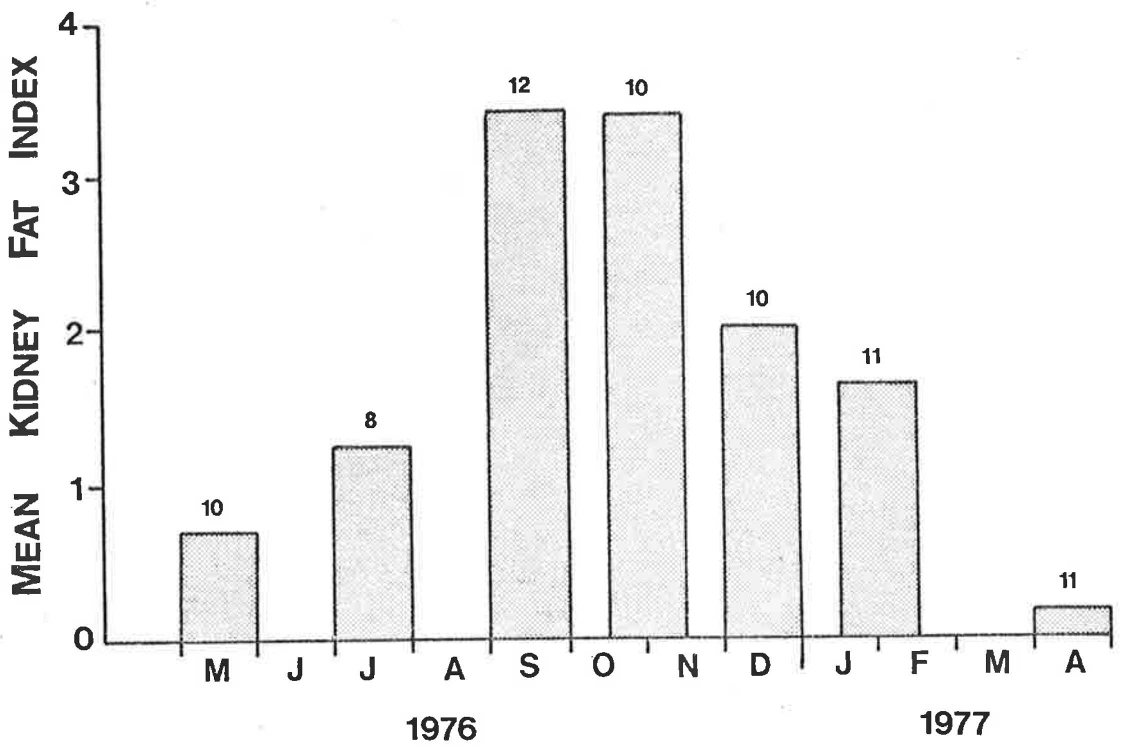
The Z_i values for Males (1966 - 1969)

	1								
	1	*2*							
	1	3	*3*						
	1	1	5	*4*					
	3	7	13	17	*5*				
	2	3	4	4	10	*6*			
	1	1	1	2	2	3	*7*		
	0	1	3	3	5	8	9	*8*	
	0	0	0	1	2	2	4	8	*9*
$Z_i + 1 =$	8	13	21	10	9	10	4		
	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8		

APPENDIX VII

SEASONAL CHANGES IN THE AMOUNT OF FAT WITHIN THE GUT CAVITY

A visual assessment of the amount of fat present in the gut cavity (kidney and mesenteric fat) was made on male wallabies that had been shot for collection of reproductive organs. The amount of fat was estimated on a 0 - 4 scale over the period May 1976 to April 1977. The results show that fat deposits are being utilized over the summer and early winter period and then gradually laid down over late winter to spring.



Seasonal changes in the amount of fat present within the gut cavity of male Kangaroo Island Wallabies. Numbers above columns represent the sample size.

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